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FRANCO PEDROTTI

DAN GAFTA

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Floristic differentiation between mid-seral communities of abandoned charcoal kilns in the forests of the Gargano Promontory (south Italy)

Franco PEDROTTI¹, Dan GAFTA^{2,*}

¹Department of Plant Diversity and Ecosystems Management Unit, University of Camerino, Camerino, Italy

²Department of Taxonomy and Ecology, Babeş-Bolyai University, Cluj-Napoca, Romania

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Abstract: We searched for patterns in species composition and richness of mid-seral communities developed on abandoned charcoal hearths that might be induced by differences in succession progress and forest context. One phytosociological relevé was performed on each of the 22 charcoal platforms located in beech (*Anemone apenninae-Fagetum*) and oak-hornbeam forests (*Doronic-Carpinetum*). The ratio of forest understorey to non-forest species richness (F/nF) at plot level was used as a proxy for the succession progress. There was a sharp differentiation of plant communities due to their floristic resemblance with the understorey vegetation of the forest type in which they were integrated. Nevertheless, these mid-seral communities still contained a number of nitrophilous weeds that were remnants of the preceding pioneer assemblages. A subgroup of communities (integrated in the beech forest) that lacked the non-forest species mentioned above (high F/nF ratio) could be ascribed to a more advanced seral stage. Species richness on charcoal platforms was not related to forest type, but that might be the consequence of the small sample size. Instead, the number of species decreased steadily with increasing F/nF ratio, which is consistent with the predictions emerging from the paradigm of ecological succession. The forest context accounted for most of the observed floristic dissimilarity between these mid-seral communities. Differences in succession progress seem to be traceable through the number of species, which declines towards more mature stages. The observed communities shared probably the same type of pioneer plant assemblage (*Alliario-Chaerophylletum temuli*) in the preceding seral stage.

Key words: *Anemone apenninae-Fagetum*, *Doronic-Carpinetum*, forest to non-forest species ratio, forest context, discriminant species, overlying tree cover, community species richness, seral stages

1. Introduction

The charcoal kiln sites represent an impressive legacy, with cultural and scientific significance, from the millennial human activity in the European woodlands (Ludemann, 2011). Although this form of forest exploitation is almost gone, it was, in the not too distant past, a significant factor shaping the Mediterranean forest landscape (Blondel, 2006; Nocentini and Coll, 2013).

Present knowledge suggests that such relict charcoal burning sites have persistent effects on the vegetation through changes in soil properties and light availability. The main cause seems to be the long chemical stability of charcoal, which allows the remains to maintain in situ as a thick layer over hundreds of years (Cheng et al., 2008; Criscuoli et al., 2014). As documented by several studies carried out in different geographic regions (Mikan and Abrams, 1995; Young et al., 1996; Wittig et al., 1999; Carrari et al., 2016), the substrate of former charcoal platforms features higher values of pH and

N content than the adjacent, undisturbed forest soil. On the other hand, the absence or very low density of overstorey trees in charcoal sites makes them look and function ecologically like small gaps (Mikan and Abrams, 1995; Carrari et al., 2016). Such alterations in soil and light conditions are generally beneficial to the low vegetation developed on charcoal platforms. In this regard, conspicuous differences in terms of species composition, richness, and abundance between charcoal kiln sites and the contiguous forest understorey were reported in central and southern Europe (Wittig et al., 1999; Carrari et al., 2016). Therefore, the charcoal burning sites can be treated ecologically as distinctive “micro-islands” within the matrix of circumscribing forest vegetation, as they display particular environmental conditions and their own synusium of plants (dependent communities), at least in early stages of succession.

In addition to the hypotheses mentioned, it is equally important to investigate the variation of species

* Correspondence: dan.gafta@ubbcluj.ro

composition between charcoal kilns abandoned at different times and located in different forest types, in order to better understand the complex determinism of the vegetation succession as well as the role of stochastic factors in these particular sites. For instance, it is likely that differences in local species pool coupled with seed dispersal limitation and the degree of substrate alteration are key factors in explaining the (probable) floristic divergence between charcoal kilns from different forest types and successional stages, respectively. However, to date, there are no studies addressing such goals.

For the purpose of this study, we chose to survey the abandoned charcoal platforms that were distributed within the woodlands of the Gargano Promontory. The uniform bedrock (limestone) and short altitudinal range pertaining to this forest area were good premises for controlling the confounding effects of these two environmental variables.

The aim of the present study was to detect patterns in species composition and richness of the plant assemblages developed on charcoal hearths that might be induced by differences in succession progress and/or forest context.

2. Materials and methods

2.1. Study area

The Promontory of Gargano is a small peninsula separated from the principal chain of the Apennines (south Italy). It is completely calcareous, with mountain-like landforms and a maximum altitude of 1065 m. The most diffused forest communities on this promontory are the beech wood [*Anemone apenninae*-*Fagetum* Gentile (1970) Brullo 1983] occurring at higher elevations (750–1000 m) in Foresta Umbra, and the oak-hornbeam wood (*Doronic-Carpinetum* Pedrotti 2007) distributed at lower altitudes (500–750 m) in Bosco Quarto (Falinski and Pedrotti, 1990; Pedrotti and Falinski, 2002; Pedrotti, 2007).

The locations of charcoal kilns were originally chosen for gentle land morphology (i.e. on plane terraces) and their close access to water supply and roads (i.e. in small valleys). The abandoned charcoal hearths look like flattened mounds with rounded bases that have been deformed by pluvial erosion.

2.2. Data collection and transformation

The floristic survey of charcoal kilns distributed in the beech and oak-hornbeam forests of Gargano was carried out in 1986–1987. A single phytosociological relevé was performed on each charcoal platform, excluding the peripheral parts of the kiln, partly modified or destroyed by paths. The relative cover of each vascular species was estimated visually in each vegetation layer. The tree species

rooted nearby the area sampled, but partially covering the target charcoal kiln with their crowns, were also recorded. The ratio of forest understorey to non-forest species (F/nF) at plot level, calculated on the basis of number of taxa, was used as a proxy for the succession progress toward the presumed climax forest. All nemoral, shade-tolerant, herbaceous species along with woody species saplings were included in the category of forest understorey species.

2.3. Data analysis

The classification of relevés (considering only the species rooted within sampled plots) was performed on the corresponding matrix of Jaccard dissimilarity via partitioning around medoids (PAM). The optimal number of partitions was assessed by means of two criteria: maximisation of mean cluster silhouette and cluster stability. The latter was estimated based on the level of bootstrap mean similarity (BMS), with values larger than 75% being considered acceptable for the distinction of plant community types. The ordination of relevés in the reduced space of species was performed through local nonmetric multidimensional scaling (NMDS). The importance of the F/nF ratio, beech tree cover (Btc), and hornbeam tree cover (Htc) in terms of proportion of floristic variance explained (r^2) was evaluated separately by linear fitting with respect to the first two NMDS axes. The species best associated with the community types distinguished were individuated by comparing species relative frequencies (rF) between the relevé clusters after adjusting for unequal group size. The amount or statistical significance of the above statistics (BMS, r^2 and rF) was estimated by 9999 random samples or permutations.

The effects of F/nF ratio and forest type on (rooted) species richness at plot level, while controlling for the effect of tree canopy cover, were tested through a generalised linear model (GLM) with negative binomial error distribution and log link function. The confounding effect of plot size on the number of species recorded was neglected as the two variables were practically independent one from the other (Spearman's coefficient = 0.0624; $P = 0.7827$). A backward removal procedure of variables was further employed in order to obtain the best explanatory model. That was assessed through the Bayesian information criterion (BIC) and the chi-square to degree of freedom ratio (χ^2/df).

All numerical analyses were carried out in R 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria) using the packages 'fpc' (Hennig, 2015), 'vegan' (Oksanen et al., 2016), 'indicpecies' (De Cáceres and Legendre, 2016), and in SAS 9.4 (SAS Institute Inc., Cary, NC, USA) using the procedure GLIMMIX (SAS Institute, 2014).

3. Results and discussion

3.1. Plant species composition

The floristic composition of communities that developed spontaneously on the former charcoal kilns matched closely the composition of the forest association (type) in which they are integrated, i.e. either *Anemone apenninae-Fagetum* or *Doronico-Carpinetum* (Table 1). Nevertheless, at the time of field sampling, these plant assemblages still contained a number of non-forest species that feature particular biological and ecological traits like short life-

span, high nitrogen demand, and preference for disturbed environments. Such species, like *Alliaria officinalis*, *Galium aparine*, and *Chaerophyllum temulum*, are frequent and/or locally abundant in the weed communities of *Alliario-Chaerophylletum temuli* Lohmeyer 1949 (Ministero dell'Ambiente e della Tutela del Territorio e del Mare, 2015). The latter is presumably the plant association that preceded (along the successional gradient) the observed communities on charcoal kilns, as suggested by the corresponding group of diagnostic species (Table 1).

Table 1. Ordered table of the floristic relevés performed on charcoal piles in the Promontorio of Gargano. All species occurring in the tree layer were not rooted within but partially covering the areas sampled. Grey-shaded scores correspond to significantly discriminant species between the two community types.

Forest area	FORESTA UMBRA											BOSCO QUARTO										
Forest type (syntaxon)	<i>Anemone apenninae - Fagetum</i>											<i>Doronico - Carpinetum</i>										
Elevation (m)	750-800 m a.s.l.											550-650 m a.s.l.										
Relevé ID	8	10	11	1	2	3	4	5	6	7	9	12	13	14	15	16	17	18	19	20	21	22
Sampled area (sq. m.)	75	50	50	110	150	75	75	75	75	110	60	150	110	50	75	60	40	90	60	40	40	60
Macroslope aspect	NW	SE	SW	N	NW	NW	NW	NW	NW	NW	S	N	NE	NW	NE	N	N	N	NW	NE	N	NW
Tree layer (t) cover (%)	90	80	80	80	70	80	80	80	80	60	90	80	70	90	80	80	90	80	80	80	80	80
Shrub layer (s) cover (%)	1	0	1	10	10	10	1	1	10	10	0	20	0	1	1	1	1	1	1	1	1	1
Herb layer (h) cover (%)	70	70	70	90	80	80	60	80	90	70	60	70	90	90	70	70	80	90	70	70	80	70
Total number of species	15	17	16	28	27	37	19	23	33	29	20	42	29	36	31	25	30	23	38	37	25	31
Woody species																						
<i>Fagus sylvatica</i> (t)	5.5	4.5	4.5	4.4	4.4	4.4	4.5	4.5	3.4	4.4	5.5	4.4
<i>Fagus sylvatica</i> (s)	.	1.1	1.1	+	+
<i>Fagus sylvatica</i> (h)	+2	+	+	+	+	.	+	+	1.2	+2	+	+
<i>Carpinus betulus</i> (t)	2.1	.	.	.	4.4	5.4	4.4	4.5	4.4	4.4	4.4	4.4	4.4	4.4
<i>Carpinus betulus</i> (s)	+	.	1.1	.	.	+	.	.
<i>Carpinus betulus</i> (h)	+	+	.	+	1.3	+	.	+	.	+	.
<i>Quercus cerris</i> (t)	2.1	.	2.1	2.1	3.1	2.2	2.2	2.1	3.1	2.1
<i>Acer obtusatum</i> (t)	.	2.1	2.1
<i>Acer obtusatum</i> (s)	.	.	1.2	.	.	+	+	.	.
<i>Acer obtusatum</i> (h)	.	+	+	+	+
<i>Acer campestre</i> (t)	1.1
<i>Acer campestre</i> (s)	+	.	.	.
<i>Acer campestre</i> (h)	+	+	.	.	.
<i>Ostrya carpinifolia</i> (t)	1.1	2.1	+	.
<i>Salix caprea</i> (t)	2.1
<i>Ilex aquifolium</i> (s)	.	.	.	+	+
<i>Ilex aquifolium</i> (h)	+	+	+	.	.	.
<i>Sorbus torminalis</i> (s)	+	.	+	.	.	.
<i>Sorbus torminalis</i> (h)	+	.
<i>Euonymus europaea</i> (s/h)	+	.	+	+
<i>Crataegus</i> sp. (s/h)	+	.	.	2.3
<i>Hedera helix</i> (h)	+	2.3	3.3	+	+	+	+	1.2	+	+	2.3	1.2	+	+	+	+	+	.	.	1.2	+	+
<i>Daphne laureola</i> (s/h)	+	+	2.2	1.1	+	+	+	+	2.2	.	.	2.2	.	+	+	.	+	+	+	+	.	+
<i>Rubus hirtus</i> (s/h)	.	.	.	+	+	1.2	.	.	1.2	+	+	+	+	+	+	+	+	.	+	.	+	+

Table 1. (Continued).

Forest area	FORESTA UMBRA												BOSCO QUARTO									
Forest type (syntaxon)	<i>Anemone apenninae - Fagetum</i>												<i>Doronico - Carpinetum</i>									
Relevé ID	8	10	11	1	2	3	4	5	6	7	9	12	13	14	15	16	17	18	19	20	21	22
<i>Ruscus aculeatus</i> (s/h)	+	.	+	+	.	.	+	.	.	+	.	2.2	.	+	.	+	.	.	+	.	.	.
<i>Malus sylvestris</i> (h)	.	.	.	+
<i>Rosa</i> sp. (h)	+
<i>Prunus spinosa</i> (h)	+
<i>Fraxinus ornus</i> (h)	+	.	.	.
Character species of <i>Quercus-Fagetum</i> Br.-Bl. et Vlieger 1937 (incl. <i>Fagetalia</i> Pawlowski 1928)																						
<i>Dentaria bulbifera</i>	1.2	3.3	+2	+2	2.2	1.2	+	+2	1.2	1.2	2.2	1.2	1.1	+	1.2	1.2	1.2	1.2	+	+2	+2	1.2
<i>Sanicula europaea</i>	+	+	1.2	+2	+	+	+	+	+	+	+	+2	+2	+	+	+	1.2	+	+2	2.2	+2	+
<i>Viola reichenbachiana</i>	+	+2	+	+	.	+	+	+	+	+2	+	+2	+	+	+	+	+	+	+	+	+	+
<i>Anemone apennina</i>	+2	+2	.	2.3	1.2	+	+	1.2	.	1.2	1.2	+2	2.3	1.2	+2	1.2	+2	1.2	+	+2	1.2	+2
<i>Cyclamen hederifolium</i>	+2	1.2	1.2	+2	+	+2	+2	+2	+2	+2	1.2	1.2	+2	+2	+2	.	3.4	.	+2	+2	+2	.
<i>Ranunculus ficaria</i>	.	.	.	1.2	1.3	+2	.	2.3	2.3	2.3	.	3.3	1.2	1.2	1.2	3.4	3.4	2.3	+2	2.2	2.2	1.2
<i>Ranunculus lanuginosus</i>	.	.	.	+	.	+	+	1.1	1.2	.	.	1.2	3.3	2.2	1.2	1.2	1.2	2.3	+	2.2	2.3	1.2
<i>Rumex sanguineus</i>	1.1	.	+	.	+	.	+	+	+2	+	1.1	+	+	.	.	+	+2
<i>Melica uniflora</i>	+	+2	+2	+2	.	+2	+2	+2	+	.	.	+	.	+2	+2	.	.
<i>Corydalis cava</i>	.	.	.	+2	+2	.	.	+	+	.	.	.	1.2	+2	+2	+2	+	.	.	+	1.2	.
<i>Euphorbia amygdaloides</i>	.	.	+2	.	.	+	+	.	.	+	+	.	+	+	+	+	.	+
<i>Carex sylvatica</i>	.	.	.	+2	.	+2	.	.	+2	.	+2	+	+2	+	+	+2	.	.
<i>Mycelis muralis</i>	+	.	.	+	+	.	.	.	+	.	.	+	.	+	+	.	.
<i>Galanthus nivalis</i>	+	+2	.	+2	.	+2	+2	.	+	.	+	+
<i>Lathyrus venetus</i>	+	.	+2	+	.	+2	.	.	.	+	+2	2.2	.	.
<i>Milium effusum</i>	+	+	+	.	+	+	+
<i>Polygonatum odoratum</i>	.	+	+	+	+	.	.	.	+	+	.	.	.
<i>Aremonia agrimonioides</i>	+	+	+	+	.	.	.	+	.	.	+
<i>Veronica montana</i>	.	+2	.	.	+2	+	+	+	.	.	.
<i>Stachys sylvatica</i>	+	.	+2	+	+
<i>Neottia nidus-avis</i>	.	.	+	+	+	.	.	+
<i>Circaea lutetiana</i>	+	+2	.	.	.	+
<i>Tamus communis</i>	+	.	.	.	+	.	+
<i>Scilla bifolia</i>	+	+
<i>Campanula trachelium</i>	+	.	+
<i>Allium ursinum</i>	+
<i>Asperula taurina</i>	+
<i>Polystichum aculeatum</i>	+2
<i>Polystichum setiferum</i>	+2
Character species of <i>Geranio striati-Fagion</i> Gentile 1970																						
<i>Galium odoratum</i>	2.3	2.3	2.3	+2	+2	3.4	+	+2	2.3	+2	1.2	2.3
<i>Arum italicum</i>	.	+	.	+	+2	.	+	+	+	+	+2	+
<i>Festuca exaltata</i>	4.5	1.2	3.4	.	.	+2	.	.	+2	+2	1.2	1.2
<i>Cardamine chelidonia</i>	+	+	+	+	+	.	1.2
<i>Mercurialis perennis</i>	.	.	.	+	.	+2	.	.	.	+
Character species of <i>Physospermo verticillati-Quercion cerris</i> Biondi et al. 2008																						
<i>Pulmonaria vallisarsae</i>	+	+	+	1.1	+	+	+	+	+	+	+
<i>Alium pendulinum</i>	+2	1.2	+2	2.3	2.2	3.3	2.3	1.2	2.3	2.3
<i>Doronicum cordatum</i>	1.2	.	2.3	+2	+2	2.3	1.2	1.3	+2	2.3

Table 1. (Continued).

Forest area	FORESTA UMBRA												BOSCO QUARTO											
Forest type (syntaxon)	<i>Anemone apenninae - Fagetum</i>												<i>Doronico - Carpinetum</i>											
Relevé ID	8	10	11	1	2	3	4	5	6	7	9	12	13	14	15	16	17	18	19	20	21	22		
<i>Cardamine graeca</i>	1.2	.	+	1.2	1.2	1.2	+	
<i>Myosotis sylvatica</i>	+2	+	+	.	+	
<i>Potentilla micrantha</i>	+	+	.	.	+	.	+	
Diagnostic species of <i>Alliario-Chaerophylletum temuli</i> Lohmeyer 1949																								
<i>Veronica hederifolia</i>	.	.	.	4.4	2.3	+	1.3	4.5	2.3	.	3.3	3.3	2.3	2.3	3.4	3.4	.	3.5	1.3	1.2	4.5	3.4		
<i>Alliaria officinalis</i>	.	.	.	+2	1.2	1.2	.	.	+	1.2	+	+2	1.2	.	.	+	+	+	+	.	+	+		
<i>Geranium robertianum</i>	.	.	.	+	+2	.	+	.	+	+2	+	.	+	+2	.	+	+	+2	1.2	+2	+2	.		
<i>Galium aparine</i>	.	.	.	+2	3.4	+2	.	+2	2.3	3.4	2.2	1.2	1.2	1.2	+2	+2		
<i>Chaerophyllum temulum</i>	.	.	.	+	+2	+2	+2	1.2	2.3	.	.	+	+2	+2	+	.	+		
<i>Geum urbanum</i>	.	.	.	+	.	+	.	.	+	.	.	+	+	.	+	+	.	.	+	.	.	+		
<i>Moehringia trinervia</i>	+2	+	.	+	+2	.	+	1.3	1.2	+2	.		
<i>Lapsana communis</i>	+	+	+	+	+	+		
<i>Urtica dioica</i>	.	.	.	+	+2	+	.	.	+	2.3		
<i>Chelidonium majus</i>	+2	.	.	.	+		
Other nitrophilous weeds																								
<i>Poa trivialis</i>	+2	.	1.3	+2	.	+	+	+2	+2	.	2.3
<i>Lamium maculatum</i>	.	.	.	+	1.2	+2	+2	+2	1.3	
<i>Anthriscus nemorosa</i>	1.2	+2	.	+	1.2	1.2	+	
<i>Sambucus nigra</i> (s)	+	.	.	.	1.2	1.1	.	.	+	1.2	
<i>Sambucus nigra</i> (h)	.	.	.	+	+	+	
<i>Stellaria media</i>	+	3.4	1.2	.	+2	
<i>Geranium lucidum</i>	+	+	.	.	.	
Accompanying species																								
<i>Pteridium aquilinum</i>	.	+	+	+	+	+	+	+	1.1	1.2	+	.	
<i>Fragaria vesca</i>	+	.	+	.	.	.	+	+	.	.	
<i>Orobancha</i> sp.	+	+	+	+	.	
<i>Astragalus glycyphyllos</i>	+	.	
<i>Aquilegia vulgaris</i>	+	
<i>Solanum dulcamara</i>	+	
<i>Atropa belladonna</i>	+	
<i>Athyrium filix-foemina</i>	.	+	
<i>Cephalanthera</i> sp. (juv.)	.	.	+	
<i>Iris foetidissima</i>	
<i>Lilium croceum</i>	+	
<i>Thalictrum aquilegifolium</i>	+	.	.	.	
<i>Festuca heterophylla</i>	+	.	.	
<i>Bromus ramosus</i>	+	.	.	
<i>Orchis</i> sp. (juv.)	+	.	.	
<i>Prunella vulgaris</i>	+	.	
<i>Trifolium pratense</i>	+	.	

Similar floristic patterns were observed in the Bialowieza Forest (Poland), where the saplings of woody species established relatively fast (5–10 years) in the former charcoal kilns located in small clearings, but the herb layer's structure was still different from that of the

surrounding old-growth forest after 24 years from the initiation of succession (Falinski, 1986). Our observations are also in accordance with the findings from beech forests in Germany (Wittig et al., 1999) and those from mixed oak woods and beech forests in Tuscany (Carrari et al., 2016).

In fact, the cited authors revealed that the differences in floristic composition of understorey vegetation between the charcoal kilns and the adjacent stands were due to several non-forest species with high nutrient demands. However, in contrast to these reports, we did not observe any differential species that might indicate higher pH in charcoal hearths than in the undisturbed forest soil. That was very likely because of the base-rich bedrock underlying the whole forest area under study. Another important aspect shared between our study and those cited above is the usual lack of adult trees rooted inside the charcoal platforms, despite the constant occurrence of tree saplings. That allowed, instead, the persistence of open-habitat weeds under more favourable light conditions as compared to the forest floor.

No vascular pyrophytes were recorded in our survey but *Funaria hygrometrica*, a bryophyte known to occur frequently in fire-disturbed habitats and coal cellars, was reported from charcoal sites in Gargano (Aleffi et al., 2009).

3.2. Classification and ordination of relevés

The optimal, numerical classification of relevés consisted of two, stable clusters that were also clearly distinctive along

the NMDS axis 1 (Figure 1). These two clusters match perfectly the empirical partitioning of relevés in two plant associations (*Anemone apenninae-Fagetum* or *Doronico-Carpinetum*) that was achieved by taking into account the occurrence of character species (Table 1). In addition, most of the diagnostic species at alliance level along with beech saplings are statistically discriminant, given their preference (high relative frequency of occurrence) for one of the two clusters (Table 1). Nevertheless, the two groups of seral communities could be easily distinguishable by taking into account only the relative cover of nearby beech or hornbeam crowns overlying the abandoned charcoal kilns, as shown by the two opposite vectors on the ordination diagram (Figure 1). This outcome suggests that the forest habitat context has contributed the most to the observed floristic divergence between these mid-seral assemblages. Actually, forest proximity is an indirect factor that acts through various processes like nutrient enrichment from litter decomposition, seed rain fall, and colonisation by stoloniferous forest herbs.

A slightly higher, mean silhouette (0.309 versus 0.297) could be achieved by separating a third, small group of relevés along the NMDS axis 2 (Figure 1), but at the

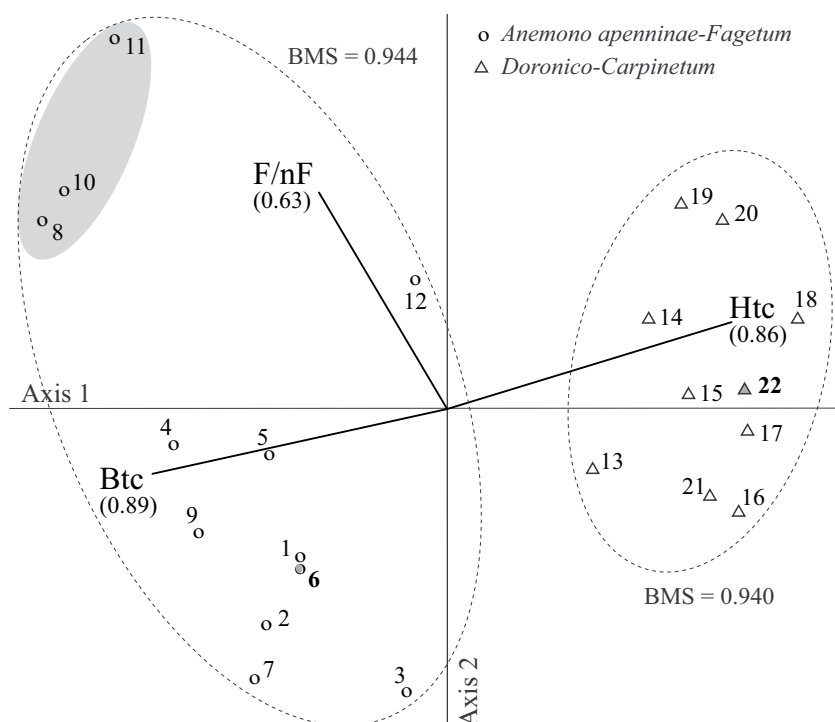


Figure 1. Local NMDS ordination of the relevés from Table 1 in the reduced species' space. The marked clusters were previously distinguished through PAM. The cluster stability is indicated by the BMS values. The importance of each external predictor represented through one vector (F/nF – forest to non-forest species ratio; Btc and Htc – beech and hornbeam tree relative cover, respectively) is expressed by the r-square value in the brackets.

expense of a much lower stability (BMS = 0.65) of that cluster. It is worth noting, however, that the F/nF vector points towards that poorly defined extra cluster, which is formed of three communities developed in beech stands (relevés 8, 10, and 11) and displaying not only the lowest species richness, but also the least number and abundance of nitrophilous weeds (Table 1). Although that subgroup of relevés could not be distinguished based on the presence of differential species, it was probably circumscribed to a more advanced seral stage, in which most of the pioneer, less stress-tolerant species were lost. Differences in terms of successional speed and/or timing of charcoal kiln abandonment might have been responsible for such floristically minor but structurally relevant differentiation.

3.3. Patterns in species richness

Although the number of species in the understorey is generally expected to decrease with the gradual

development of the forest canopy, the observed species richness was not affected by the cover degree of the tree layer (Table 2). The forest type had also no significant effect on the number of species recorded on charcoal kilns (Table 2), even though the species pool in oak-hornbeam forests is usually larger than in beech forests. The small sample size, determined by the limited number of abandoned charcoal sites extant in the study area and suggested by the high variance in species richness observed on the charcoal kilns located in the beech forest (Table 1), may have prevented the detection of a significant difference.

The F/nF ratio was the only predictor that showed a significant effect on species richness (Table 2). By modelling this relationship in the log-log space, a steady decline in the number of species with increasing F/nF ratio was disclosed (Figure 2). Such an outcome is in accordance with the paradigm of ecological successions (Begon et

Table 2. Standardised coefficients along with their statistical significance of the variables used to predict the species richness at plot level via GLM.

Predictor variable	Standardised coefficients	t value	Prob. (> t)	Fit statistics
Forest type (beech wood)	-0.104	-0.48	0.6383	Chi-sq./df = 1.21 BIC = 152.98
Tree layer relative cover	0.031	0.14	0.8902	
log(F/nF ratio)	-0.984	-3.85	0.0012	
Intercept	3.309	74.87	<0.0001	

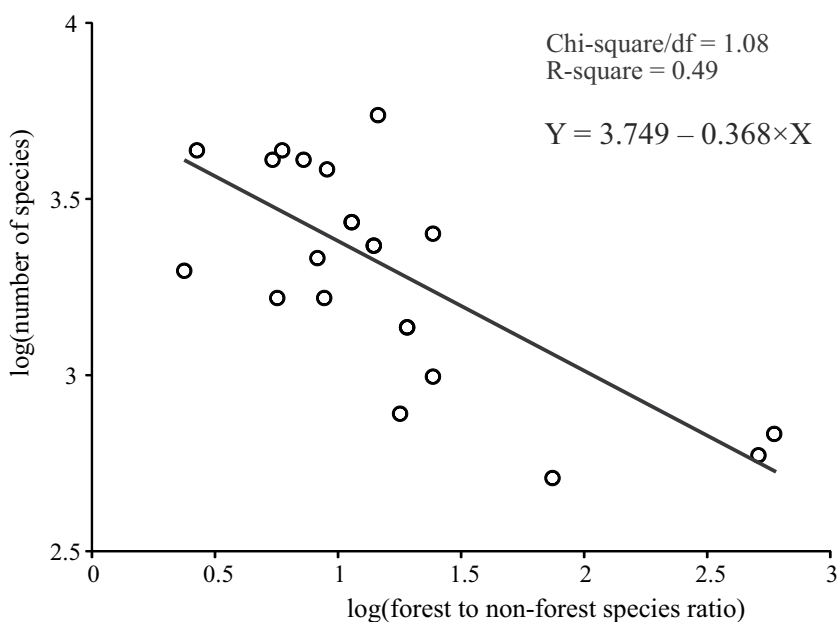


Figure 2. GLM fitted line in log-log space of the number of species recorded at plot level as a function of the forest to non-forest species ratio (F/nF). Both regression coefficients are significantly different from zero at 0.1% threshold of alpha probability.

al., 2006), which predicts a decline in species richness towards mid-late seral stages as a consequence of the high competition for light. In this regard, the forest understorey species are more competitive and can eliminate those adapted to open or disturbed habitats.

In conclusion, the mid-seral communities that developed on the former charcoal hearths are rather inertial in the sense of persistence of several nitrophilous weeds alongside forest herbs and saplings. However, the differentiation of these communities from the circumscribing forest understorey is less conspicuous

on base-rich soils than on acidic soils. The species-rich communities hold a relatively large proportion of non-forest species and appear successional retarded. Changes in floristic composition followed more or less convergent pathways in the early stages of succession (i.e. under strong abiotic stress), as inferred from the remnant species of the prior pioneer assemblages. Later on, the forest (biota) context turned into the most important driver of vegetation dynamics by accounting for most of the observed floristic dissimilarity between these mid-seral communities.

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