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Research paper

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Abstract

An understanding of contemporary and likely future biodiversity requires knowledge of how past human societies have shaped diversity patterns. Here, we use long-term pollen data sets extending from lowlands to subalpine environment in the Carpathian region (Romania) with the aim of exploring the relationship between landscape openness, anthropogenic disturbance, elevation and vegetation richness over the Holocene. We found that landscape openness represents a significant driver of pollen richness: The more open sites from mid (440–750 m) and high elevations (1550–1850 m) showed on average greater diversity than more forested upland sites (1050–1360 m). For the first time, our results show pollen richness patterns along elevation gradients that remain constant over the Holocene. Although significant only over the last 3000 cal. yr BP, these elevational patterns become accentuated with stronger evidence of anthropogenic impact. We also found a strong link between diversity change and major land use strategies of prehistoric societies, demonstrating the potential of pollen richness to be used as a tool to depict the ecological impact of human disturbance on diversity. Most distinct episodes of enhanced floristic richness are evident during the Roman Period (2000 cal. yr BP), and over the last 500 cal. yr BP. Recent anthropogenic activity negatively impacted diversity in mountainous areas mainly through plantations; the lack of sites in agriculture landscapes however limits our inference for this type of setting. The maintenance of habitat diversity is key to maintaining high levels of diversity. While there is temporal consistency in the diversity pattern in records from similar climate and vegetation settings, comparison of diversity from different vegetation assemblages and levels landscapes openness should be interpreted cautiously.

Keywords

Carpathian, diversity, elevation gradient, fire, Holocene, land use, landscape openness, level of disturbance, pollen richness

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Introduction

Latitudinal and elevational diversity gradients occur across scales (Field et al., 2009; Hillebrand, 2004). Complex hierarchical interactions between species richness, spatial scales, and processes controlling diversity have been identified, and operate over different temporal scales i.e. years to million years (Willis and Whittaker, 2002). Large-scale variation in diversity is mainly because with a change in latitude or elevation there is a change in the abiotic determinants of the habitats, including temperature, precipitation, energy, and area (Field et al., 2009; Willis and Whittaker, 2002). At smaller scales, variability in microclimate, biotic and abiotic interactions, and disturbances (natural and anthropogenically driven) shape diversity patterns (Billeter et al., 2008; Pärtel et al., 2007; Svenning, 2002; Whittaker et al., 2001; Willis and Whittaker, 2002).

Plant diversity is currently decreasing at a global scale but has increased at continental and regional scales because new species have been introduced faster than native species have gone extinct (Hobbs et al., 2009). Recent anthropogenic activities are considered to have increased vegetation similarity across regions, a phenomenon termed *biotic homogenization* (McKinney, 2008; Olden and Rooney, 2006; although see Feurdean et al., 2010). Yet, it is widely suggested that land-use change will continue to represent a threat to global biodiversity and result in many plants and animals going extinct (Thomas et al., 2004).

Because fossil pollen records represent a first order approximation of the past plant occurrence they can be used to examine temporal and spatial scale changes in diversity and contribute to understanding the contemporary diversity. For example, many contemporary plant communities have developed in close association with human activity, i.e. type of subsistence and settlements (Behre, 1981, 1988; Berglund et al., 2008; Brun, 2009; Pärtel et al., 2007). It has also been suggested that local species diversity is maximized at intermediate disturbance (fire, human impact, agriculture, grazing, deforestation), and not

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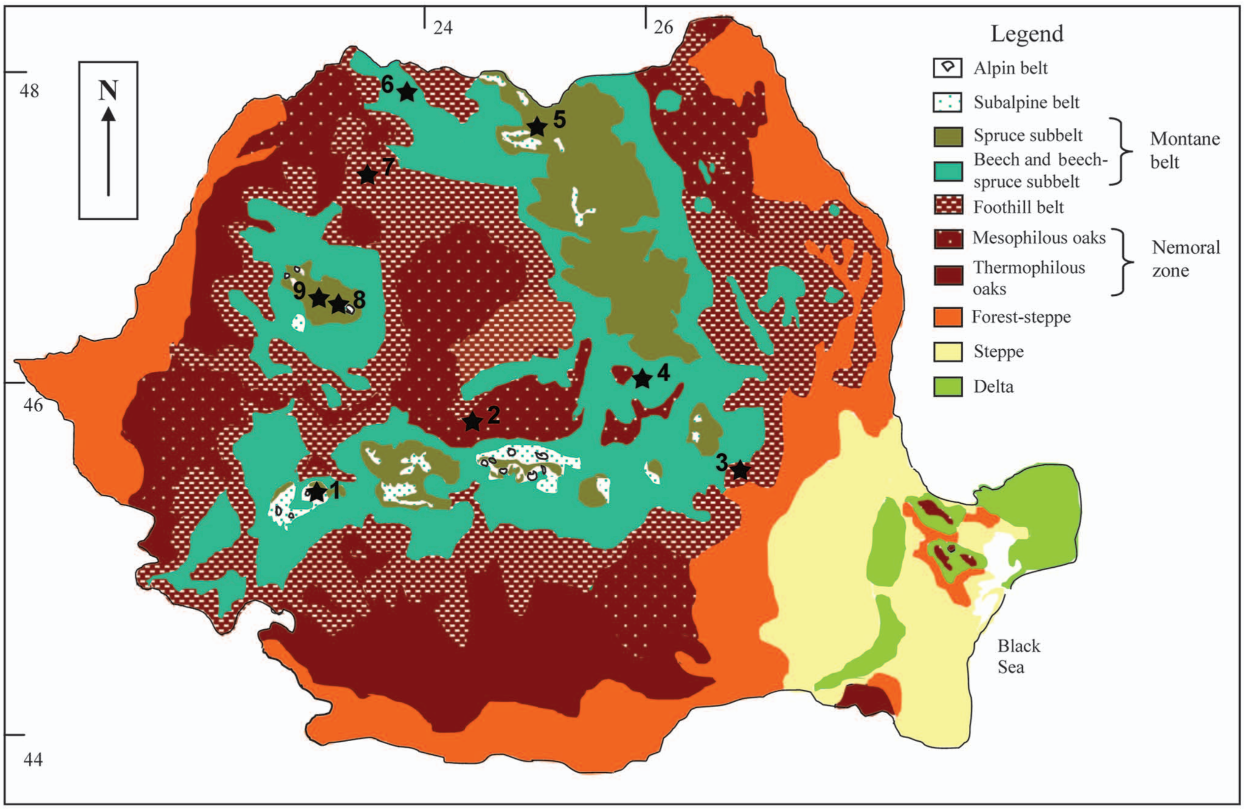

Figure 1. Schematic representation of the distribution of vegetation zones and elevational forest belts in Romania. The location of the study sites is as follows: 1: Taul Zanoguții, 1840 m; 2: Avrig, 440 m; 3: Bisoca, 890 m; 4: Mohoş, 1050 m; 5: Poiana Stiol, 1520 m; 6: Preluca Tiganului, 730 m; 7: Turbuța, 275 m; 8: Călineasa, 1360 m; 9: Molhaşul Mare, 1224 m (colour figure available online).

when disturbance is too weak/rare or too strong/frequent (Connell, 1978; Grime, 1973). In temperate regions, plant species diversity is enhanced in more heterogeneous and semi-open landscapes and therefore exhibit higher floristic diversity than forested or agricultural landscapes which are more homogenous (Billeter et al., 2008). However, most neo- and palaeoecological studies on the long-term relationship between human impact and vegetation diversity are from northern European landscapes, with distinct woodland composition and land-use history than eastern Europe (Birks and Line, 1992; Brun, 2009; Meltsov et al., 2012; Odgaard, 2001). Thus far, changes in long-term floristic richness across different vegetation types in central-eastern Europe have not been explored, neither has the long-term richness–elevation pattern in Europe more broadly.

In this paper, Holocene pollen records from lowlands to subalpine environments in the Carpathians were used to examine: (1) the influence of spatial scale and landscape openness on pollen richness; (2) how pollen richness varies with elevation and over time; and (3) the effect of anthropogenic influences on pollen richness. We highlight the importance of using long-term data in understanding contemporary and the likely future trends in biodiversity.

Here we use pollen richness as an expression of vegetation diversity within the pollen source area. We hypothesize that semi-open landscapes in the study area would host higher floristic diversity when compared with forested or very open, intensively used landscapes. We also hypothesize that the long-term trends in vegetation diversity will generally be positively correlated with early anthropogenic activity, and explore which periods of anthropogenic activity had the greatest diversity and which the lowest. Further, we expect that pollen richness patterns over time will be largely comparable in areas characterized by rather similar climate and vegetation settings. If this assumption is true we then demonstrate that there is potential to compare pollen richness trends across sites from similar settings and consequently to infer the drivers behind this pattern.

Study area

The modern climate in the study region (Romania) is continental temperate. However, the northwestern part where the sites Preluca Ţiganului, Molhaşul Mare, Călineasa, Poiana Ştiol are situated is influenced by a western oceanic climate, the southwestern part where Tăul Zănoguții is located by warm air masses from sub-Mediterranean region, whereas the eastern part where Mohoş and Bisoca are influenced by cold and dry air masses from the Russian plain (Academia Română, 2002, 2004). Changes in diversity were inferred based on nine pollen records situated in different massifs and at elevation ranging between 275 and 1840 m, thus representing a composite elevation gradient. Although our sites do not represent a continuous elevation gradient, they cover representative vegetation from each elevational belt in the Carpathians (Figure 1). Details on the site location, modern vegetation composition and basins size are provided in Table 1.

Materials and methods

Measuring diversity change through time using palynological richness

To examine trends in diversity, a rarefaction analysis (Figure 2) was applied to each pollen data set (Howard, 1968) using the Psimpoll software (Bennett, 2003). The pollen counts range between 250 and

Table 1. Characteristics of the vegetation zones and elevational belts in Romania (after Cristea, 1993; Doniţa 1962) and of the present vegeation types surrounding each study site.

Site: elevation (m) and size (ha)	Modern regional vegetation zones and belts in Romania	Modern local vegeation composition around the study site	References
Turbuţa (275, 1.5)	Forest steppe (< 300 m)	Patchy forests dominated by *Q. petraea* and *Q. robur* with isolated presence of *Carpinus betulus* and *Fagus sylvatica*.	Feurdean et al., 2007
Avrig (440, 1)	Foothill forest belt (300–600 m)	Patchy forests dominated by *Quercus petraea* with a local occurrence of *Quercus robur, Carpinus betulus, Fagus sylvatica, Alnus, Betula* and *Picea abies*.	Tanţău et al., 2006
Preluca Ţiganului (730, 1)	Lower montane forest belt dominated by *Fagus sylvatica* (600–1000 m)	*Fagus sylvatica* forests with isolated occurrences of *Carpinus betulus, Quercus, Tilia, Corylus avellana, Fraxinus excelsior, Ulmus, Betula, Picea abies* and *Pinus*.	Feurdean, 2005
Bisoca (890, 1.5)	Similar as above	*Fagus sylvatica* forests with locally abundant *Picea abies, Alnus glutinosa, Betula pendula, Betula verrucosa*.	Tanţău et al., 2009
Mohoş(1040, 30)	At the limit between middle montane forest belt (*Fagus sylvatica*) and upper montane forest belt (*Picea abies*) (1000–1200 m)	Local vegetation dominated by *Pinus sylvestris, Betula pubescens, Betula pendula, Alnus glutinosa.*	Tanţău et al., 2003
Molhaşul Mare (1224, 3)	Upper montane forest belt (*Picea abies*, 1200–1800 m)	*Picea abies* dominated forests with *Fagus sylvatica* stands and with locally presence of *Pinus mugo, Abies alba, Betula verrucosa, Sorbus aucuparia*.	Feurdean and Willis, 2008a
Călineasa (1360, 1)	Similar as above	Similar as above.	Feurdean et al., 2009
Poiana Ştiol (1540, 2.6)	At the limit between upper montane forest belt (*Picea abies*) and subalpine vegetation	*Picea abies* and subalpine vegetation locally consisting of *Pinus mugo, Pinus cembra, Sorbus aucuparia, Salix silesiaca, Juniperus communis ssp. nana*, and *Rhododendron myrtifolii*.	Tanţău et al., 2011
Tăul Zănoguţii (1840, 0.05)	The subalpine belt (1800–2000 m)	Dense stands of *Pinus mugo ssp. mugo* with a few scattered individuals of *Pinus cembra*	Fărcaş et al., 1999

800 grains per sample at each site studied. All terrestrial pollen and spores were included and the lowest pollen count (T_n) was used to standardize the size of the pollen counts at each site. A few pollen-poor samples, where this sum could not be reached, were excluded from the analysis. Rarefaction analysis is an interpolation method that estimates how many pollen and spore types would have been found if all the samples had the same count size, and therefore it reduces bias in richness caused by different pollen count sizes (Birks and Line, 1992; Gotelli and Colwell, 2001).

The sedimentary basins vary from small to medium size (0.05–3 ha), except one site that is much larger (Mohoş, *c*. 30 ha). The size of the basin controls the pollen source area and hence the spatial scale of the study. The relevant pollen source area is also dependent on vegetation patchiness, the size and spatial distribution of the patches, and the pollen productivity and fall speed of the plant taxa involved (Hellman et al., 2009; Sugita, 1994). Based on empirical and modeling studies on the composition of the pollen rain it can be assumed that the main pollen source area for pollen entering sites smaller than 1 ha (Turbuţa, Avrig, Preluca Ţiganului, Bisoca, Tăul Zănoguţii) is a few kilometers around the basins, for those of 2–3 ha (Molhaşul Mare and Poiana Ştiol) up to *c*. 20 km radius, whilst at Mohoş (30 ha) of few tens of kilometers (Gaillard et al., 2008). With the spatial record of our sites, the estimated temporal variation in diversity should mainly be within landscape or γ diversity (Whittaker, 1977).

Studies on changing diversity over time have suggested that palynological richness provides a good understanding of diversity changes within vegetation units through time (Berglund et al., 2008; Birks and Birks, 2008; Birks and Line, 1992; Feurdean et al., 2012a; Fleneley, 2005; Meltsov et al., 2012; Weng et al., 2007; Willis et al., 2007). It must also be recognized, however, that pollen-based estimates of past plant diversity are a mix of taxonomic resolutions (family, genus, species), and can be biased by pollen productivity and dispersal mechanism, basin size, sediment accumulation rate, sampling effort (i.e. pollen sum), and evenness (Feurdean et al., 2012a; Odgaard, 2001; Peros and Gajewski, 2008; Seppä, 1997; van der Knaap, 2009; Weng et al., 2006).

Measuring human impact in the fossil pollen records

A schematic representation of the main trends in tree dynamics over the Holocene in the region is provided in Figure 3. Further, we used the percentages for total non-arboreal pollen (NAP) as proxy for landscape openness, i.e. the amount of non-forested area. To obtain information about nature and magnitude of human activities on the vegetation (Table 2; Figure 4) we used several events in the fossil records (Behre, 1981; Brun, 2009, 2011; Marinova et al., 2012): (1) the appearance of pollen from cultivated plants and associated weeds or so-called primary anthropogenic indicators (*Cerealia*-type, *Secale, Triticum*-type, *Hordeum*-type, *Avena*-type, *Zea, Centaurea cyanus, Agrostemma githago*); (2) the rise in herbaceous pollen types associated with pastures/meadows and ruderals or so-called secondary anthropogenic indicators, i.e. *P. media/major, P. lanceolata, Artemisia*, Asteraceae, *Cannabis, Urtica, Rumex, Polygonum aviculare-type*, (see full list in Table 2); (3) the decline in primary forest constituents (*Fagus sylvatica,*

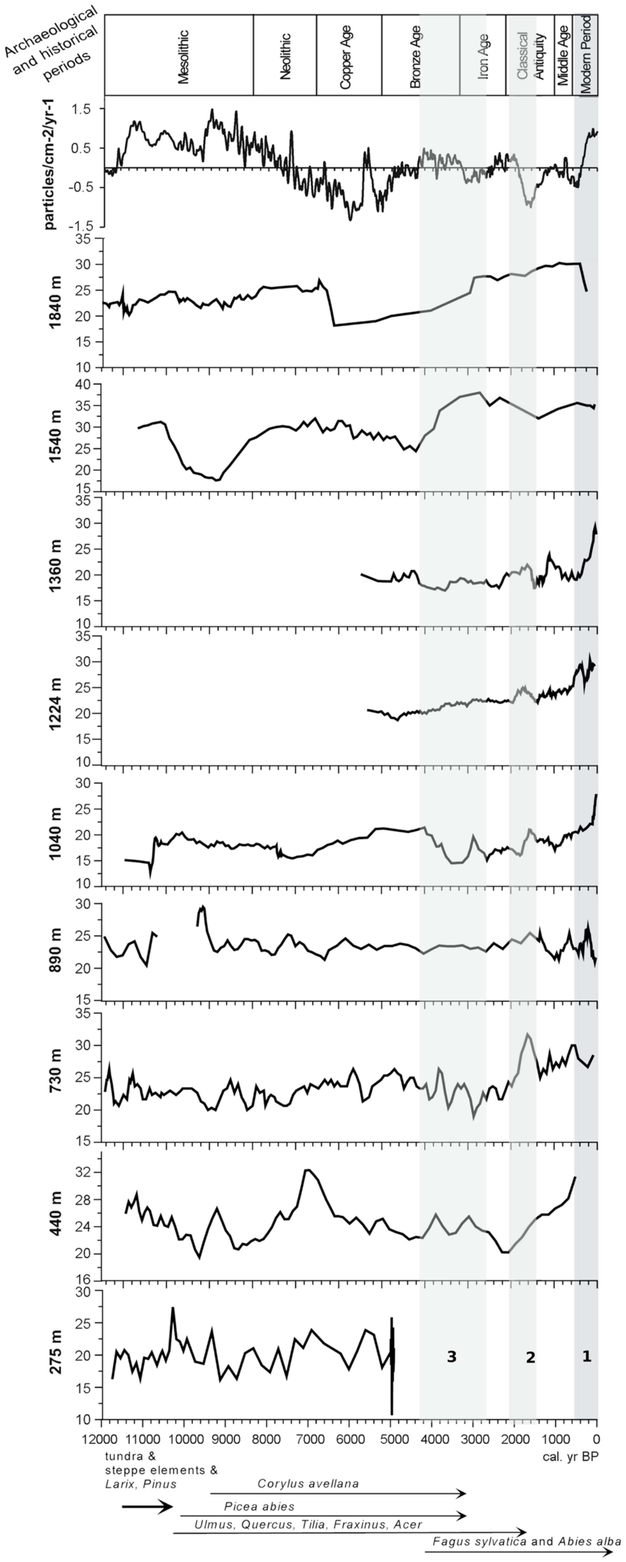

Figure 2. Pollen richness presented alongside composite elevation gradient. Archaeological and historical periods, charcoal records (after Feurdean et al., 2012b), and the dynamics of the main tree forest constituents are also shown. Different grey shades highlight the periods of progressively increasing pollen richness. The sites were classified as follows; below 440 m: lowlands; between 440 and 750 m: mid elevations; 900 and 1360 m: upper elevations; above 1530 and 1850 m: high elevations.

Abies alba, Picea abies, Tilia, Ulmus, Acer, Fraxinus excelsior, Corylus avellana), (4) the increase in the secondary forest elements (*Alnus, Betula, Cornus, Fraxinus ornus, Carpinus orientalis/ Ostrya type, Pinus, Sorbus, Sambucus*, and *Viburnum*), and (5) the presence of pollen from arboriculture (*Juglans, Castanea, Vitis, Prunus, Malus, Pyrus*). In addition, fire activity identified through charcoal records is also recognized as an important tool for humans to clear the forests and manage the land (Bowman et al., 2009; Feurdean et al., 2012b; Rius et al., 2012).

To evaluate how richness is affected by the basin size and landscape openness, and how this relationship varies with elevation, we used scatter plots of pollen richness with the size of the sedimentary basins (Figure 5a), NAP (Figure 5b) and elevation (Figure 5c). Data were grouped into consecutive 500 yr time slices for the first 1000 years and in 1000 yr time slices for the remaining Holocene period for each record. We consider the sites < 440 m to be lowlands, sites between 440 and 750 m as mid elevation, sites between 900 and 1360 m as upper elevation, and above 1530 m as high elevation.

To determine the effect of landscape openness and anthropogenic impact on vegetation diversity, pollen richness values at each individual site and at all sites combined were regressed against NAP and anthropogenic pollen indicators (Figure 6a, b; Table 3) using both linear and nonlinear (polynomial) models. The sum of anthropogenic pollen indicators includes pollen of primary anthropogenic indicators (*Cerealia*-type, *Secale*-type, *Hordeum-type, Zea, Centaurea cyanus, Juglans*) and selected secondary anthropogenic indicators such as those related to livestock breeding, ruderalization, and arboriculture (*Plantago lanceolata, P. media/major, Rumex acetosella, Cannabis, Sinapis, Urtica, Polygonium aviculare, Juglans, Castanea, Prunus*) which are more likely to increase under human impact. We used mostly primary anthropogenic indicators because in eastern Europe many of the secondary anthropogenic pollen indicators (for example *Artemisia*, Chenopodiaceae, Asteraceae Liguliflorae) originate from plants occurring naturally in the study region and their increase does not always represent greater human impact (Marinova et al., 2012; Willis, 2007).

To determine whether the diversity–elevation pattern remain constant over the Holocene, pollen richness values for each time slice were individually regressed against the elevation using both linear and nonlinear (logarithmic and polynomial) models (Table 3).

Results

The influence of spatial scale and landscape openness on pollen richness

Scatter plots between pollen richness and the size of the sedimentary basins show no clear relationship between the two parameters at any given time period (Figure 5a).

For all sites combined, the best-fit model for pollen richness and non-arboreal pollen (proxy for openness) was polynomial (R^2=0.17.2, P<0.001) as compared with linear (R^2=0.10, P<0.001) (Figure 6a). Modelling results for individual sites also show that the polynomial model better describes the relationship between the pollen richness and non-arboreal pollen compared with a linear model (Table 3). This relationship is positive at all sites: the greater the landscape openness, the higher the pollen richness.

Variation in pollen richness with elevation and over time

The best-fit model for species richness and elevation was polynomial compared with linear or logarithmic models. Sites from mid (440–750 m) and high elevations (1550–1850 m) show on

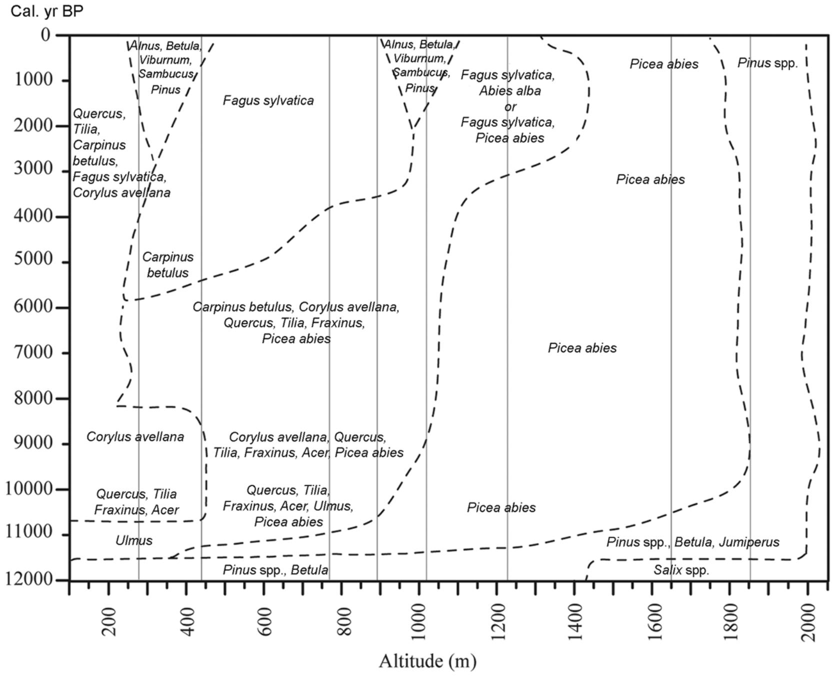

Figure 3. Schematic representation of the temporal and spatial variation in main forest constituents in Romania.

average greater diversity than sites from upper elevations (1050–1360), although this pattern is significant only over the last 3000 years (Figure 5b, Table 3). From 3000 cal. yr BP to the present the pattern was mostly consistent over time (Figure 5c, Table 3).

Most sites show high pollen richness values at the beginning of the Holocene (i.e. between 11,500 and 10,000 cal. yr BP) when the inferred vegetation was mixed deciduous-coniferous forest (*Pinus, Picea abies, Betula, Quercus, Tilia, Fraxinus excelsior, Acer*) with abundant non-arboreal pollen types (NAP) including grasses, steppe herbaceous elements, and ferns (Figures 2, 3). This time interval is also characterized by highest charcoal input in the region (Figure 2). From *c*. 10,500 cal. yr BP to between 7000 and 5000 cal. yr BP, pollen richness decreased to the lowest values for most sequences although the magnitude of decline is less evident at elevations below 440 m (Figure 2). This period is coincident with the development of *Picea abies* and *Corylus avellana* forests and the lowest proportion of non-arboreal pollen types (Figures 3, 5b). Charcoal values decrease markedly between 8000 and 4500 cal. yr BP (Figure 2). The interval 5000–3500 cal. yr BP is characterized by inconsistent trends in pollen richness across sites. Pollen richness increased progressively at all sites between *c*. 3500 and 2000 cal. yr BP onwards, and displays the highest values in most sequences between 1000 cal. yr BP and the present (Figure 2). This interval coincides with the decline in primary forest constituents (*Fagus sylvatica, Quercus, Carpinus betulus*) and a parallel expansion of secondary forest elements (*Alnus, Betula, Cornus,Carpinus orientalis/Ostrya-type, Pinus, Sorbus, Sambucus*, and *Viburnum*) and of primary and secondary anthropogenic herbaceous indicators (Figure 3). Short-term declines in pollen richness are evident between *c*. 1500 and 1000 cal. yr BP, 600 and 400 cal. yr BP and in the most recent samples. There are many individual peaks in pollen richness at each site with little temporal correlation among sites (Figure 2). At sites with charcoal records (Molhaşul Mare, 1224 m; Călineasa,1360 m) there is a strong positive association between the increase in pollen richness and the charcoal input (Figure 2).

Anthropogenic influence on pollen richness

For all sites combined modelling results indicate that a polynomial model (R^2=0.11, P<0.001) best described the positive relationship between the pollen richness and anthropogenic pollen indicators (Figure 6b). The best-fit model for pollen richness and anthropogenic pollen indicators at individual sites was also polynomial (Table 3), and this relationship was positive at all sites: the higher the anthropogenic pollen indicators, the higher the pollen richness.

Discussion

The influence of scale and landscape openness on diversity

The size of the sedimentary basins generally influences diversity by its control on the spatial scale of the pollen record, i.e. the larger the basin size, the greater the spatial scale of vegetation record (Gaillard et al., 2008) and thus the diversity expected. Our results, however, show that the basin size had little influence on the general trends pollen richness; this is likely because most of our basin sizes were small (eight out of nine sites were 0.05–3 ha) (Figure 5a). Surprisingly, however, even the large basin (30 ha) does not show greater diversity than the smaller basins (Figure 5a). Because of limited pollen dispersal, the pollen of herbaceous taxa are normally poorly represented in larger sites (Broström et al., 2008); this could explain why the large site shows similar diversity to smaller ones.

Landscape openness (NAP) instead had a significant influence (R^2=0.18, P<0.001) on pollen richness at our sites (Figures 5, 6b). Mean landscape openness, as evident from NAP percentages, varied between 3% and 40%, with sites with larger openness in low to mid (275–730 m) and high elevations (1550–1850 m) showing greater pollen richness than forested uplands (1050–1360 m) (Figure 5b). The proportion of the landscape that was open was greatest over the last 500 years, although high values were also observed for the early Holocene (before 9000 cal. yr BP) and at

Table 2. Pollen indicators of anthropogenic influence and land use types in Romania, taken from Saˇvulescu (1964), Behre (1981), Ciocârlan (2000), Brun et al (2009, 2011). The time of their first occurrence (cal. yr BP) in at least one pollen diagram is also indicated. The colour codes mark their abundance in different types of habitat: light grey (rare/low occurrence), intermediate grey (medium occurrence), dark grey (very abundant). This colour coding was only applied for taxa identified at species and genera level since family level contains species occurring in different types of habitat. Pollen types marked with asterisk represent primary anthropogenic indicators, while all others are secondary anthropogenic indicators.

Pollen type	First presence in the pollen diagrams (cal. yr BP)	Cultivated habitats	Ruderal	Pastures	Forest grazing	Arbori-culture
Cerealia*	7000	×				
*Secale**	6600	×				
*Triticum-t**	1500	×				
*Avena-t**	1500	×				
*Hordeum-t**	1500	×				
*Zea**	500	×				
*Centaurea cyanus**	500	×	×			
*Agrostemma githago**	500					
Papaveraceae	11,000	×	×			
Polygonum aviculare-t	> 11,500	×	×	×		
Rumex acetosa/acetosella	> 11,500		×	×	×	
Rumex spp.	> 11,500	×	×	×	×	
Sanguisorba minor	> 11,500			×		
Cannabis/Humulus	> 11,500	×	×			
Urtica	> 11,500		×	×	×	
Sinapis	> 11,500	×	×	×		
Brassicaceae	> 11,500	×	×	×		
Fabaceae	> 11,500	×		×		
Plantago lanceolata	> 11,500	×	×	×	×	
P. media	> 11,500		×	×	×	
P. major	> 11,500	×	×	×		
Artemisia	> 11,500	×	×	×		
Chenopodiaceae	> 11,500		×	×		
Asteraceae Tubuliflorea	> 11,500	×	×	×	×	×
Asteraceae Liguliflorea	> 11,500	×	×	×	×	×
Dipsacaceae	> 11,500			×		
Apiaceae	> 11,500	×	×	×	×	×
Ranunculus spp.	> 11,500	×	×	×	×	×
Filipendula vulgaris	> 11,500		×	×	×	
Potentilla-t	> 11,500		×	×	×	
Trifolium	500	×	×	×	×	×
Campanula	> 11,500	×	×	×	×	
Melampyrum	> 11,500	×		×	×	×
Polypodiaceae	> 11,500	×	×	×	×	
Polypodium vulgare	> 11,500		×	×	×	
Pteridium aqulinium	7500			×	×	×
*Juglans**	2000					×
Castanea	9000					×
Cornus	9000				×	×
Prunus-t	9000			×	×	×

times in the past 3000 years. Lowest landscape-openness values occurred between 8000 and 4000 cal. yr BP (Figure 5b). While the more open landscapes with higher diversity in the early Holocene were a result of the occurrence of remnant glacial mosaic of herbs and shrubs (*Artemisia*, Chenopodiaceae, Poaceae, Asteraceae, *Juniperus, Ephedra*), the late-Holocene landscape openness and pollen richness increase appears primarily to be a product of human activities (Figures 4, 5). High burning activity in the region was inferred between 11,500 and 8000 cal. yr BP, during the Bronze Age, late Iron Age, and over the last millennium (Feurdean et al., 2012b) and therefore it is possible that disturbances by fire may have promoted a more patchy and diverse landscape (Figures 3, 4).). In addition, the presence of large herbivores in the early Holocene is thought to have kept the landscapes more open (Vera, 2000). Our finding corroborates others in that a significant opening up of the primeval forests along with the advancement of grassland in lowland Europe occurs after 3000 cal. yr BP (Mitchell, 2005; Pärtel et al., 2007).

Even considering that the openness is likely to be under-represented in the pollen records, our results demonstrate that the high mountain forests in the Carpathians remained closed until relatively recently, i.e. the last millennium. Although

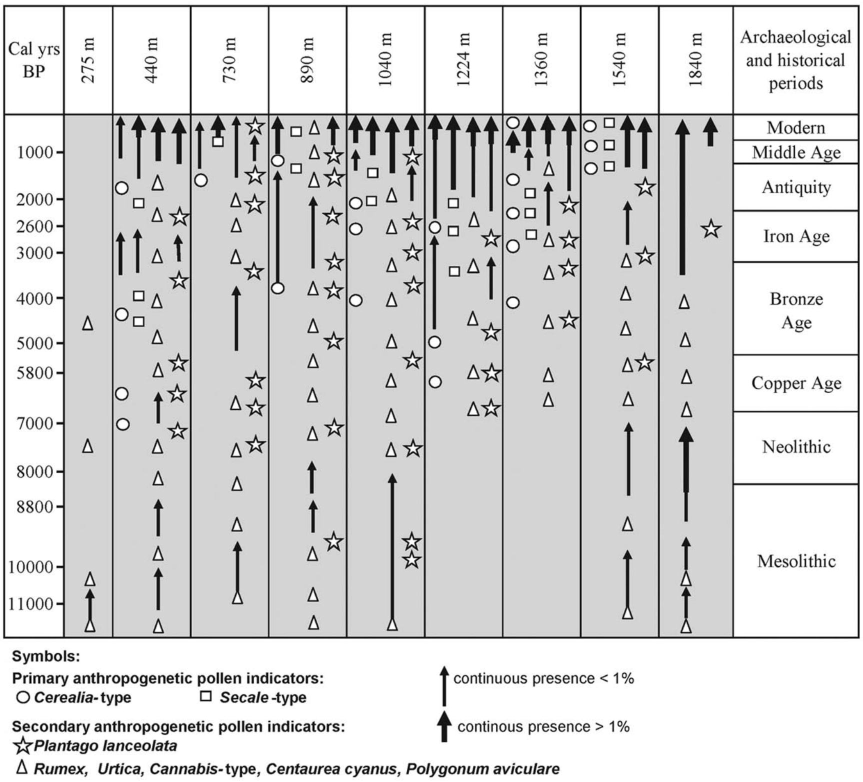

Figure 4. Schematic representation of the primary and secondary anthropogenic pollen indicators at the nine study sites. The arrangement of the sites follows an altitudinal gradient. Archaeological and historical periods are also provided.

Table 3. Relationship between the pollen richness and non-arboreal pollen type (proxy for openness) and anthropogenic pollen indicators in both linear and nonlinear (polynomial) models at each individual site (a) and between the pollen richness and elevation in both linear and nonlinear (logarithmic and polynomial) models.

(a) Site	NAP		Anthropogenic pollen indicators	
	Linear	Polynomial	Linear	Polynomial
Turbuța	0.054	0.055	0.005	0.005
Avrig	0.12***	0.19***	0.22***	0.22***
Preluca Tiganului	0.058**	0.058**	0.07**	0.12***
Bisoca	0.03*	0.16***	0.21***	0.22***
Mohoş	0.40***	0.47***	0.51***	0.53***
Molhaşul Mare	0.61***	0.62***	0.28***	0.33***
Calineasa	0.22***	0.23***	0.53***	0.59***
Poiana Stiol	0.16**	0.17**	0.20***	0.25***
Taul Zanoguții	0.04*	0.07*	0.007	0.03
(b) Time (cal. yr BP)	Linear	Logarithmic	Polynomial	
Present	0.33	0.25	0.76**	
250	0.0006	0.016	0.12	
500	0.02	0.007	0.62**	
1000	0.17	0.009	0.37*	
2000	0.25	0.18	0.33*	
3000	0.30	0.13	0.45**	
4000	0.003	0.003	0.12	
5000	0.03	0.02	0.19	
6000	0.20	0.17	0.23	
7000	0.33	0.27	0.35	
8000	0.03	0.04	0.03	
9000	0.02	0.04	0.03	
10,000	0.03	0.03	0.04	
11,000	0.19	0.16	0.20	

Notes: Significant values are indicated with asterisks: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

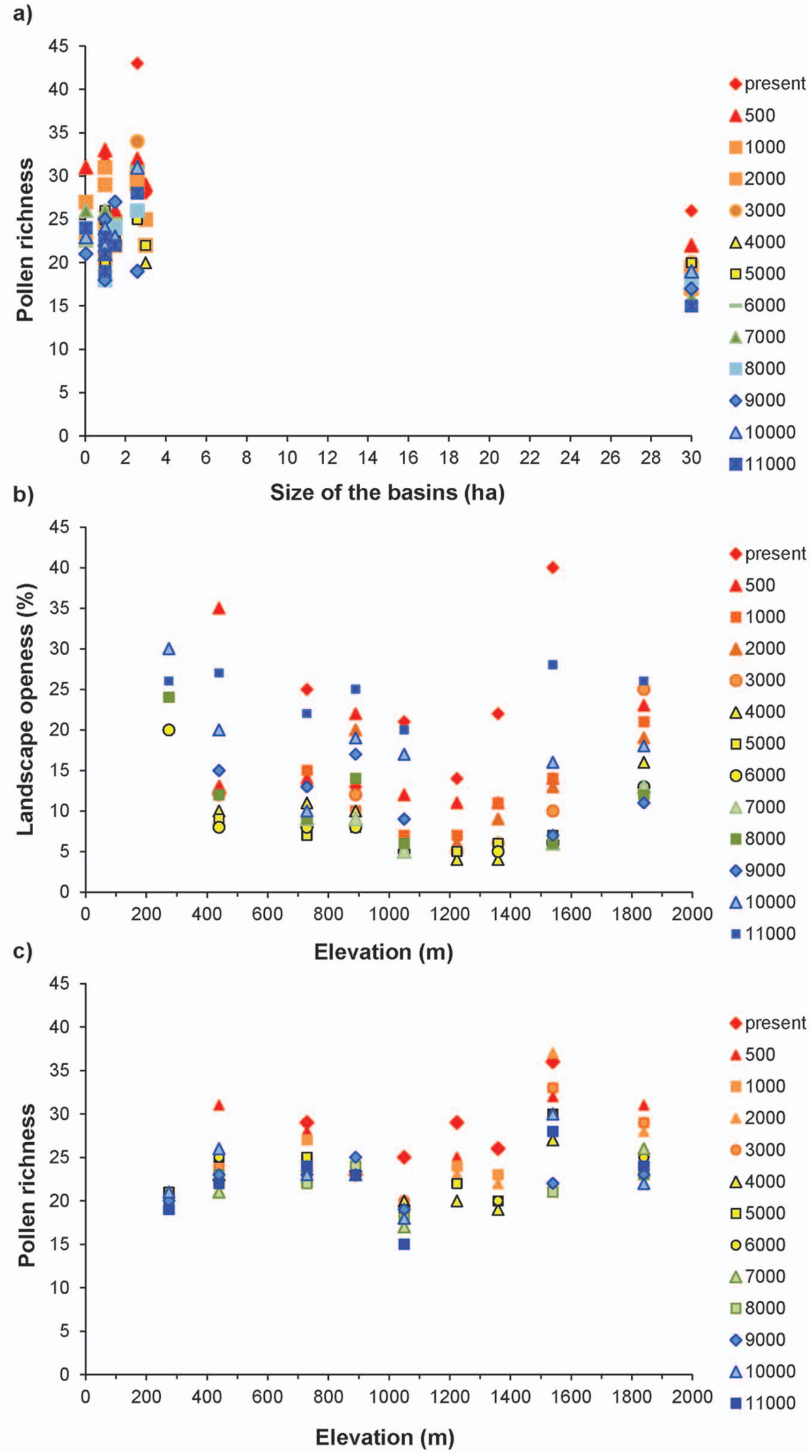

Figure 5. Variation in (a) size of the basin, (b) landscape openness (c) and pollen richness throughout time presented along composite elevation gradient. The values represent mean non-arboreal pollen types and pollen richness, respectively, over 1000 yr intervals except for the last 1000 yr where 500 yr intervals were used (colour figure available online).

there are no studies specifically addressing the influence of landscape openness on diversity in central-eastern Europe, our findings are in agreement with results from northern Europe indicating that semi-open landscapes show greater floristic richness than forested ones (Berglund et al., 2008; Meltsov et al., 2012).

Elevational diversity changes with time

While results from this study show that sites from mid (440–750 m) and high elevations (1550–1850 m) had higher diversity over time than those in uplands (1050–1360 m (Figure 5c), this pattern was only statistically significant over the past 3000 cal. yr BP

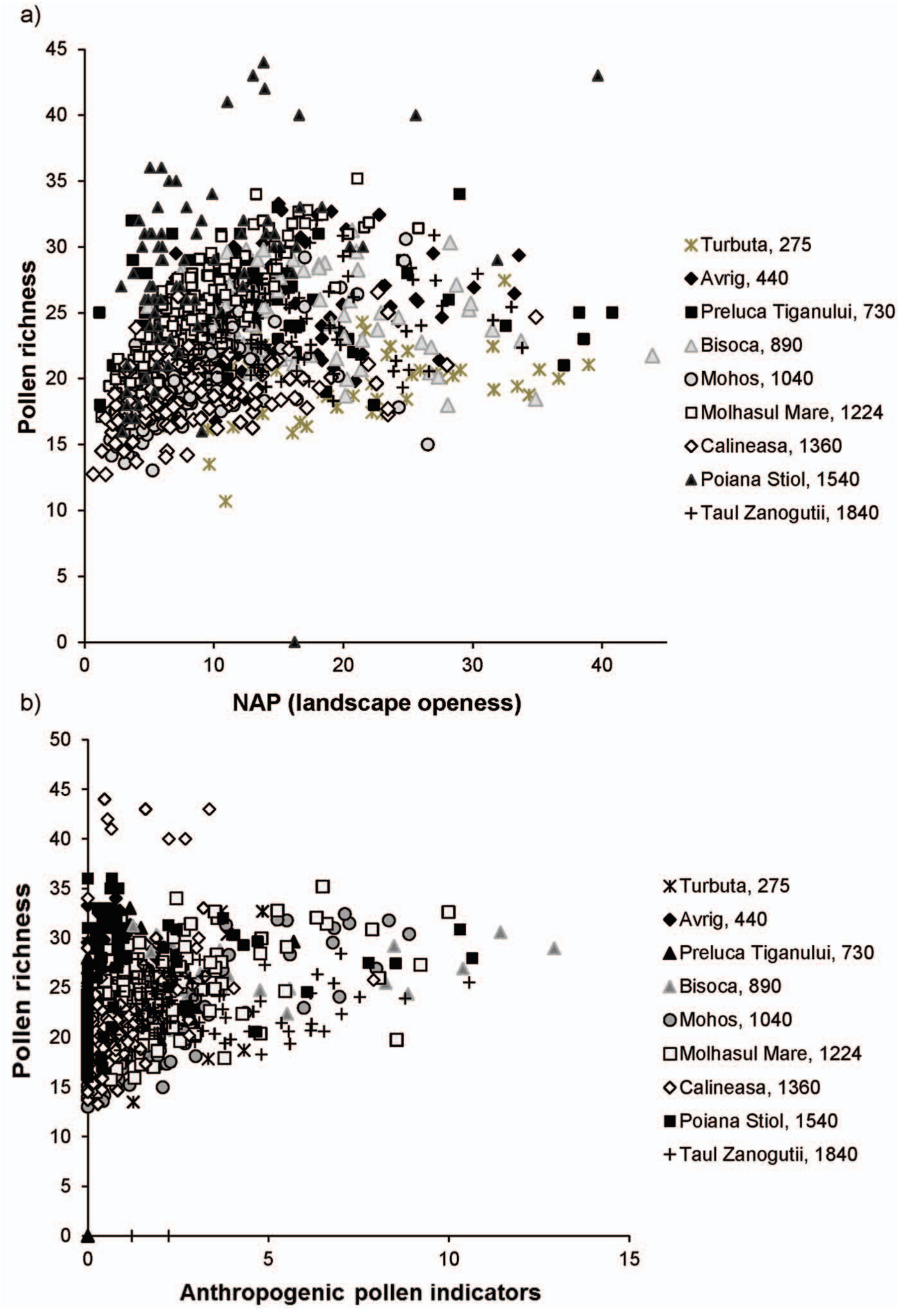

Figure 6. Relationship between (a) pollen richness and landscape openness at all sites combined using polynomial regression (R^2=0.17.2, $P < 0.001$) and linear regression (R^2=0.10, $P < 0.001$), and (b) pollen richness with percentages of anthropogenic indicators using polynomial regression (R^2=0.11, $P < 0.001$) and linear regression (R^2=0.10, $P < 0.001$) (colour figure available online).

(Figure 5c, Table 3). Importantly, even if not significant at all time intervals the overall pollen richness elevation gradient remained constant over time (the Holocene). It should be noted that for the last 5000 years no data are available from elevations below 400 m. The past 3000 cal. yr BP coincides with stronger evidence of anthropogenic impact on the landscapes and would thus suggest that anthropogenic impacts have altered the general, long-term diversity–elevation trends by increasing the discrepancies in pollen richness across elevations (Figure 5c). Because pollen richness values are temporally consistent in sequences situated in largely similar climate and vegetation settings this implies that there is potential to compare diversity trends across these sequences. However, a direct comparison of diversity at sites located in different vegetation assemblages and landscapes openness is less reliable.

We also found that some sites from low and high elevations show greater temporal variability in pollen richness and NAP, whilst mid elevations were more stable (Figure 5c). It is acknowledged that elevation-richness trends tend to be less clear than the latitudinal trends (Hillebrand, 2004), however, results from this study do not fit either of the two well-documented diversity patterns: monotonic decline in diversity with increased elevation or a mid-elevational peak (Hillebrand, 2004; Kraft et al., 2012). We suggest that this is because spatial scale strongly affected the long-term elevation diversity trends. For example, high elevation, floristically diverse landscapes receive uphill pollen transport (Fărcaş et al., 1999) meaning that the pollen assemblages are indicative of vegetation coming from wider elevational range (Pellatt et al., 1998). This implies that the relative importance of regional versus local processes controlling diversity at high elevations shifts in favour of more regional ones (i.e. altitudinal variation in temperature, vegetation, area); this contrasts with predominantly local controllers (i.e. microclimate, biotic interactions, disturbance by grazing and local fire) at mid elevations surrounded by closed forest.

Nevertheless, the composition of forests appears to have also affected richness at individual sites. Mixed deciduous forests composed of *Quercus* but also including *Ulmus, Tilia, Fraxinus*, and *Corylus avellana* (Figure 3) were predominant at low to mid elevations during most of the Holocene (Feurdean et al., 2011; Tanţău et al., 2006). Of these forest types *Quercus*-dominated are regarded as having the most diverse understory shrub and herbaceous layers when compared with coniferous forests (Barbier et al., 2008). In contrast, upland elevation sites, characterized by lowest diversity, were surrounded by closed forests dominated by *Picea abies* (11,500–0 cal. yr BP; *c.* 1200–1600 m), *Fagus sylvatica* (the last 4800 cal. yr BP, *c.* 400–800 m) or a mixture between the two species (*c.* 800–1300 m) (Fărcaş et al., 1999; Feurdean and Willis 2008; Feurdean et al., 2009; Tanţău et al., 2003, 2009) (Figure 2). *F. sylvatica* and *P. abies* forests have lower understory diversity than mixed deciduous stands (Barbier et al., 2008). However, some other coniferous genera such as *Larix* and *Pinus*, taxa that occurred in floristically diverse landscapes in our sequences during early Holocene, can exhibit great understory diversity (Figure 2). Thus, the increase in the past fossil floristic diversity with the shift in the dominant tree species, including the transition from boreal to deciduous dominant forest ecosystems is in general agreement with a gradient of modern vegetation across Europe (Barbier et al., 2008). The enrichment of past floristic richness with the advancement from boreal to deciduous forest has also been documented in Scandinavia (Berglund et al., 2008).

The relationship between pollen richness and anthropogenic impact

Previous studies on the effect of anthropogenic impact and diversity in Europe have documented an enrichment of flora by humans at landscape scales, a pattern strongly related to the developments in farming methods and human settlements (Andric, 2007; Berglund et al., 2008; Birks and Line, 1992; Brun, 2009; Colombaroli et al., 2007; Kreuz et al., 2005). Higher resolution records have also depicted recent diversity declines due to changes in agricultural systems (Berglund et al., 2008; Brun, 2009). Until now, however, changes in richness with elevation and how this relationship varies with anthropogenic influence have not been explicitly explored.

A common feature in our pollen records is the isolated occurrence of primary anthropogenic indicators and the discontinuous presence of the secondary anthropogenic pollen indicators at all sites between 8800 and 3500 cal. yr BP (Figure 4), (Fărcaş et al., 1999; Tanţău et al., 2003, 2006, 2011a, 2011b), although particularly rare in the upland sites (Figure 4). These records suggest small-scale human impact (e.g. forest clearing, grazing and cultivation) occurred before 3500 cal. yr BP (Figures 2, 3). Palaeobotanical evidence for Neolithic sites stems mainly from south and southwest Romania and indicates that the late Neolithic cultures cultivated a variety of crops (e.g. wheat (*Triticum*), barley (*Hordeum*), oat (*Avena*), peas (*Pisum sativum*), and *Vicia ervilia*)) and species-poor weed flora was also found at these sites (Cârciumaru, 1995; Fischer and Rösch, 2004). In contrast to the few Neolithic artifacts found in mountainous areas, a comparably high number have been recorded in the lowlands (Maxim, 1999; Perşoiu et al., 2011; Repertoriul Arheologic National, available from: http://ran.cimec.ro/); this suggests it is likely that the lowlands were more densely populated and consequently were more affected by humans than the uplands. Indeed good agreement exists between the high number of artifacts and the elevated values in pollen richness in lowlands during the Neolithic, and in particular after 7500 cal. yr BP. Modelling results for western Europe suggest a high area per capita (*c.* 6.5 ha) was needed by Neolithic people until about 2500 years ago when the area needed declined (4.5 ha) (Kaplan et al., 2011); this implies a large forest area would have been needed for human subsistence (cultivation, pasture, timber, etc.). In agreement with our pollen records, simulations of the rate of deforestation obtained by Kaplan et al. (2009) for our region indicate that mountains areas in eastern Europe appear to have retained large tracts of their natural forests until at least *c.* 1000 years ago and that only the lowlands were really affected by prehistoric land use practices. However, the occurrence of anthropogenic indicators in the two lowland records was not significantly greater than at other sites (Figure 4). One explanation for this pattern is that given the widespread forest cover in lowlands during the spread of the Neolithic Culture (Figure 3), the existing small forest openness impeded the detection of high values of anthropogenic pollen indicators; this is especially problematic where core basins are located away from the settlements. It is well documented that the detection of crop and weed pollen is difficult in densely forested landscape, particularly when cultivated fields close to settlements are far from sampling sites (Brun, 2009; Kreuz et al., 2005). Archaeobotanical data indicates that many of the wild plants such as *Cornus mas, Corylus avellana* and *Sambucus nigra/ebulus, Vitis, Prunus type (Prunus, Malus, Pyrus*) were used as food resources by the Mesolithic and Neolithic communities (Marinova et al., forthcoming).

At a few sites, mainly those from mountainous zones, a steady increase in diversity from about 4000 cal. yr BP (Figure 2) corresponds to the Bronze Age/early Iron Age (4000–2500 cal. yr BP). Although these archaeological periods are characterized by the cultivation of new crops in the region, like millet (*Panicum miliaceum*), free threshing wheat and lentils (*Lens esculenta*) (Cârciumaru, 1995; Fischer and Rösch, 2004), the dominant signal is for a change in land use strategies, such as the increasing use of higher mountain areas for pasture (e.g. seasonal pastoral activities) (Sherratt, 1981). Our pollen records indeed indicate an increase in grazing pressure: the continuous and abundant occurrence of secondary anthropogenic pollen indicators, particularly *Plantago lanceolata* and *Rumex*, are strong indicators of livestock during this time (Fărcaş et al., 2003; Feurdean and Willis, 2008; Feurdean et al., 2009, 2010; Tanţău et al., 2003, 2006, 2009, 2011a, 2011b). Often the vegetation changes were associated with peaks in charcoal (Feurdean et al., 2012b), pointing to the use of fire to increase the grazing area. Elsewhere in the Southern and Western Balkans (Andric, 2007; Huttunen et al., 1992; Marinova et al., 2012; Tonkov and Marinova, 2005) and in the Alps, the Iron and Roman Age intensification of pastoral activities was also related to forest burning (Röpke et al, 2011; Tinner et al., 2003) suggesting that this land management represents a regional tendency.

Another distinct rise in diversity across many elevations is evident at the beginning of the Roman Period (2000 yr) and reached the maximum between 1000 and 100 cal. yr BP (from the Middle Ages onwards) or close to the present day (Figures 3, 5). Interestingly all upper elevation sites (980–1360 m) show a notable diversity rise (Figure 2). The number of settlements and archeological artifacts in NW Romania peaked during the Roman period (Perşoiu et al., 2011). Key changes in the land use during the Roman period are the introduction of new crops such as rye (*Secale cereale*), oat (*Avena sativa*), faba bean (*Vicia faba*) and arboriculture (*Juglans regia*), the spread of intensive agriculture at a larger-scale, and the increased demand for wood for construction, fortifications, and mining (Cârciumaru, 1995; Wollmann, 1996). In the pollen records the onset of this diversity rise from about 2000 cal. yr BP is represented by large-scale forest clearance (with *Fagus sylvatica* and *Abies alba* recording the greatest decline), burning, pastoral activities and arable farming at lower elevation (Bodnariuc et al., 2002; Fărcaş et al., 1999, 2003; Feurdean et al., 2010, 2012b; Rösch and Fischer, 2000; Tanţău et al., 2011b). Our pollen data thus document the formation of a more fragmented landscape and increase in ecozone boundaries.

The Middle Ages rise in diversity (1000 yr onwards) is evident at many elevations but mainly at those between 1000 and 1540 m. The intensification of agro-pastoral activities at sites located in deep mountainous regions (1200–1360 m) occurred later, generally only from about 1000–500 cal. yr BP with these sites showing a corresponding delayed rise in diversity (Figures 3, 5).

Superimposed on this pattern of a general increase in diversity, there are two short term-episodes of diversity declines in the last 1500 years. The first one is evident after the Roman collapse, during early Middle Ages/Dark Ages (1500–1000 cal. yr BP), and the second during the ‘Little Ice Age’, i.e. 500–300 cal. yr BP (Figure 3). Climatically, both episodes are characterized by cooler/wetter conditions that appear to affect the yield production: the pollen data indicate a drastic reduction in agro-pastoral activities, particularly at mountainous sites (Feurdean et al., 2009).

Some sequences from the mountains (Molhaşul Mare, Călineasa, Mohoş, Bisoca) show a decline in pollen richness in the uppermost (most recent) samples which could be temporally coincident with massive deforestation followed by commercial tree planting and the abandonment of grazing and agriculture in the high mountains and subsequent forest regeneration (last 50 yr) (Figure 3). Biodiversity decline in both native and alien flora during the last century has been documented in Europe and came about as a result of the replacement of traditional farming by modern agriculture, the use of herbicides and fertilizers, and increased urbanization (Robinson and Sutherland, 2002). In most places in Europe the current flora includes up to 50% alien species (Brun, 2009).

Summarizing the evidence above, our data indicate floristic richness increased from the late Neolithic onwards with the periods of most rapid increase being in the late Bronze Age/early Iron Age (3500 cal. yr BP), during the Roman Age (2000 cal. yr BP), and with the onset of Middle Ages (the last 500 cal. yr BP). However the pollen richness pattern is not entirely synchronous across sites, but shows a complex pattern with a rise in diversity occurring later at upland sites. This in agreement with palaeoecological and modeling results, which show that the mountains in southeastern Europe were outside the main economic area of the prehistoric population for a longer time and consequently changes in these areas are seen later (Kaplan et al., 2009; Marinova et al., 2012). Noteworthy, however, is the fact that anthropogenic indicators are native and become widespread due to prehistorical land-use changes (animal husbandry, mowing, agricultural farming, burning activity, forest clearance). These activities provided new habitats or increased the extent of open area, and resulted in the formation of more fragmented landscape units and consequently increased ecozone boundaries (i.e. highlight environments, forest fragments and edges, grazing and various cultivated areas). This is particularly true of many of the extra-zonal vegetation elements, such as grasslands, that are naturally weak competitors and for which late-Holocene human activity enhance their dispersal ability and facilitated a range shift (Pärtel et al., 2007; Svenning, 2002). It also appears that the continuous enlargement of open landscapes has also permitted species movements between habitats, leading to an initial (2700 cal. yr BP) increase in vegetation similarly (homogenization) across the region, followed by differentiation in the past 200 years due to strong human influence (Feurdean et al., 2010).

Concluding remarks

Results from nine pollen records situated on composite elevation gradient indicate that:

(1) The extent of open landscape (NAP) represents an important driver of pollen richness and supports the hypothesis that the semi-open sites show greater diversity than more forested one. However, the lack of sites from intensive agricultural landscapes limits the degree to which we can test the effect of extremely open landscapes on diversity. We also found positive relationships between pollen richness and anthropogenic indicators (representing the development of human societies), therefore demonstrating the potential of pollen richness to be use as a tool to infer human disturbance-diversity co-evolution. Increased levels of anthropogenic disturbance (via the introduction of new crops, but mainly by the creation and/or enlargement of the existing landscape openings which favoured species movement) between 1000 and 100 years (Middle Ages) increased diversity to one of the highest levels. If this period of highest pollen richness in our records is taken as the baseline for the ideal disturbance level to maximize diversity, it can be speculated that this is analogue to the ecological intermediated level of disturbance for which one should aim if the goal is to benefit habitat diversity for both native and introduced plants. Pastoral activity, however, appears to be the strongest land use to enhance the diversity of native plants. We suggest that keeping a diversity of habitats is the key to maintaining current levels of diversity. Recent anthropogenic activity (mainly plantations), however, negatively impacted diversity in the mountainous areas. Developing managements plans based on long-term ecological data has been attempted for reserves or other areas of high conservation value in mountainous areas in Europe, and often an historical biodiversity level close to that of Medieval period is considered the best mimic for conserving a high level of biodiversity (Agnoletti, 2007; Feurdean et al., 2009).

(2) Our results emphasise the existence of elevation gradients in pollen richness (i.e. lower richness in the uplands and greater richness at mid and high elevations) but this

elevation gradient pattern was significant only over the last 3000 cal. yr BP. Since this time interval (last 3000 yr) coincides with stronger evidence of anthropogenic impact we suggest that humans have altered the general, long-term diversity–elevation trends by increased discrepancies in pollen richness across elevations. Importantly, the pollen richness–elevation gradient remained constant over the Holocene, and there was consistency in the diversity pattern across sites from similar elevations and therefore situated in comparable climate and vegetation settings. Diversity results across elevations with markedly different vegetation assemblages and landscapes openness, however, cannot be compared.

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