

Natural regeneration patterns of *Fagus sylvatica* L. in canopy gaps of a low-elevation European beech forest in central Italy

Gianluigi Mazza^{1*}, Ugo Chiavetta¹

Received: 14/04/2025 Accepted: 2/03/2026 Available online: 31/03/2026

ABSTRACT Understanding natural regeneration in European beech (*Fagus sylvatica* L.) forests is crucial for sustainable management and climate adaptation. This study compared natural regeneration and gap characteristics in two central Italian forests: Bassano Romano, with recent management, and Monte Raschio, a UNESCO-protected old-growth site. Regeneration density was significantly higher in Bassano Romano, likely due to progressive canopy openings from shelterwood management, while Monte Raschio showed greater broadleaved species diversity, suggesting gap-driven regeneration. Despite similar mean gap sizes (~500 m²), Monte Raschio exhibited higher variability. Regeneration was denser along warmer, sunnier gap edges, confirming microclimatic influences. The medium- and small-size gaps seems to favour the regeneration in both forest areas, most likely because they can create the best conditions for beech natural regeneration. Indeed, regeneration height increased up to medium-sized gaps (~500 m²). The linear mixed model results indicate that differences between the two forests account for a significant portion of the total variance when included as a random effect.

The findings suggest that shelterwood systems tend to reinforce beech dominance, whereas gap-cutting promotes greater species diversity. This underscores the need for a balanced management approach that aligns regeneration objectives with biodiversity conservation. Adaptive management emerges as a key strategy for maintaining long-term resilience and functional stability in temperate forests.

KEYWORDS: Seedlings, saplings, treefall gap, old-growth forests, thermophilic beech forest, linear mixed models.

Introduction

Natural forest dynamics and close-to-nature management strategies rely on the integration of natural processes, including natural regeneration (Nagel et al. 2013). This approach is particularly significant for old-growth forests with high naturalistic value, as they provide essential ecosystem services. These include biodiversity preservation, conservation of priority habitats, carbon sequestration and cycling, as well as recreational, spiritual, and cultural benefits for society (De Groot et al. 2002, Paletto et al. 2021, De Assis Barros et al. 2022).

The development of natural regeneration is strongly influenced by the canopy gaps characteristics (Schliemann and Bockheim 2011), which regulate light availability on the forest floor, as well as drought conditions and evapotranspiration rates, especially during summer at lower elevations. These factors also influence competition dynamics between species (Muscolo et al. 2014).

Although different definitions exist, a canopy gap can generally be defined as an opening in the forest canopy through all canopy layers to at least a reference threshold height of about 2 m above ground level or below (Schliemann and Bockheim 2011). Consequently, the canopy gap size plays a crucial role in ecological dynamics by altering light conditions and impacting the microclimate (Schliemann and Bockheim 2011, Muscolo et al. 2014). Canopy gaps create unique microenvironments, modifying temperature, humidity, and wind patterns. The extent of these modifications depends on gap size, influencing both seedling establishment and species competition over time. Larger gaps allow increased light penetration, supporting light-demanding species while

potentially suppressing shade-tolerant plants. This dynamic is essential for understanding forest succession and biodiversity. Over time, gap size determines the rate and type of species regeneration. Small gaps close within a few years and may favour slower-growing or shade-tolerant tree species, while larger gaps persist longer and can accelerate the growth of pioneer species (Feldmann et al. 2018).

Natural gaps are generally formed by wind, snowfall, insects, disease, or other disturbances such as drought and fire. However, other factors may also be responsible for gap formation, such as the interaction between soil properties and root system patterns (Clinton and Baker 2000, Lin et al. 2004, Scharenbroch and Bockheim 2007).

Artificial gaps are mainly the result of silvicultural treatments, which in recent decades have been designed to mimic natural disturbances and naturally restore forests, preserving ecosystem functions while optimising harvesting (Abrari Vajari et al. 2012). These treatments allow for controlling the size, shape, location, and formation timing as a proxy for naturally created gaps. However, in many cases, artificial gaps differ significantly from natural ones because felled trees are often removed, leaving stumps and root systems in the ground. In contrast, in natural gaps, fallen trees remain, often with the root ball exhumed from the soil but still attached. These natural gaps are not free of soil disruption (Clinton and Baker 2000). Therefore, soil disruption and biomass removal differ between artificial and natural gaps, making it difficult to generalise between the two gap types (Schliemann and Bockheim 2011).

In Mediterranean climatic conditions, canopy gap characteristics have an even more pronounced impact

1 - CREA – Research Centre for Forestry and Wood – Italy

* Corresponding author: gianluigi.mazza@crea.gov.it

on natural regeneration, especially under ongoing climate change. In Mediterranean forests, canopy gaps expose the forest floor to intense solar radiation, particularly during the summer when evapotranspiration rates peak. This can exacerbate water stress for seedlings and saplings, limiting the success of less drought-tolerant species, particularly in larger canopy gaps, where the increased soil exposure to sunlight can lead to more rapid moisture loss. Understanding the interaction between gap characteristics and local environmental conditions is crucial for predicting forest regeneration outcomes.

Fagus sylvatica L. (European beech) is a tree species widely distributed across Europe, historically valued for its economic relevance in timber production and managed mainly by the silvicultural uniform shelterwood system, which involves the gradual removal of trees over several cycles to encourage natural regeneration (Nocentini 2009, Wagner et al. 2010). In recent years, it has gained substantial naturalistic importance due to its role in biodiversity conservation, particularly within old-growth beech forests (Leuschner 2020).

The study site is in a low-elevation thermophilic beech forest in central Italy within the Regional Natural Park of Bracciano-Martignano. The site comprises two areas with different management histories: one left to natural evolution for at least 60 years and another subjected to silvicultural interventions until the 2000s. The presence of *F. sylvatica* is closely linked to favourable soil and microclimate conditions, partly due to the proximity of Lake Bracciano, which mitigates the effects of summer drought. However, in recent years, Lake Bracciano has experienced a significant drop in water levels due to intensive water extraction. This, combined with rising temperatures and increased drought, has intensified water loss, impacting negatively the vulnerability of the surrounding forest ecosystems (Mazza et al. 2020, Mazza et al. 2024). In the beech forest, for example, some decay phenomena can be observed, as evidenced by the attack of lignivorous pathogenic fungi such as *Biscognauxia nummularia*, a secondary causal agent of cortical cancer, which is closely related to drought conditions and water stress.

In this context, we hypothesize that the regeneration of *F. sylvatica*, being near its low-elevation distribution limits, is likely to become increasingly sensitive to competition with the better drought-adapted species of the mixed mesophilic forests under current climate warming. We also hypothesize that the physical characteristics of gaps, such as aspect, location and distance from boundaries (edge effects), have a significant influence on regeneration dynamics by favouring different species or growth strategies, leading to variations in species composition, growth patterns and biodiversity.

Under these hypotheses, our study aims to assess a potentially significant effect of the two different management histories on the main regeneration patterns of *F. sylvatica* and the other broadleaves species (e.g., *Quercus cerris* L., *Carpinus betulus* L., *Acer* spp., *Ulmus* spp., etc.), and their relationships with the gap characteristics.

Materials and methods

Study site

The study site, which belongs to the Mediterranean biogeographical region, is a Special Area of Conservation (SAC) – IT6010034, Faggete di Monte Raschio ed Oriolo – of about 712 hectares within the Regional Natural Park of Bracciano-Martignano in central Italy (42.10° N – 12.10° E), at about 450 m a.s.l. SAC IT6010034 encompasses the following habitats of EU interest: 1) 9210 – ‘Faggete degli Appennini di *Taxus e Ilex*’ and 2) 9260 – ‘Foreste di *Castanea sativa*’. The first of these habitats is listed as a priority in Annex II of Directive 43/92/EC.

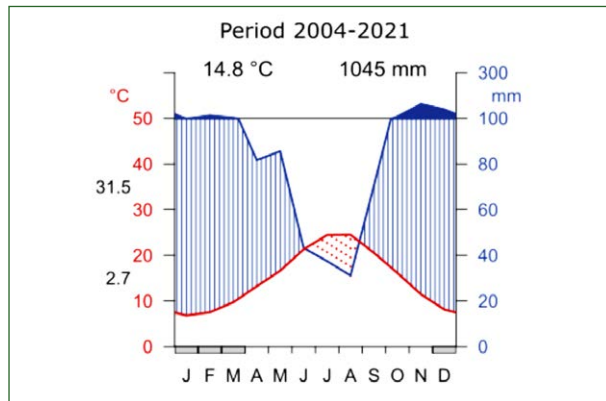
The study site includes two main beech forest areas, Monte Raschio (MR), within the municipality of Oriolo Romano and Bassano (BS), within the municipality of Bassano Romano. These are significant examples of relict beech forests of about 120 years-old (Mazza et al. 2024), serving as evidence of the beech stands that once thrived at much lower altitudes several thousand years ago. During the Ice Ages, around 10,000 years ago, the advance of glaciers forced mountain vegetation to migrate downward. It was only after the ice retreated that beech trees gradually returned to higher elevations, leaving behind isolated forests at lower altitudes where the climate remained favourable. In both areas, the dominant layer of the beech stands consists of *F. sylvatica* trees, with isolated or grouped *Q. cerris* and, secondly, *Castanea sativa* Mill. Within the understorey, several species are widespread, mainly individually, such as *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Acer pseudoplatanus* L., *Acer campestre* L., *C. betulus* L., *Ilex aquifolium* L., *Sorbus torminalis* and *domestica* L., *Prunus avium* L., and some trees of *Ulmus glabra* Huds. The shrub and herbaceous layers are poorly developed due to the dense tree canopy cover. It is mainly composed of *I. aquifolium*, *Crataegus monogyna* Jacq., *Ruscus aculeatus* L., with a lesser presence of *Cornus sanguinea* L., *Corylus avellana* L. and *Sambucus nigra* L., besides the natural regeneration of *F. sylvatica*.

The soils belong mainly to the type of Andosol, typically found in volcanic areas, and usually contain high proportions of glass and amorphous colloidal materials, resulting in very fertile soils (Mattei et al. 2010). They are characterized by a sandy loam texture and are very porous with good drainage.

Climate data were recorded at the Bassano Romano meteorological station (Piano Mola - 457 m a.s.l.) for the period 2004-2021 (Fig. 1). The climate is typically Mediterranean with a total mean annual precipitation (MAP) of 1,045 mm concentrated mainly in winter (32.3 %) and autumn (32.2 %) and a dry summer in which July and August are the driest months with 37.5 and 36.2 mm of rainfall, respectively. The mean annual temperature (MAT) is 14.8 °C. The study site falls under the Mediterranean biome, category Temperature Deciduous Forest, and specifically Warm temperate moist forest. The bioclimate is Mediterranean Pluviseasonal oceanic, the

thermotype is Upper mesomediterranean and the ombrotpe is sub-humid lower (Pesaresi et al. 2017).

Figure 1 - Climatic characterization of the study area (Walter & Lieth climatic diagram). Mean annual temperature – MAT and the total mean annual precipitation – MAP (top). Mean maximum temperature of the warmest month and mean minimum temperature of the coldest month (beside the left y-axis). The dotted area in the Walter & Lieth climatic diagram indicates seasonal water deficit.



Forest management history and description

The beech forest area of Monte Raschio (MR) consists of high-density stands of either single-layered or two-layered high forests. Following the decline of the railway sleeper market several decades ago, traditional silvicultural interventions with economic purposes have ceased completely. This has led to a significant increase in the density of the forest stands that constitute the beech forest, a process accelerated by the site's high fertility. It is considered a secondary old-growth forest, with stands actively managed in the past but left to natural evolution for at least 60 years. The Monte Raschio beech forest is a priority habitat (9210 – Apennine beech forests with *Taxus baccata* L. and *Ilex aquifolium* L., EU Habitats Directive), and it is the 33rd natural UNESCO heritage site “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe”.

The beech forest area in the municipality of Bassano Romano has a different history. According to the available information, the forest was intensively and indiscriminately exploited, particularly during the post-war period. Afterwards, it was decided that the forest should be subject to moderate harvesting. Subsequently, due to a shortage of provisions and a marked uniformity of age across the population, silvicultural interventions based on the uniform shelterwood system were prescribed. There is little and fragmentary information about the regularity and type of cutting that followed this management plan. Presumably, the cycle of uniform shelterwood system cuttings was not fully respected in many cases. However, it appears that the chestnut coppice was regularly used until 1997, the oak coppice until 1991 and the high forest until 1986. After this, all cutting was omitted, but two sections were moderately thinned in 2002. In summary, two decades of heavy harvesting were followed by a subsequent two decades of conservation, after which there was another two decades of no cutting (except for coppicing).

This fluctuation in interventions has had a peculiar effect on the entire forest. Regeneration spread widely through the forest in the first twenty years and became established in the second, before declining dramatically or ceasing altogether in the final years. A forest management plan was subsequently drawn up for the beech stands owned by the Agricultural University of Bassano Romano for the 2005–2014 period.

Natural regeneration assessment

The field survey of natural regeneration took place in autumn 2021, from September to mid-November, in gaps of various sizes in the forest canopy, both natural, resulting from falls, and artificial, resulting from old cuts.

According to Runkle (1992), the most difficult and arbitrary aspect of defining the gap in a forest stand is when it merges with the lower layers through vertical ingrowth. Thus, gaps are usually considered filled or re-closed when the next sub-dominant canopy layer has reached 2/3 of the dominant tree height (Runkle 1992, Feldmann et al. 2018). This is not the case in our old-growth forest, where the dominant layer is clearly distinct from the underlying canopy layers without any canopies merging.

The identification of these gaps was first done at the desk through satellite imagery (from Google Earth – Fig. 2) and then validated in the field, confirming or appropriately shifting the sampling points and adding others based on their characteristics (accessibility, representativeness, etc.). Some locations were excluded because they were old logging staging areas, roads, or inaccessible due to excessive shrub cover, mainly consisting of *R. aculeatus* L. After confirming the validity of each gap, we determined their area using satellite images. The gaps were then divided into three classes (“small”, “medium”, “big”) based on quantile thresholds, computed from the cumulative distribution of total gap area. This procedure identifies the 33rd and 66th percentiles as class boundaries, ensuring that each class contains one third of the total gap area.

Then, within each gap, two perpendicular transects of 1 m width and variable length, depending on the gap size, were positioned to record the following parameters: species, height, health status, growth stage and position on the linear axis of the transect. The first transect was aligned with the major radius of the gap, while the second transect was oriented orthogonally (90°) to the first (Fig. 3). The regeneration density was reported per square metre, based on the area of the two perpendicular transects.

The natural tree species diversity was evaluated using the Shannon index. Health status was assessed qualitatively (good, medium, poor) based on leaves number and vigour, considering signs such as chlorosis, curling, and necrotic lesions. The growth stage was evaluated and classified according to the following scheme: i) seedling (first stage) – seedling born in the current year's growing season, still evident presence of cotyledons or maximum number of 5 leaves; ii) seedling (second stage) – seedling born maximum two previous growing seasons, character-

Figure 2 - Study site (red box) and sampling plots of natural regeneration in the two parts of the thermophilic beech forest (MR: Monte Raschio, BS: Bassano Romano; the numbers indicate the eight gaps).

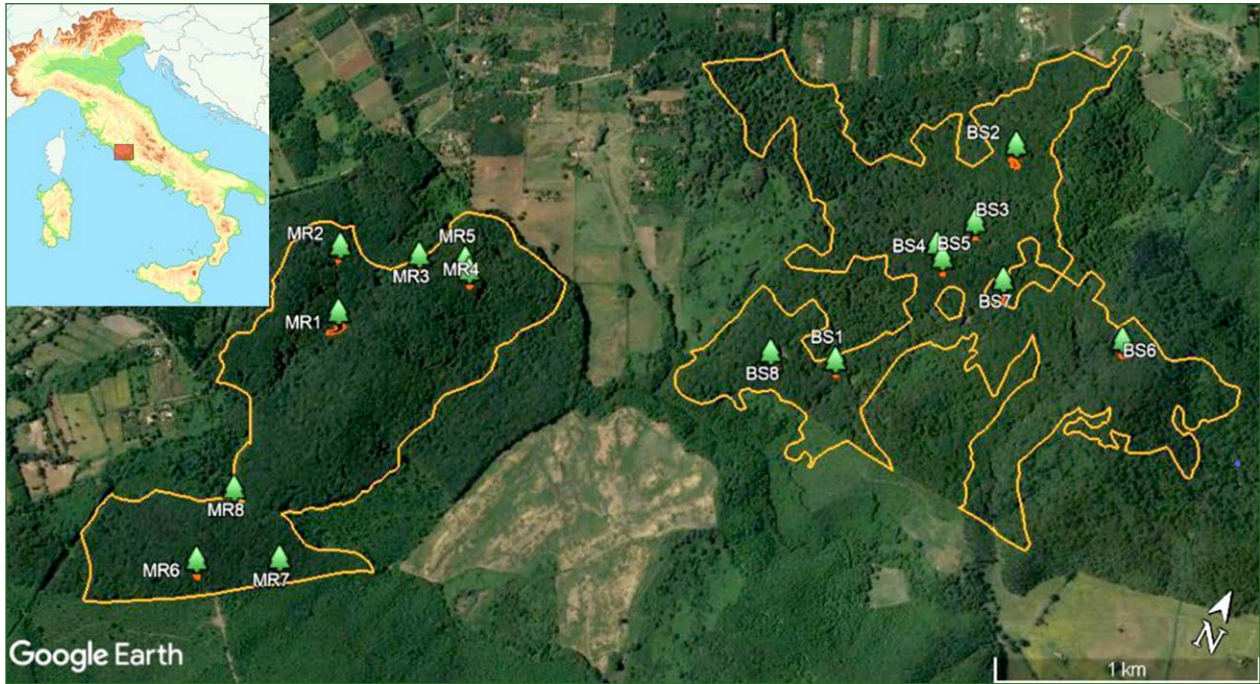
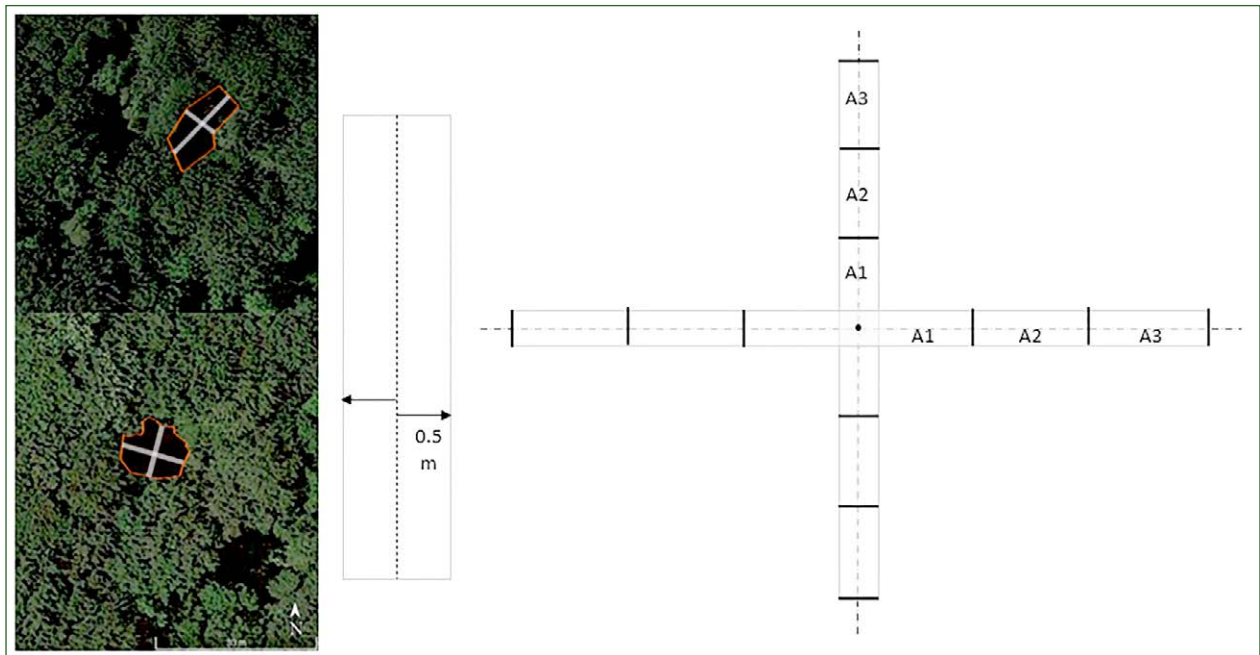


Figure 3 - Two examples of cross-transects within the examined gaps, along with a schematic representation of the survey transects used to assess patterns of natural regeneration. The three sections that divide each of the four semi-transects are labelled A₁, A₂ and A₃.



ized by a substantial number of leaves and not more than 50 cm in height; ii) sapling – seedling now established with evident presence of woody parts and height more than 50 cm (Giannini et al. 2010, Feldmann et al 2020).

Additionally, natural regeneration patterns within each gap were analysed based on distance from the centre, in order to assess significant differences between central and peripheral areas. For this purpose, we divided each of the four semi-transects into three sections, each representing one third of their length, following the

scheme shown in Figure 3 (A₁ is the central section, A₂ the intermediate one, and A₃ the outermost one).

Statistical analysis

Significant differences in natural regeneration parameters between the two forest areas (Monte Raschio and Bassano) were analysed after testing the normal distribution of the data using the Kolmogorov-Smirnov test and the Barlett test for homogeneity of variance. When the normality test failed, the non-parametric Wilcoxon

Table 1 - Number of individuals per hectare and mean height of natural regeneration in Bassano (BS) and Monte Raschio (MR). FS: *F. sylvatica*, Other: other broadleaves, T₁ e T₂: transect. The letters S (small), M (medium), and B (big) indicate the gap size classes.

ID gap	T ₁ (m)	T ₂ (m)	Area (m ²)	N° m ⁻²		Mean Height (cm)	
				FS	Other	FS	Other
BS1	30.5	20.8	310 (S)	1.05	0.66	22.5	24
BS2	38.0	30.0	810 (B)	1.31	0.35	10.3	7.7
BS3	38.5	17.5	300 (S)	2.50	0.02	54.1	35
BS4	32.0	21.3	350 (S)	2.14	–	8.2	–
BS5	31.0	26.2	440 (M)	2.52	0.12	47.8	105
BS6	42.7	39.0	980 (M)	3.73	0.27	13.9	22.4
BS7	34.0	27.6	510 (M)	0.21	0.67	21	10.9
BS8	31.0	27.0	450 (M)	2.38	0.60	44.8	36.9
MR1	30.5	43.0	1200 (B)	1.22	–	24.6	–
MR2	37.6	25.5	430 (M)	0.43	0.75	14.8	109
MR3	38.5	30.5	560 (M)	0.74	0.03	13.2	19.5
MR4	29.1	20.5	330 (S)	1.07	0.02	12.4	240
MR5	52.0	38.6	1010 (B)	0.22	–	20	–
MR6	29.7	15.8	290 (S)	1.43	0.02	24.4	550
MR7	34.6	16.0	310 (S)	0.14	0.91	11.4	56.2
MR8	23.5	13	200 (S)	0.44	1.26	14.9	14.1
	Mean length	Mean area	N° m ⁻²	Mean Height (cm)			
BSTOT	34.7 ± 4.5	26.2 ± 6.7	518.8 ± 247.4	1.98	0.32	28.3	32.3
MRTOT	34.4 ± 8.6	25.4 ± 11.1	541.3 ± 367.2	0.71	0.37	19.0	67.9

Mann-Whitney (W) test for two independent groups of samples and the non-parametric Kruskal-Wallis test for analysis of variance by ranks for more than two independent groups instead of one-way analysis of variance (ANOVA) were used. Correction for multiple comparisons of significance levels was checked using the Bonferroni method.

Additionally, given the nested study design (gaps within sites and multiple transects per gap) and the inclusion of various variables (e.g., gap size, aspect and distance from the gap edge), we employed a linear mixed-effects model (LMM) to analyse the impact of key factors on regeneration height for all species together, as well as for the target species *F. sylvatica*. We used the Akaike Information Criterion (AIC) for selecting the best model, the marginal R squared (R²_m) values to consider the fixed effects, and the conditional R squared values (R²_c) for fixed plus the random effects (Nakagawa & Schielzeth 2013). R²_c–R²_m quantifies the added value of random effects. We performed all the analyses mentioned above in the R software environment (R Core Team 2025, version 4.5.2).

Results

We identified sixteen gaps, equally distributed between the two study areas and covering a similar total and mean area: about 4,150 and 4,330 m², and 518.8 (± 247.4) and 541.3 (± 367.2) in Bassano (BS) and Monte Raschio (MR), respectively (Tab. 1). A total of 1,631 regeneration individuals of the different species were re-

corded in the transects within the gaps. Only *F. sylvatica* was present in all the gaps; the other broadleaf species were absent from two gaps at MR (MR₁ and MR₅) and one gap at BS (BS₄) (Tab. 1). Regarding the three classes of gap size, the grouping was as follows: two big, two medium and four small in MR, and one big, four medium and three small in BS.

Natural regeneration characteristics

In the Bassano beech forest (the managed forest area), a higher number of beech natural regeneration was found, while the other broadleaves tree species were more abundant in Monte Raschio beech forest (Tab. 1 and Fig. 4). Overall, the natural regeneration of beech (N°m⁻²) was about 2.8 times higher in BS than in MR, but also with a 2.3 times higher variability. Conversely, the other broadleaved species (e.g., *F. ornus*, *Acer spp.*, *O. carpinifolia*, *C. betulis*) were more abundant in MR, albeit only slightly (0.9 times higher than in BS). MR also exhibited greater species diversity than BS, as indicated by the Shannon diversity index, both with and without beech individuals included (0.94 vs. 0.64 and 0.69 vs. 0.51, respectively).

According to the different growth stages, the number of beech individuals per square meter was always higher in BS than in MR, especially for the sapling stage (18.2 times higher – Fig. 4). Using 50 cm as the threshold to define established regeneration (sapling), its proportion relative to potential regeneration (seedling at both I° and II° stage) is 25.1% in BS and only 3.5% in MR (Fig. 4). In contrast, the overall higher number of the other broadleaved species found in MR compared to BS was mainly relat-

Figure 4 - Number of individuals per square meter of natural regeneration of *F. sylvatica* alone and compared to the other broadleaves species according to their different growth stages in Bassano (BS) and Monte Raschio (MR). Vertical bars indicate the standard deviation.

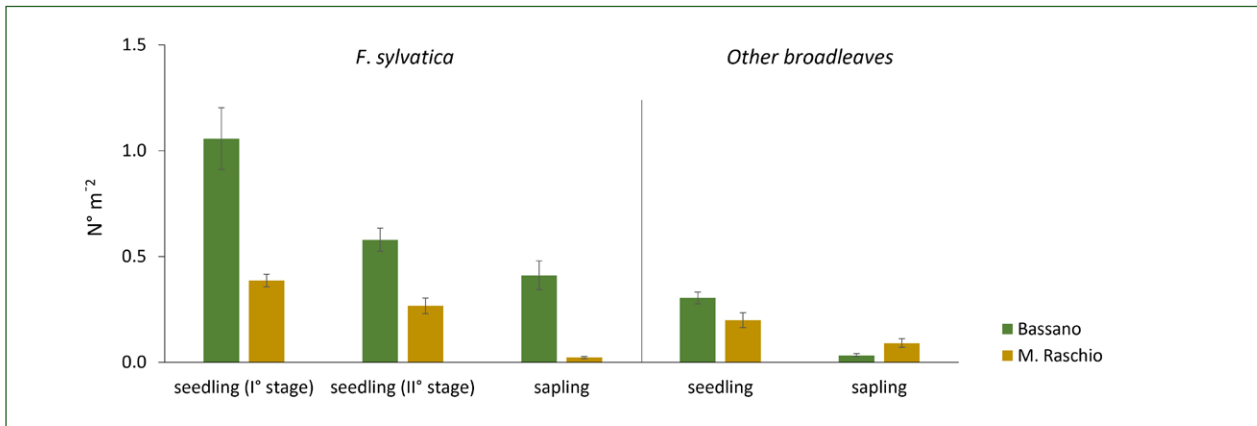
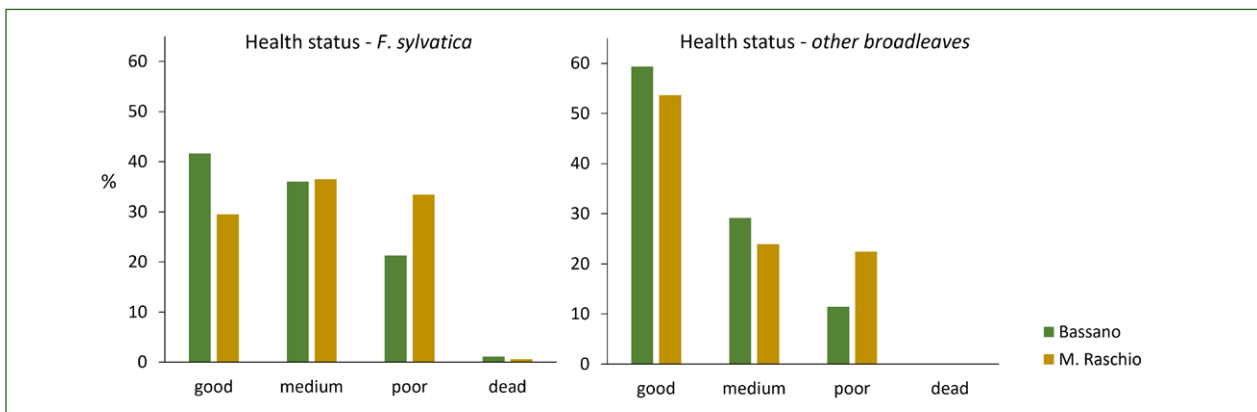


Figure 5 - Percentage distribution of individuals of *F. sylvatica* and the other broadleaves species across qualitative classes of health status.



ed to the sapling stage rather than the seedling stage (2.8 times, $P < 0.001$) (Fig. 4).

The mean height of beech was significantly greater in BS than at MR ($P < 0.001$), while the mean height of the other broadleaves species was greater in MR ($P < 0.001$) (Tab. 1). Concerning the height of the sapling stage, which is an important parameter because it determines the ability of natural regeneration to reach the establishment phase and survive (Giannini et al. 2010), the mean height of beech was significantly greater in BS than in MR (79.9 vs. 54.7 cm, $P < 0.001$).

The health status monitoring revealed a higher percentage of individuals in good growing conditions in BS, both for beech (41.6 vs. 29.5 %) and, to a lesser extent, for the other broadleaves species (59.4 vs. 53.6 % - Fig. 5). In contrast, a higher percentage of beech individuals with a poor health status was observed in MR (33.4%) than in BS (21.3 %). A similar pattern, though less pronounced, was observed for the other broadleaves species, with 22.5% of individuals in poor health status at MR compared to 11.5% at BS.

Effects of gap characteristics

Considering the size of the gaps, the frequency distribution of regeneration is more concentrated in medium-sized gaps in BS and in small gaps in MR, particu-

larly for other broadleaf species (Fig. 6). Regarding the distance from the gap centre, at BS, the highest number of beech regeneration was found in section A3, furthest from the gap centre, followed by section A1, closest to the gap centre. For the other broadleaves species, section A3 had the fewest individuals (although this was not statistically significant). At MR, the central section (A1) had the highest number of regeneration individuals, particularly for the other broadleaves species (Fig. 6). Regarding the aspect of the gap, we found less variability at MR than at BS. However, a common pattern emerged: the frequency distribution of regeneration based on aspect was higher for southern exposures at both BS and MR (Fig. 6).

The effect of gap characteristics on regeneration height showed contrasting patterns in the two forest areas (Fig. 7). For beech regeneration, the tallest individuals were found at the BS site, where gap size and aspect had a greater significant influence than the distance from the gap centre. Indeed, the greatest beech regeneration was found in small and medium-sized gaps compared to large ones ($P < 0.001$), and along east and west aspects ($P < 0.001$). Regarding the other broadleaves species, the east aspect had the greatest significant influence on height enhancement ($P < 0.001$), followed by the west aspect ($P < 0.05$) (Fig. 7). At MR, the height of the other

Figure 6 - Frequency distribution of individuals of *F. sylvatica* and the other broadleaves according to the gap characteristics in Bassano (BS) and Monte Raschio (MR).

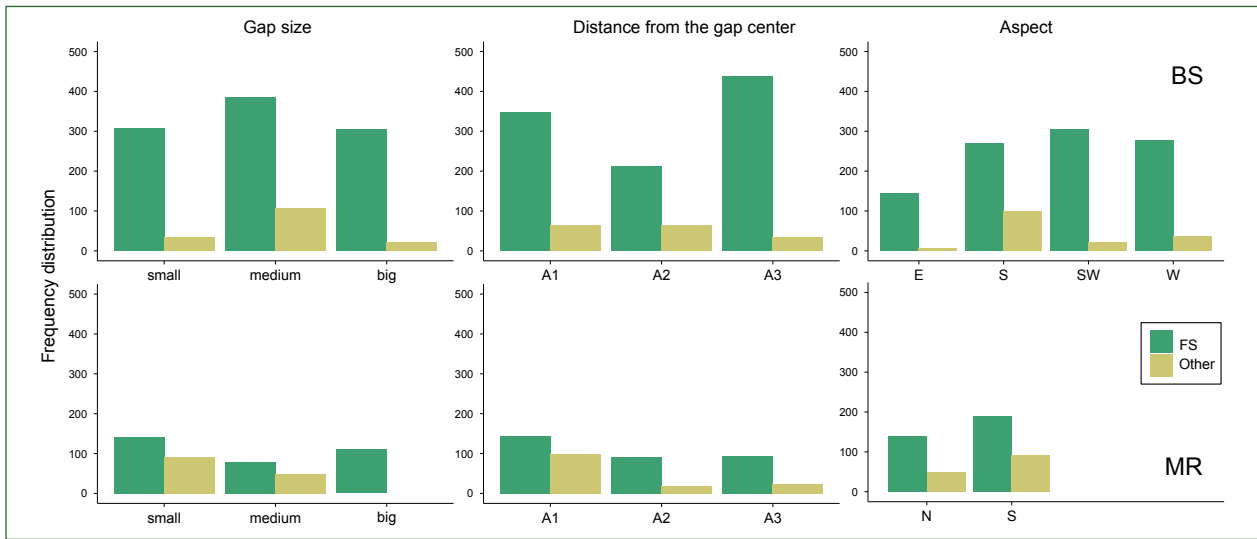
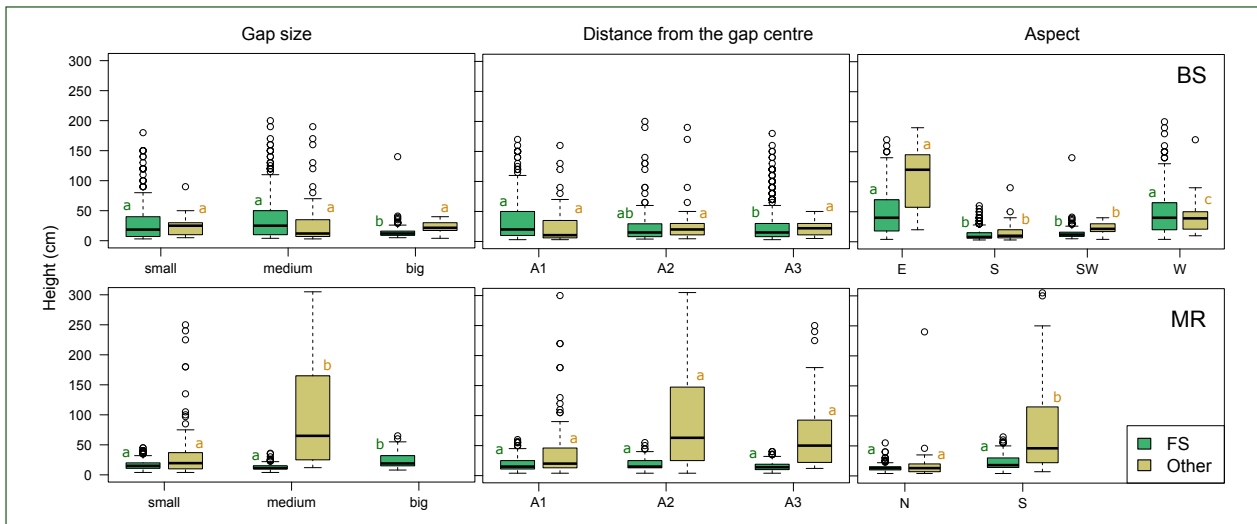


Figure 7 - Boxplots showing the height distribution of beech and other broadleaf trees according to the characteristics of the gaps in Bassano (BS) and Monte Raschio (MR). Different letters indicate significant differences among groups according to the pairwise comparisons between group levels with correction for multiple testing.



broadleaves species was significantly greater than at BS ($P < 0.001$). Gap characteristics had a strong influence on height enhancement, with medium-sized gaps, intermediate and outermost sections, and the south aspect having a significant positive influence ($P < 0.001$) (Fig. 7).

Finally, based on the results of the LMM, we found a significant effect of aspect ($P < 0.001$) and gap size ($P < 0.05$) on the height variability of beech regeneration, as well as an interaction between the distance from the gap centre and gap size ($P < 0.001$), specifically between the outermost section A3 and medium-sized gaps. The selected best model explains that 37% of the overall height variability is attributable to environmental factors (gap characteristics), while a further 39% is explained by the random effects included in the model (i.e. SIC). This suggests that the remaining variance is derived from differences between sites (Tab. 2).

When analysing the other broadleaves species, aspect

Table 2 - Summary of the LMM (Linear mixed-effects model) statistics for *F. sylvatica* only (Model_FS) and for the other broadleaves species (Model_Other). AIC: Akaike Information Criterion, N° parameters includes fixed and random () effects, R²m: marginal R squared, R²c: conditional R squared, NumDF: Numerator Degrees of Freedom (number of parameters estimated for the effect).

	AIC	N° parameters	R ² m	R ² c
Model_FS	12070	13 (+1)	0.37	0.39
Model_Other	3524	16 (+1)	0.23	0.41
Model_FS: F. sylvatica only. Random effect: SIC				
Predictors	NumDF	F-value	p-value	
Aspect	4	120.8	0.0000	
Gap size	2	3.96	0.0052	
distance centre : gap size	4	11.17	0.0000	
Model_other: the other broadleaves species. Random effect: SIC				
Aspect	4	7.8	0.0000	
Gap size	2	3.46	0.0315	

and gap size remained significant predictors of height ($P < 0.0315$). However, the effect of gap size was weaker ($P < 0.05$), and no significant interaction was detected. However, the model was less capable of explaining the overall variance, with marginal and conditional R^2 values of approximately 0.23 and 0.41, respectively (Tab. 2).

Overall, there are significant differences between sites, and the main ecological pattern is clear: height growth variability is determined by exposure and gap size.

Discussion

Our survey showed a higher presence of natural beech regeneration in the BS area, characterized by a more active and recent management than in the MR UNESCO site for all developmental stages. The same pattern was observed for the health status, with more individuals of both beech trees and other broadleaves tree species in good health conditions.

The average gap size was comparable between the two areas (518.8 m² in BS, from 310 to 980 and 541.3 m² in MR, from 200 to 1,200) but MR showed a higher variability. According to the literature, these gaps can be classified as large, although size thresholds may vary between studies and forest types. Bagnato et al. (2021), in a European beech high forest, considered the following sizes: small, 200 m²; medium, 400 m²; and large, 600 m². In an old-growth European beech forest, the gap size ranged from 116 to 1,410 m² (Naaf and Wulf 2007). In a forest type dominated by European beech (90%), small, medium and large gaps were 280, 530 and 1,150 m², and in a mixed forest type dominated by Norway spruce and European beech (50% Norway spruce, 30% European beech) they were 280, 765 and 905 m² (Hammond and Pokorny 2020). Furthermore, no significant difference in size was observed between naturally occurring gaps and those artificially created by logging in managed forests (Feldmann et al. 2018, Stiers et al. 2019). This finding suggests that the origin of the gap—whether natural or artificial—does not significantly impact the overall pattern of natural regeneration when other conditions, such as microclimate, are consistent. However, the more active and recent silvicultural interventions at the BS beech forest may have significantly altered the stand structure, resulting in progressive canopy opening and changes in the light environment, triggering continuous regeneration processes in the understory. Indeed, the uniform shelterwood system, the common silvicultural approach used to promote the natural regeneration of *F. sylvatica*, involving the gradual removal of mature trees over multiple cutting cycles, ensures optimal conditions for seedling establishment and growth (Barna 2008, Nocentini 2009, Wagner et al. 2010). Progressive canopy openings allow increased light penetration, stimulating seedling development while preventing excessive sun exposure that could cause desiccation (Madsen and Hahn 2008, Muscolo et al. 2017, Tinya et al. 2020). These growing conditions favour the shade-tolerant nature of *F. sylvati-*

ca, promoting its growth and reducing competition from pioneer and/or shade intolerant species. Indeed, gradual harvesting limits competition from fast-growing species and allows beech seedlings to establish dominance, fostering continuous natural regeneration under the forest canopy. Accordingly, we found more abundant natural regeneration of *F. sylvatica* in the European beech forest of BS (about three times higher than in MR), with a significantly greater mean height and a higher percentage of individuals in good growing conditions. The LMM results suggest that the site (BS vs. MR), which also include different management practices, has a significant influence as a random effect in explaining the variance. These results may confirm uniform shelterwood system as an appropriate method for favouring natural regeneration and maintaining a stable beech-dominated stand with minimal disruption, as widely reported in the literature (Nocentini 2009, Wagner et al. 2010, Janík et al. 2016).

Another silvicultural method to manage European beech forests and ensure sustainable growth, natural regeneration, ecosystem resilience, and biodiversity conservation is the gap-cutting technique (Madsen and Hahn 2008, Aszalós et al. 2023). It is increasingly recognized as a viable method to enhance tree species diversity and improve forest structure by increasing structural heterogeneity and promoting vertical and horizontal diversity. By creating small to medium-sized canopy openings, removing clusters of trees, gap-cutting promotes light penetration, encouraging species diversity by allowing both shade-tolerant and shade-intolerant species (Kovács et al. 2020, Aszalós et al. 2023). This method promotes structural diversity with multiple age classes and is better suited for mixed-species forests where gaps can enhance diversity, encourages mixed regeneration, so integrating beech with other species. It seems to align with our results, suggesting that gap-cutting may be closer to the MR beech forest, as the gap opening may simulate the natural gaps within the continuous forest cover. Indeed, the density of the other broadleaved species and their mean height are significantly higher at MR than at BS (Tab. 1). The medium- and small-size gaps seems to favour the regeneration in both forest area, because they can create the best conditions for beech natural regeneration, providing the right balance between light availability, microclimate stability, and competition control (Bagnato et al. 2021).

Tree height increased up to medium-sized gaps (~500 m²), where light conditions are likely optimal for seedling and sapling growth. In contrast, height declined slightly in larger gaps, probably because higher solar radiation, elevated temperatures, and increased evapotranspiration create drier and more stressful microclimatic conditions, which can limit regeneration growth. In small gaps, reduced light availability appears to be the main constraint on growth—especially on northern aspects, where incoming radiation is naturally lower (Muscolo et al. 2014). Overall, the relationship between gap size and height growth seems to be non-linear: regeneration benefits

from the improved light environment of intermediate gaps, but growth diminishes again in the largest gaps due to increasingly unfavourable moisture and temperature conditions.

Our results also showed a relevant spatial pattern on the regeneration distribution within the gap, with higher regeneration density the other broadleaves species toward the edges in the warmer and sunnier (south/southeast) exposures. In contrast, in gaps with cooler (north-dominant) exposures, there doesn't seem to be a significant difference between the edges and the centre of the gap. For beech regeneration, there was a slight spatial distribution within the gap, with higher densities towards the edges and in the centre of the gap. However, the results of the linear mixed model did not show a significant effect of distance from the edge, nor any strong significant interaction with other gap characteristics. Indeed, despite for the European beech regeneration and the regeneration of shade-intolerant species there is a significant relationship between regeneration density and spatial position within the gap (Hammond and Pokorný 2020, Bagnato et al. 2021, Orman et al. 2021), different and contrasting results have been reported in the literature. In a European beech-dominated forest in southern Denmark (0-29 m a.s.l.), a gap-cutting experiment revealed a higher presence of regeneration outside than in the centre of gaps, although the difference was not significant (Madsen and Hahn 2008). In a beech forest in southeastern Slovenia at 860-890 m a.s.l., the highest regeneration density was found along the edges of gaps rather than in the centre (Vilhar et al. 2015). In contrast, in a mountain European beech forest at 1,450 m a.s.l. in southern Italy, higher beech regeneration density was found in the central area of gaps compared to the outermost area (Bagnato et al. 2021), as well as in a temperate European beech-Norwegian spruce-dominated mixed forest in southern Czech Republic (210-575 m a.s.l., Hammond and Pokorný 2020). These results were also consistent with the study by Orman et al. (2021) in an old-growth forest in central Poland at 375-580 m a.s.l., where the highest densities of European beech seedlings were observed in the centre of the gap.

These results can support the management strategies, for example, in driving the gap-opening characteristics according to the dominant stand aspect. However, further investigations considering the spatial pattern of the micrometeorological conditions within gaps with different physical characteristics are necessary for a more meaningful statistical significance of the ecological requirements for seedling establishment and growth.

Uncertainties and limitations of the study

Despite providing insights into how gap characteristics influence tree species regeneration, this study is subject to several limitations that should be considered when interpreting the results. First, the absence of microclimate measurements—such as light availability

(e.g., photosynthetically active radiation – PAR), soil moisture, and temperature—limits our ability to directly link regeneration patterns to the environmental gradients typically associated with different gap sizes. Similarly, the lack of data on browsing pressure represents a substantial uncertainty, as variations in ungulate density or hunting regimes between the two forest types could strongly affect seedling survival and growth, potentially confounding the observed gap effects. In addition, the study did not quantify the average height of the vegetation surrounding the gaps, which can influence light penetration and microclimatic conditions within the gap, thereby affecting regeneration outcomes. Other unmeasured biotic and abiotic factors, including seed rain variability, soil nutrient status, understory competition, and small-scale disturbance history, may also influence regeneration dynamics but were not explicitly quantified. Together, these gaps in information constrain the strength of causal inferences and highlight the need for more integrative, multi-factor studies to fully understand how gap characteristics shape tree regeneration processes.

Conclusions and perspectives

Overall, our findings suggest poor regeneration potential for some ageing stands. They point out the need for appropriate management strategies for conservation and maintaining the ecological and social role of such marginal priority habitats of special naturalistic interest. In low-elevation beech forests under Mediterranean climatic conditions, implementing gap-cutting may be an effective management strategy, as it promotes mixed regeneration and ensures structural diversity with various age classes. However, it is crucial to monitor the increasing pressure from drought-adapted tree species. Consequently, specific conservation strategies for beech forests are essential to prevent a shift in dominance from *F. sylvatica* to other broadleaved species, such as oaks. Climate-adaptive tree-oriented silvicultural strategies based on selective thinning may reduce growth decline and the related higher mortality risk of *F. sylvatica* in low-elevation forests under ongoing climate change. The appropriate management strategies, coupled with research efforts to find and introduce more drought-tolerant genotypes and proveniences, may enhance resilience and promote the coexistence of *F. sylvatica* with more drought-adapted species for habitat conservation.

Acknowledgments

This work was supported by the Project “LakeFagus”, funded by the Regional Natural Park of Bracciano-Martignano (Lazio region, Italy). The authors would like to thank the Director and the personnel from the Regional Natural Park of Bracciano-Martignano, especially Dr. Salvatore Mineo, for field assistance and collaboration.

References

- Abrari Vajari K., Jalilyvand H., Pourmajidian M.R., Espahbodi K., Moshki A. 2012 - *Effect of canopy gap size and ecological factors on species diversity and beech seedlings in managed beech stands in Hyrcanian forests*. Journal of Forestry Research 23: 217–222. <https://doi.org/10.1007/s11676-012-0244-6>
- Aszalós R., Kovács, B., Tinya F., Németh C., Horváth C.V., Ódor P. 2023 - *Canopy gaps are less susceptible to disturbance-related and invasive herbs than clear-cuts: Temporal changes in the understorey after experimental silvicultural treatments*. Forest Ecology and Management 549: 121438. <https://doi.org/10.1016/j.foreco.2023.121438>
- Bagnato S., Marziliano P.A., Sidari M., Mallamaci C., Marra F., Muscolo A. 2021 - *Effects of gap size and cardinal directions on natural regeneration, growth dynamics of trees outside the gaps and soil properties in European beech forests of southern Italy*. Forests 12: 1563. <https://doi.org/10.3390/f12111563>
- Barna M. 2008 - *The effects of cutting regimes on natural regeneration in submountain beech forests: species diversity and abundance*. Journal of Forest Science 54 (12): 533–544. <https://doi.org/10.17221/42/2008-JFS>
- Clinton B.D., Baker R. 2000 - *Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses*. Forest Ecology and Management 126: 51–60. [https://doi.org/10.1016/S0378-1127\(99\)00082-1](https://doi.org/10.1016/S0378-1127(99)00082-1)
- De Assis Barros L., Venter M., Elkin C., O Venter O. 2022 - *Managing forests for old-growth attributes better promotes the provision of ecosystem services than current age-based old-growth management*. Forest Ecology and Management 511: 120130. <https://doi.org/10.1016/j.foreco.2022.120130>
- De Groot R.S., Wilson M.A., Boumans R.M.J. 2002 - *A typology for the classification, description and valuation of ecosystem functions, goods and services*. Ecological Economics 41(3): 393–408. [https://doi.org/10.1016/S0921-8009\(02\)00089-7](https://doi.org/10.1016/S0921-8009(02)00089-7)
- Feldmann E., Drößler L., Hauck M., Kucbel S., Pichler V., Leuschner C. 2018 - *Canopy gap dynamics and tree understorey release in a virgin beech forest, Slovakian Carpathians*. Forest Ecology and Management 415: 38–46. <https://doi.org/10.1016/j.foreco.2018.02.022>
- Feldmann E., Glatthorn J., Ammer C., Leuschner C. 2020 - *Regeneration Dynamics Following the Formation of Understorey Gaps in a Slovakian Beech Virgin Forest*. Forests 11(5): 585. <https://doi.org/10.3390/f11050585>
- Giannini T., Cutini A., Gugliotta O.I., Manetti M.C. 2010 - *Tree canopy cover and natural regeneration into strictly protected forest areas: the MaB reserve of Montedimezzo (Isernia, Italy)*. Annals of Silvicultural Research (36): 87 – 96. DOI: 10.12899/ASR-823
- Hammond M.E., Pokorný R. 2020 - *Effects of gap size on natural regeneration and microenvironmental soil conditions in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst) dominated mixed forest*. Plant, Soil and Environment 66: 607–615. <https://doi.org/10.17221/397/2020-PSE>
- Janík D., Král K., Adam D., Hort L., Samonil P., Unar P., Vrska T., McMahon S. 2016 - *Tree Spatial Patterns of *Fagus sylvatica* Expansion over 37 Years*. Forest Ecology and Management 375: 134–145. <https://doi.org/10.1016/j.foreco.2016.05.017>
- Kovács B., Tinya F., Németh Cs., Ódor P. 2020 - *Unfolding the effects of different forestry treatments on microclimate: results of a 4-year experiment*. Ecological Applications 30(2): e02043 <https://doi.org/10.1002/eap.2043>
- Leuschner C. 2020 - *Drought response of European beech (*Fagus sylvatica* L.) - a review*. Perspectives in Plant Ecology, Evolution and Systematics 47: 125576. <https://doi.org/10.1016/j.ppees.2020.125576>
- Lin Y., Hulting M.L., Augspurger C.K. 2004 - *Causes of spatial patterns of dead trees in forest fragments in Illinois*. Plant Ecology 170: 15–27. <https://doi.org/10.1023/B:VEGE.0000019017.41546.eb>
- Madsen P., Hahn K. 2008 - *Natural Regeneration in a Beech-Dominated Forest Managed by Close-to-Nature Principles - A Gap Cutting Based Experiment*. Canadian Journal of Forest Research 38: 1716–1729. <https://doi.org/10.1139/X08-026>
- Mattei M., Conticelli S., Giordano G. 2010 - *The Tyrrhenian margin geological setting: from the Apennine orogeny to the K-rich volcanism*. In G.G. Funicello R (a cura di), The Colli Albani Volcano: 7–27
- Mazza G., Becagli C., Proietti R., Corona P. 2020 - *Climatic and anthropogenic influence on tree-ring growth in riparian lake forest ecosystems under contrasting disturbance regimes*. Agricultural and Forest Meteorology 291: 108036. <https://doi.org/10.1016/j.agrformet.2020.108036>
- Mazza G., Monteverdi M.C., Altieri S., Battipaglia G. 2024 - *Climate-driven growth dynamics and trend reversal of *Fagus sylvatica* L. and *Quercus cerris* L. in a low-elevation beech forest in Central Italy*. Science of the Total Environment 908: 168250. <https://doi.org/10.1016/j.scitotenv.2023.168250>
- Muscolo A., Settineri G., Bagnato S., Mercurio R., Sidari M. 2017 - *Use of canopy gap openings to restore coniferous stands in Mediterranean environment*. iForest 10: 322–327. <https://doi.org/10.3832/ifor1983-009>
- Muscolo A., Bagnato S., Sidari M., Mercurio R. 2014 - *A review of the roles of forest canopy gaps*. Journal of Forestry Research 25: 725–736. <https://doi.org/10.1007/s11676-014-0521-7>
- Naaf T., Wulf M. 2007 - *Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps*. Forest Ecology and Management 244: 141–149. <https://doi.org/10.1016/j.foreco.2007.04.020>
- Nagel T.A., Zenner E., Brang P. 2013 - *Implications for Integrated Forest Management. Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity*. Research in Old-Growth Forests and Forest Reserves. European Forest Institute: Freiburg, Germany: 44–50.

- Nocentini S. 2009 - *Structure and management of beech (Fagus sylvatica L.) forests in Italy*. iForest 2: 105–113. <https://doi.org/10.3832/ifer0499-002>.
- Orman O., Wrzesinski P., Dobrowolska D., Szewczyk J. 2021 - *Regeneration growth and crown architecture of European beech and silver fir depend on gap characteristics and light gradient in the mixed montane old-growth stands*. Forest Ecology and Management 482: 118866. <https://doi.org/10.1016/j.foreco.2020.118866>
- Paletto A., Pieratti E., De Meo I., Agnelli A.E., Cantiani P., Chiavetta U., Mazza G., Lagomarsino A. 2021 - *A multi-criteria analysis of forest restoration strategies to improve the ecosystem services supply: an application in Central Italy*. Annals of Forest Science 78: 7. <https://doi.org/10.1007/s13595-020-01020-5>.
- Pesaresi S., Biondi E., Casavecchia S. 2017 - *Bioclimates of Italy*. Journal of Maps 13 (2): 955–960. <https://doi.org/10.1080/17445647.2017.1413017>
- Runkle J.R. 1992 - *Guidelines and Sample Protocol for Sampling Forest Gaps*. General Technical Report PNW-GTR-283. Forest Service: Washington, DC, USA.
- Sardans J., Peñuelas J. 2013 - *Plant-soil interactions in Mediterranean forest and shrublands: Impacts of climatic change*. Plant Soil 365: 1–33. <https://doi.org/10.1007/s11104013-1591-6>.
- Scharenbroch B.C., Bockheim J.G. 2007 - *Pedodiversity in an old-growth northern hardwood forest in the Huron Mountains, Upper Peninsula, Michigan*. Canadian Journal of Forest Research 37: 1106–1117. <https://doi.org/10.1139/X06-312>
- Schliemann S.A., Bockheim J.G. 2011 - *Methods for studying treefall gaps: A review*. Forest Ecology and Management 261: 1143–1151. <https://doi.org/10.1016/j.foreco.2011.01.011>
- Stiers M., Willim K., Seidel D., Ammer C., Kabal M., Stillhard J., Annighöfer P. 2019 - *Analyzing spatial distribution patterns of European Beech (Fagus sylvatica L.) regeneration in dependence of canopy openings*. Forests 10: 637. <https://doi.org/10.3390/f10080637>
- Tinya F., Kovács B., Aszalós R., Tóth B., Csépanyi P., Németh C., Ódor P. 2020 - *Initial regeneration success of tree species after different forestry treatments in a sessile oak-hornbeam forest*. Forest Ecology and Management 459: 117810. <https://doi.org/10.1016/j.foreco.2019.117810>
- Vilhar U., Rožnberger D., Simončič P., Diaci J. 2015 - *Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps*. Annals of Forest Science 72: 253–266. <https://doi.org/10.1007/s13595-014-0424-y>
- Wagner S., Collet C., Madsen P., Nakashizuka T., Nyland R.D., Sagheb-Talebi K. 2010 - *Beech regeneration research: from ecological to silvicultural aspects*. Forest Ecology and Management 259: 2172–2182. <https://doi.org/10.1016/j.foreco.2010.02.029>