Journal of Insect Conservation (2025) 29:52
https://doi.org/10.1007/s10841-025-00678-4

ORIGINAL PAPER

Click beetles (Elateridae) identify conservation units in Oriental and European beech forests

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Received: 15 January 2024 / Accepted: 23 April 2025 / Published online: 14 June 2025

Abstract

Beech trees form major parts of lowland temperate forests in the Western Palearctic. To protect biodiversity, many beech forests have been designated as World Heritage Sites or established as networks of beech forest reserves. However, the insect communities within these protected forests have not been well explored. In this study, elaterids (Elateridae, Coleoptera) in 26 beech forests, from France in the west to Iran in the east, were sample to identify conservation clusters and hotspots of biodiversity. Sampling was mostly carried out using window traps and all specimens were identified to the species level. A total of 118 species were identified including one previously unreported species. Community composition analyses that focused on rare species identified five clusters comprising distinct communities: (i) the Hyrcanian Forest in Iran, (ii) the Lesser Caucasus in Türkiye, Georgia and Armenia, (iii) the Greater Caucasus in Georgia, (iv) the Pyrenees and (v) a cluster made up of forests from Central Europe, the Balkan region and the Carpathians. After controlling for sampling effort (individuals), the highest richness was found in the Caucasus region. The proportion of endemics was highest in the Oriental beech forests of the Caucasus and in Hyrcanian forests. These findings highlight the unique biodiversity of beech forests and support calls for intensified conservation actions in beech forests, particularly in the Caucasus and Hyrcanian regions, which should be prioritized for conservation efforts, due to their unique fauna.

Implications for insect conservation Our study underscores the importance of protecting beech forests, especially in the Caucasus and Hyrcanian regions, as they host unique and endemic insect species critical for biodiversity conservation.

Keywords Click beetles · Endemic species · Forest conservation · *Fagus sylvatica* · *Fagus orientalis* · Hill numbers

Introduction

Eurasian beech forests form a belt from Western Europe to Iran and are dominated by two species, European beech (*Fagus sylvatica* L.) and Oriental beech (*F. orientalis* Lipsky). However, the classification of these forests into different habitats has challenged botanists for at least a century (Willner et al. 2017; Gholizadeh et al. 2020) and, more recently, also the planners of continent-wide protected area systems, such as Europe's Natura 2000 (Bohn et al. 2007). Advances in genetic methods over the last two decades have repeatedly yielded new insights into the origin of West Eurasian beech forests (Renner et al. 2016) and have confirmed the distinction of the two beech species (Jiang et al. 2022). In Europe, progressive climate change has led to interest in *F. orientalis* in European forestry, as this species is considered to be better suited to higher temperatures and drought (Mellert et al. 2016). In fact, there is evidence of *F. orientalis* forests in Italy during the interglacial period (Paffetti et al. 2007). Overall, beech species worldwide have a relatively similar niche width, independent of their distribution area (Cai et al. 2021). However, considerations of assisted migration in European forest management have also given rise to a debate about the effects of such tree species selection on biodiversity. The increased awareness of the importance of near-natural beech forest ecosystems of both

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Fagus species has also led to targeted protected area designations and to the awarding of World Heritage Site status.

Despite the high physiognomic similarity of the forest ecosystems of *F. orientalis* and *F. sylvatica* and their overlap in Bulgaria, there have been very few comparative studies of the biodiversity across *Fagus* species. This knowledge gap has complicated arguments in support of increased conservation efforts across West Eurasia. Only in exceptional cases, such as deadwood and old trees and a study that investigated tree-related microhabitats on living trees across both *Fagus* species (Courbaud et al. 2022; Mamadashvili et al. 2023), has it been possible to transfer findings from areas of European beech to those of Oriental beech.

Among insects, beetles (Coleoptera) have been used in many ways to evaluate the impact of land use and/or biogeographical context in beech forests (Lachat et al. 2012; Gossner et al. 2013; Hagge et al. 2019). Click beetles (Elateridae) form the largest family of beetles in the superfamily Elateroidea and are one of the most ecologically diverse families of beetles in terms of habitats and foraging strategies (Laibner 2000; Bouchard et al. 2009). They also play an important role in many ecosystem, either as herbivores, predators or fungivores, with forests and grasslands harboring the greatest local richness of species (Scurlock et al. 2002).

Click beetles have been regularly used as model groups of organisms in ecological studies of the impact of forest management type. In the rainforests of Indonesia, different land-use types were shown to affect the abundance, diversity and species composition of click beetles (Kasmiatun et al. 2020). Horák & Rébl (2013) found that the species richness of click beetles in an ancient pasture woodland benefitted from a high level of sun exposure. Similarly, Mladenović et al. (2018) observed that click beetles in plantation forests mostly preferred sun-exposure, but also spruce trees. A study of mature oak forests and spruce plantations showed that tree species structured the species composition of click beetles and accounted for the very high diversity of these insects in oak forests (Loskotová and Horák 2016). In European beech forests, an increase in the richness of click beetles with the amount of deadwood was observed (Müller et al. 2008). Similarly a study in the silver fir (*Abies alba*) relic forests of Italy found that click beetles responded to spatial patterns of forest structure (Parisi et al. 2016). Click beetle diversity in hardwood forests in the USA is also responsive to different management strategies (Stewart 2013). A long-term experiment in similar forests in the USA also showed that click beetles respond positively to openings and deadwood (Thomas 1995). Among natural disturbances, click beetles in boreal forests are sensitive to fires, with many species favored by fire events. Finally, click beetles have been included in zoogeographical studies in Türkiye and in Northern and Northwestern Caucasus (Penev and Alekseev 1996; Zamotajlov et al. 2010; Platia et al. 2018).

In the present work, click beetle data were compiled from 26 old growth and production beech forests, extending from France in the west to Iran in the east, to address the following research questions:

1. How similar are click beetle species communities in beech forests in the different regions and under different management?
2. Which beech forests harbor (a) the highest richness, (b) proportion of endemics and (c) proportion of saproxylic species?

Material and methods

Study sites

The study area covered a wide geographical distribution of both *F. sylvatica* and *F. orientalis*, extending from France, Germany, Bulgaria, Ukraine, Türkiye, Georgia, Armenia, and finally to Iran (Fig. 1). Among these countries, Bulgaria is the only one in which the two *Fagus* species overlap. Old growth and production forest stands were sampled in each country, with the exception of Bulgaria, from which data were obtained only from old growth forests. Study plots varied from 65 to 1497 m above sea level and were dominated by beech trees but admixed with hornbeam (*Carpinus* spp.), oak (*Quercus* spp.), maple (*Acer* spp.), lime (*Tilia* spp.) and in some areas with spruce (*Picea* spp.), pine (*Pinus* spp.) and fir (*Abies* spp.). Each site contained a particular type of deadwood, such as snag and log, stump and crown or dead standing (or lying) trees.

Sampling methods

Beetle sampling was implemented during warm seasons, from April until October, between 2018 and 2022. The single flight interception and pair of pitfall traps were set up at each plot, close to deadwood objects. Only in Switzerland and one forest in Iran flight interception traps were exclusively used. However, as most elaterids are collected by flight traps, we assumed that this limitation can be neglected, which was supported by additional analyses (see Statistical analyses). For both types of traps, a copper sulphate and Rocima solution served as the collecting fluid. The traps were emptied every 2–4 weeks. Collected insects were placed in tubes containing 75% ethanol and refilling the solution in the traps. The specimens were identified by Antoine Brin in France, Vasyl Chumak and Maksym Chumak in Ukraine and Switzerland, Alex Szallies in Switzerland, and Boris Büche in Germany. All other material was determined by Andrea Jarzabek-Müller. Two species from Türkiye were identified by Giuseppe Platia.

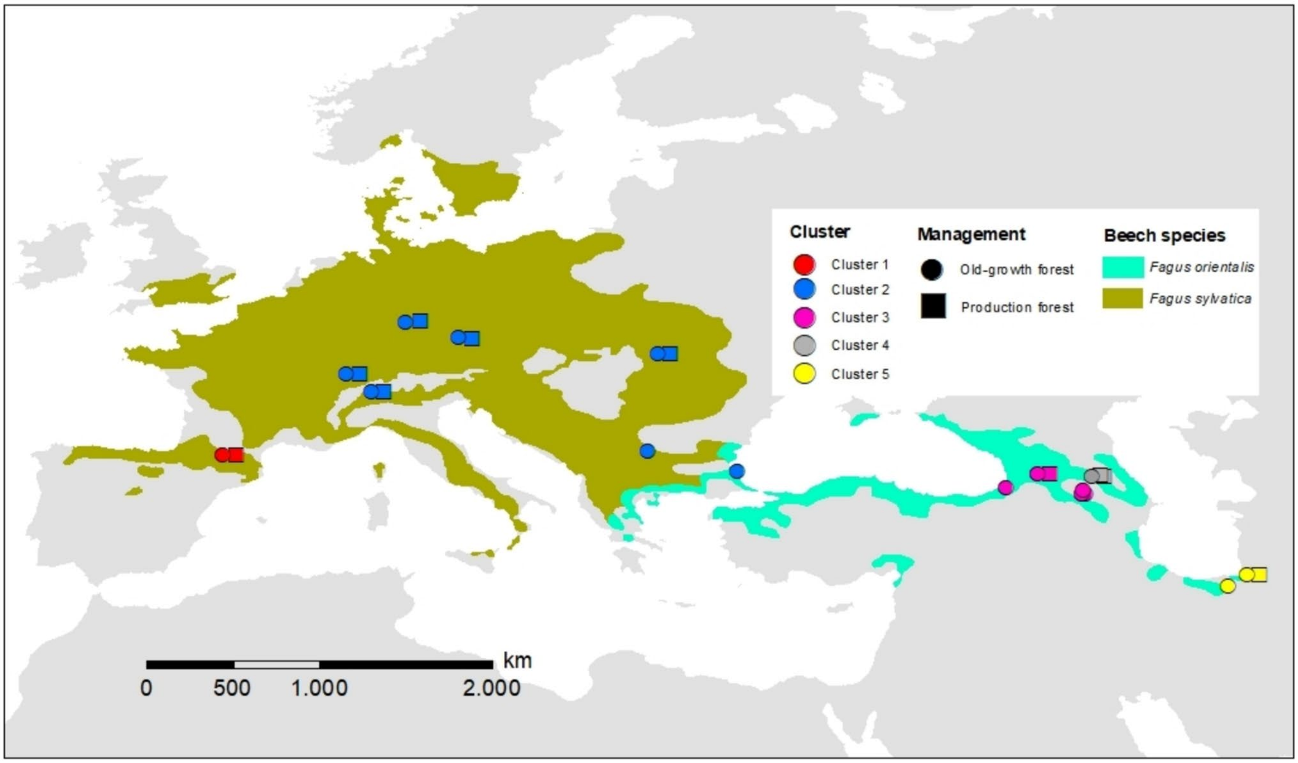

Fig. 1 Global distribution of *Fagus sylvatica* and *F. orientalis* and the location of the 26 forests investigated for click beetle communities. Note that some locations have been shifted to increase visibility. Colors indicate the clusters identified in the ordination by distance matrix focusing on rare species (q = 0, Fig. 2)

Statistical analyses

All analyses were conducted at the forest level, combining all specimen from one forest, with the data analyzed using R 4.2.3 (R Core Team 2022). Since the sampling effort was related to the number of traps, which affected the number of specimens and led to variations in sample completeness, methods for the ordination of elaterid communities and diversity analyses were used, taking into account unobserved species (Chao et al. 2014a) (see Supplementary material, R code). Among ecologists, a consensus has emerged that Hill (1973) numbers (effective numbers of species) should be used to incorporate species abundance/evenness into species diversity and into composition measures (Ellison 2010). However, Chao et al., (2014a, b) demonstrated that the Jaccard index ($q = 0$), the Horn index ($q = 1$) and the Morisita-Horn index ($q = 2$) can replace the Hill numbers q = 0, 1, 2, representing rare, common, and dominant species, respectively, as diversity measures. Therefore, in this study diversity and dissimilarity in species composition (Chao et al. 2023, pp. 4–8) was estimated for a standardized sample coverage for all forests, while also considering unseen species, using the packages spadeR and iNEXT (Linderman et al. 2012; Hsieh et al. 2016). To identify groups of forests with similar elaterid species composition we applied non-metric Multi-dimensional Scaling (NMDS) to the distance matrices using function metaMDS in vegan. To test the overall significance of the visual identified groups we applied the function anosim in vegan. Since some clusters were represented only by two or three forests, we refrained from a formal post-hoc test between the clusters. Finally, a rank-abundance curve was calculated for all species based on their occurrence in the 26 forests. To test for sensitivity of our results to the fact that Switzerland and one site in Iran had not used pitfall traps, we reanalyzed the data set reduced to flight traps only. For details to all analyses including analyses on raw data without considering unseen species in the ordination, see R code. All data and R code to reproduce the findings are available here: https://doi.org/10.6084/m9.figshare.27506826

Results

Among the 6875 recorded specimens in this study, representing 118 different click beetle species (see Table 2), one species (*Idolus* sp.), found in two forests in Georgia, was newly discovered and is now described as *Idolus caucasicus*, Jarzabek-Müller (2025). All other specimens could be identified to the species level. The most widespread species was

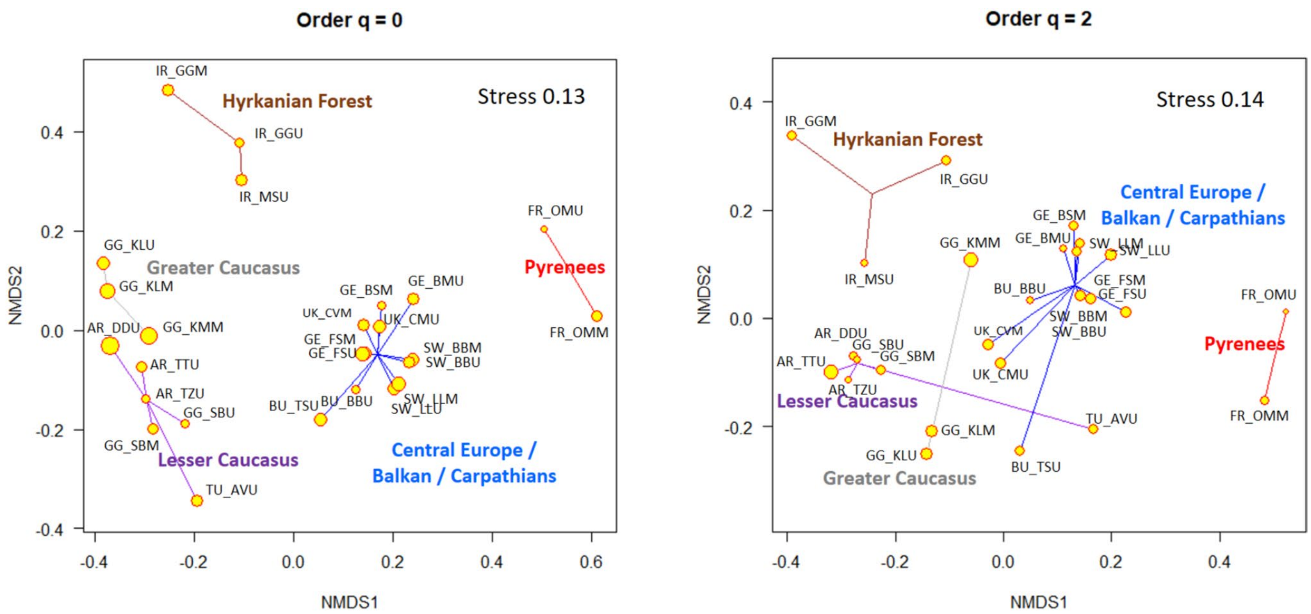

Fig. 2 Non-metric ordination of the distance matrix for rare species (Jaccard similarity) and dominant species (Morisita-Horn similarity) under consideration of unseen species. Stress values indicate the robustness of the findings (for abbreviation of the forests, see Table 1). ANOSIM statistic for q0: R 0.95, $p=0.001$ and for q2: R 0.82, $p=0.001$

Table 1 The 26 beech forests investigated for elaterid species

Forest	Latitude	Longitude	Elevation	Country	Region	Forest type
AR_DDU	40.947	45.208	1232	Armenia	Ditaven	Unmanaged
AR_TTU	40.912	45.077	1327	Armenia	Teghut	Unmanaged
AR_TZU	41.122	44.923	1298	Armenia	Tavush	Unmanaged
BU_BBU	43.176	23.122	1067	Bulgaria	Berkovitsa	Unmanaged
BU_TSU	42.107	27.788	298	Bulgaria	Tsarevo	Unmanaged
FR_OMM	42.987	0.973	917	France	Occitania	Managed
FR_OMU	42.990	0.966	950	France	Occitania	Unmanaged
GE_BMU	49.099	13.246	748	Germany	Bavaria	Unmanaged
GE_BSM	49.066	13.306	786	Germany	Bavaria	Managed
GE_FSM	49.930	10.562	452	Germany	Franconia	Managed
GE_FSU	49.861	10.500	389	Germany	Franconia	Unmanaged
GG_KLM	41.843	46.272	800	Georgia	Kakheti	Managed
GG_KLU	41.841	46.325	837	Georgia	Kakheti	Unmanaged
GG_KMM	41.918	46.096	931	Georgia	Kakheti	Managed
GG_SBM	41.963	43.449	1006	Georgia	Samtskhe Javakheti	Managed
GG_SBU	41.980	43.450	1101	Georgia	Samtskhe Javakheti	Unmanaged
IR_GGM	36.733	54.392	881	Iran	Golestan	Managed
IR_GGU	36.728	54.393	959	Iran	Golestan	Unmanaged
IR_MSU	36.150	53.405	1573	Iran	Mazanderan	Unmanaged
SW_BBM	47.221	7.415	932	Switzerland	Bettlachstock	Managed
SW_BBU	47.219	7.410	833	Switzerland	Bettlachstock	Unmanaged
SW_LLM	46.255	8.665	910	Switzerland	Lodano	Managed
SW_LLU	46.239	8.695	691	Switzerland	Lodano	Unmanaged
TU_AVU	41.237	41.854	800	Turkey	Artvin	Unmanaged
UK_CMU	48.221	23.651	521	Ukraine	Carpathian Ruthenia	Unmanaged
UK_CVM	48.269	23.621	755	Ukraine	Carpathian Ruthenia	Managed

Table 2 Distribution of 118 elaterid species in beech forests

Species	France (2)	Germany (4)	Switzerland (4)	Ukraine (2)	Bulgaria (2)	Türkiye (1)	Armenia (3)	Georgia (5)	Iran (3)
Adrastus dolini								1	
Agriotes acuminatus		2			1				
Agriotes bogatschevi								3	
Agriotes tauricus								1	
Agriotes danieli									2
Agriotes infuscatus					1	1	2	3	1
Agriotes integricollis							2		
Agriotes lineatus								1	
Agriotes litigiosus				1	1				
Agriotes obscurus		1							
Agriotes pallidulus		2		1					
Agriotes pilosellus		2	3		2				
Agriotes sputator		1							
Agriotes starcki								1	
Agriotes ustulatus				1					
Agrypnus murinus					1				
Ampedus aethiops		1	1						
Ampedus balteatus			2						
Ampedus biformis									2
Ampedus brunnicornis			1						
Ampedus cinnabarinus							1	1	
Ampedus elegantulus				2					1
Ampedus elongatulus	1		2						
Ampedus erythrogonus		1	4	1					
Ampedus hjorti									1
Ampedus lenkoranus							3		2
Ampedus melanurus			1	1					
Ampedus nigerrimus		1	1	1					
Ampedus nigrinus		2	2						
Ampedus pomonae				2					
Ampedus pomorum		2	4	2	1			1	
Ampedus quercicola			4		1				
Ampedus rubellus								1	
Ampedus rufipennis					2			2	1
Ampedus sanguineus			3	1					
Ampedus sinuatus					1	1	2	1	1
Anostirus castaneus		2	1	1					
Anostirus purpureus		2	2	1					
Anostirus sulphuripennis			1						
Athous mokrzecki					1				
Athous haemorrhoidalis		3	4	2	2				
Athous vittatus		4	4	2	2	1			
Athous proximus					1				
Athous austriacus					2				
Athous circassiensis								1	
Athous circumductus								3	

Table 2 (continued)

Species	France (2)	Germany (4)	Switzerland (4)	Ukraine (2)	Bulgaria (2)	Türkiye (1)	Armenia (3)	Georgia (5)	Iran (3)
Athous turcicus						1			
Athous subfuscus		4	4	2	1			1	
Athous abkhazianus								1	
Athous dasycerus					1				
Athous artvinensis						1			
Athous circassicus							3	2	
Athous hyrcanicus									2
Athous astrabadensis									1
Athous bicolor				1					
Athous emaciatus			1						
Athous laevistriatus	1								
Athous longicornis	1								
Athous mandibularis	2								
Athous mollis				1					
Athous rosinae									3
Athous zebei		3	4						
Brachygonus megerlei			3		1				
Calambus bipustulatus			1		1				
Cardiophorus gramineus								1	
Cardiophorus kryzhanovskyi								2	
Cardiophorus nigerrimus			2						
Crepidophorus mutilatus				1					
Ctenicera cuprea			1						
Dalopius marginatus		4	4	1					
Denticollis linearis	2	4	2	2	1				
Denticollis parallelicollis							2	3	
Denticollis rubens		3	3	2				1	
Diacanthous undulatus				2					
Dicronychus cinereus			1				1		
Dicronychus decorus								1	
Dicronychus marani					2				
Drapetes talyschensis									2
Drasterius bimaculatus								1	
Drilus concolor			2		1		1		
Drilus fulvitarsis								1	
Drilus novoathonius								1	
Elater ferrugineus									1
Elathous brucki									1
Hemicrepidius hirtus		1	1						1
Hemicrepidius niger			3						
Hemicrepidius nigritulus						1	1	3	
Hypoganus inunctus			2		1				

Table 2 (continued)

Species	France (2)	Germany (4)	Switzerland (4)	Ukraine (2)	Bulgaria (2)	Türkiye (1)	Armenia (3)	Georgia (5)	Iran (3)
Hypoganus stepanovi									1
Idolus adrastoides							1	2	
Idolus picipennis	2		1	1					
Idolus caucasicus							2		
Ischnodes sanguinicollis				2					
Lacon mertliki									1
Lacon punctatus								1	
Limoniscus wittmeri									1
Limonius minutus				1					
Limonius poneli							1		
Megathous menentriesi									3
Melanotus castanipes	1	2	4	1					1
Melanotus crassicollis					1				
Melanotus dichrous					1				
Melanotus villosus		3		2	2		3	5	1
Nothodes parvulus	1	2	4		2				
Paraphotistus impressus			2						
Pheletes aeneoniger			1						
Pheletes quercus			1						
Procraerus carinifrons								1	
Procraerus stepanovi									2
Procraerus tibialis	1			2					
Prosternon admirabilis									1
Prosternon tessellatum			1	1	1				
Pseudocrepidophorus flavescens					2		1		
Sericus subaeneus			1						
Stenagostus probosus							1		
Stenagostus rhombeus			2	1	2				
Stenagostus rosti								3	
Synaptus filiformis				2					

The Elaterid beetles are identified on species level and given nomenclature is from the Global Biodiversity Information Facility (GBIF). The number of forests surveyed is shown in parentheses. The numbers in the table describe the number of forests a species was recorded

Melanotus villosus, followed by *Athous vittatus*, *A. subfuscus*, *A. haemorrhoidalis*, *Denticollis linearis* and *Ampedus pomorum* (Fig. 3). Reducing the data to flight traps only ended up in 6743 specimens of 112 species.

The non-metric multidimensional scaling (NMDS) ordination focusing on rare species (q0, Fig. 2a) showed a clear separation of five clusters, comprising species in: (i) the western Pyrenees, (ii) all Central European sites up to the first *F. orientalis* occurrence in eastern Bulgaria, (iii) all sites in the Lesser Caucasus, (iv) the Greater Caucasus and (v) the Hyrcanian forest of Iran. This pattern was relatively robust also for dominant species in the ordination by distance matrix (q2, Fig. 2b), but with some outliers. ANOSIM analyses provided highly significant values for the five cluster. The higher ANOSIM R value for q0 supports statistically the visually more distinct clusters when focusing on rare species (see Fig. 2).

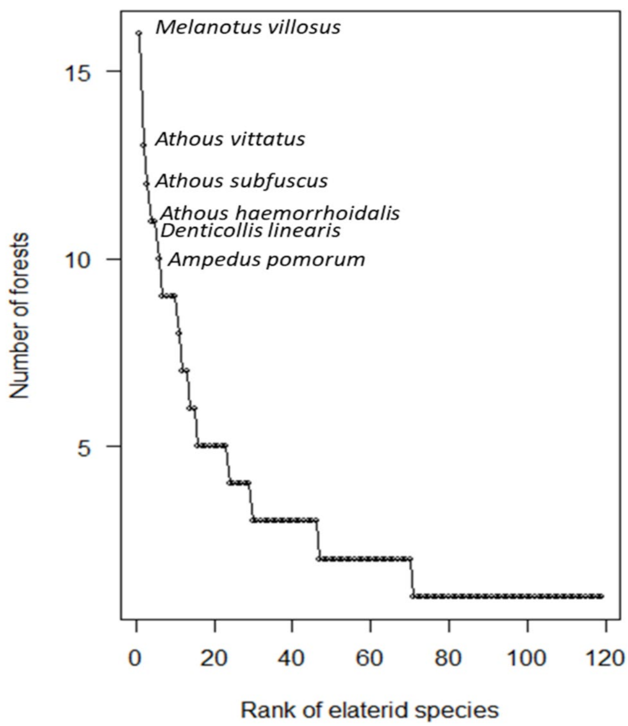

Fig. 3 Rank frequency curve for the 118 identified species. Note that ~ 50 species occurred in only one forest; the other 68 species were recorded in two or more forests

Table 3 Results of linear models for four measures of elaterid community diversity and composition in 26 beech forests; *t* values are shown, ***$p < 0.001$

Predictor	Diversity q0	Diversity q2	Saproxylics (%)	Endemics (%)
Elevation	− 0.87	− 1.47	0.26	0.89
Forest Type: Unmanaged	− 0.76	− 1.05	− 0.39	− 0.48
Longitude	1.38	1.37	0.61	4.75***

The coverage-standardized diversity was high in forests in Switzerland and Southern Germany, but particularly in the Caucasus region. This was also the case for dominant species, with a high diversity determined particularly in Ukraine forests. A high proportion of saproxylics was detected in the Caucasus and in Central Europe, and a high proportion of endemics (in descending order) in the Hyrcanian and Caucasus forests, the Pyrenees and Eastern Europe. Testing the impact of elevation, management status and Longitude on all four-measure revealed only a significant increase of the proportion of endemic species towards the east where the *Fagus orientalis* forests are located (Table 3). All results were also robust for the removal of all individuals caught in pitfall traps (see Supplementary Material).

Discussion

Our comparison of elaterid species in forests of *F. sylvatica* and *F. orientalis* revealed many similarities among communities, with several species occurring in both forests. This observation provides further support for the view that, for the fauna in Central Europe, the use *F. orientalis* in silviculture is unlikely to be problematic (Mellert et al. 2016). However, from a conservation perspective, based on biodiversity indicators such as total species richness or the number of endemics or other functional groups, different hotspots were identified at the continental scale, as also determined in global comparisons of biodiversity of, e.g., birds or fishes (Orme et al. 2005). For elaterid assemblages in beech forests, this study identified a number of clusters as well as differences in biodiversity and different proportions of endemics. The respective patterns seemed to be related to biogeography, isolation, climate history and evolution, all of which result in the historical expansion and subsequent colonization of species within specific geographical ranges (Bruchmann and Hobohm 2014; Gutiérrez-Rodríguez et al. 2017; Manes et al. 2021).

In Europe, the Pyrenees mountains form one of the few glacial refuges for *F. sylvatica* (Magri et al. 2006). The high variation in topography as well as the presence of both near-natural forests and forests excluded from glaciation might explain why the Pyrenees are one of Europe's most species-rich mountain ranges, hosting, for example, 3652 plant species, of which 119 are endemics (Gómez et al. 2022). In their report on *Saxifraga longifolia*, an endemic species of the Pyrenees, Pomeda-Gutiérrez et al. (2023) referred to the Pyrenees as a "cradle" of plant diversity. Similar species-forming evolutionary processes in the Pyrenees have been shown for mammals (Gillet et al. 2017), amphibians (Valbuena-Ureña et al. 2018) and spider species (Kronestedt 2007). These findings are in line with the results of this study, showing that, for elaterid species in the studied European beech forests, the Pyrenees hosts the largest proportion of endemics.

Most European beech forests are concentrated in Central Europe, where they cover a wide area (Fig. 3); however, these forests are relatively young. When beech trees recolonized the area after the last glaciation (Magri et al. 2017), around 6000–5000 years ago, humans were intensively using forests and thus actively destroying natural ecosystems, with consequent habitat loss and degradation and, in turn, a decline in the number of rare species in many regions (Gossner et al. 2013; Eckelt et al. 2018). The recent response to this long-term negative trend has included the designation of protected areas as refuges for the surviving rare species (Berg et al. 1994; Peterken 1996; Bengtsson et al. 2000). However, these protected beech forests contain very few, if any, old-growth stands (Glatzel 1991; Schulze et al. 2016; Ammer et al. 2018).

Despite a similar or even more destructive land-use history in the Balkan region, its forests are still considered to be a European hotspot for biodiversity, based on the high proportion of endemics. The Balkan region lies at the crossroads of Europe and Asia (Griffiths et al. 2004) and represents a refugium from the Pleistocene, sheltering almost 8000 plant taxa, of which ~ 2700 are endemic (Stevanović et al. 2007). This was demonstrated by Guéorguiev et al. (1997) for endemic Balkan ground beetles (Carabidae) in Bulgaria. During geological history, many biogeographical territories collided in the Balkan region, resulting in a fauna that is extremely heterogeneous and includes many endemic and relict species (Makarov and Dimitrijević 2008). This is in line with the proportion of endemics determined in this study (Fig. 4D). Here it is important to note that the endemic species in our studied beech forests are often not restricted to beech forests and can occur in other broadleaf forests, e.g. in lower elevation with more mixed forests (Müller et al. 2016a, b). For European beech, the Carpathian Mountains, with their relatively large number of primeval forests, form an important backbone of biodiversity, as reflected by the relatively high diversity of elaterids (Fig. 4B). However, while 12% of the flora in the Carpathians is endemic (Voloscuk 1999), this is not the case for beech-forest-inhabiting elaterids. For example, the diversity of elaterids present in the primeval Uholka forests was similar to that in degraded forests in Germany and Switzerland.

The Caucasus ecoregion, by contrast, is unique, as the separation over millennia into the high mountains of the Greater (north) and Lesser (south) Caucasus, the Black Sea (west) and the Caspian Sea (east) created biogeographical islands (Zazanashvili et al. 2020) that gave rise to many endemic species. The specific diversity of the vegetation (trees, shrubs, herbs) dates back to the Tertiary period, especially in the Colchic region of the Black Sea basin, which was shaped mainly during the end of the Middle Sarmatian, 11–12 million years ago (Shatilova et al. 2011; Nakhutsrishvili et al. 2015). The Western Caucasus is one of the few regions of Europe where the human impact has been small, such that it provides a refugium characterized by a unique floral and faunal diversity with high endemism. This accounts for the designation of this region as a World Heritage Site under UNESCO Natural Criteria ix and x (UNESCO 1999). In addition, because ecosystems of the Caucasus survived the last Ice Age, the Colchic refugium (Georgia, Russia, and Türkiye) hosts many endemic species. This is also supported by the significant increase of endemic species towards the east (Table 2). Together with Armenia, Azerbaijan and Georgia, the North Caucasus portion of the Russian Federation and northeastern Türkiye and part of northwestern Iran, this region is one of the world's 34 biodiversity hotspots recognized thus far (Mittermeier

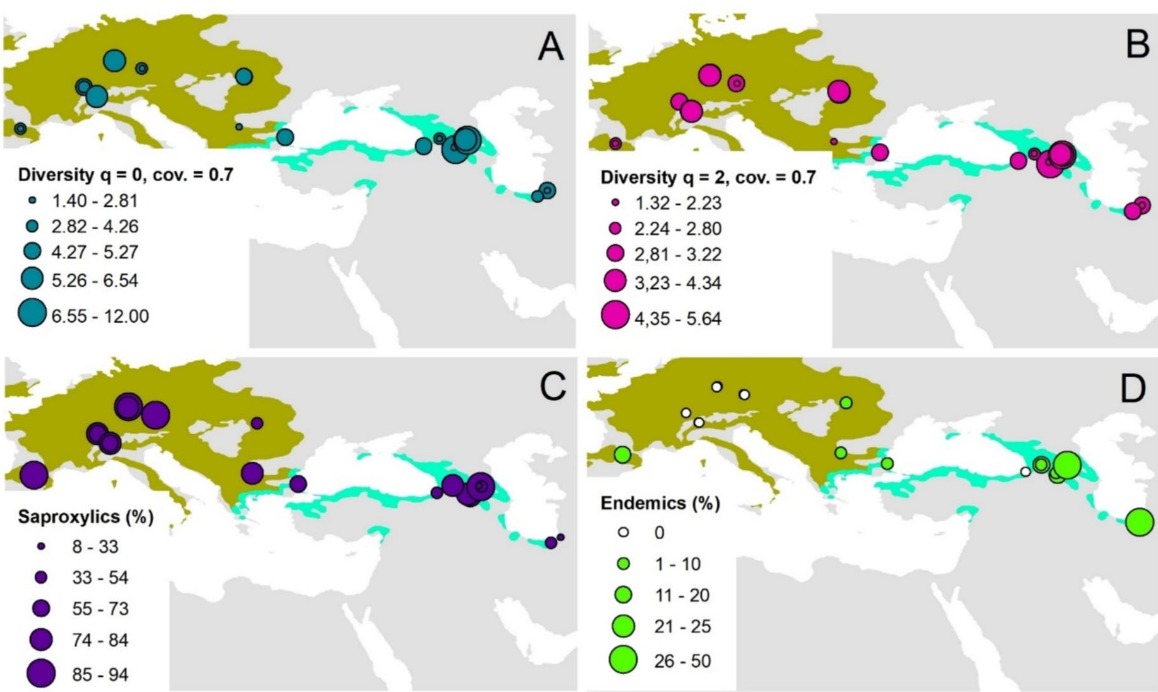

Fig. 4 Site-specific richness **A** of click beetles calculated from the same sample coverage; **B** diversity of dominant species ($q = 2$). The proportions of **C** saproxylic beetle individuals and **D** endemics per forest site

et al. 2004). The temperate forests of the Caucasus form one of the most diverse and unique temperate forest ecosystems globally, with more than twice the plant and animal diversity found in adjacent regions of Europe or Asia (Williams et al. 2006; Zazanashvili and Mallon 2009). This assessment is supported by studies on elaterids. Orlov (1994) described several species unique to the Caucasus region, while Chantladze (1988) reported new records of click beetles in western Georgia, including endemic species. Magomedova (2017) examined the species composition of the elaterid genus *Agriotes* in the Caucasus region and found that species diversity was highest in the northern Caucasus, similar to our results. The importance of the geographical and climatological isolation of the Greater Caucasus mountains for diversity and endemics, as shown in our study of elaterids, was also demonstrated in a study of Tenebrionids (Abdurkhmanov and Nabozhenko 2015).

The last group of beech forests identified in our study as important for insect diversity consists of those in the Hyrcanian region, south of the Caspian Sea. In these forests, the numbers of endemics or highly threatened species are as high as those in Europe [Fig. 4D, (Müller et al. 2016a, b)]. However, in terms of species composition, Hyrcanian forests form a very distinct community (Fig. 2), which seems to be the product of their geographical history, isolation and climate (Safarov 1979; Nakhutsrishvili et al. 2015). Beech forests in the Hyrcanian belt are 25–50 million years old and the conservation of their ecosystems promoted speciation, with many endemics in all species groups (Mathew et al. 2000; Javidkar et al. 2007). To this day, even for well-studied species groups, such as beetles, newly discovered species are still being reported from the beech forests of Hyrcanian forests (Löbl and Ogawa 2016; Bussler 2017; Müller and Schuh 2021). This is true also for elaterids (Jarzabek-Müller et al. 2017; Kundrata et al. 2019).

As noted above, the importance of the larger Caucasus Ecoregion for rare and endemic species, demonstrated even in our elaterid data from beech forests, was recognized by its designation as a UNESCO Worlds Heritage Site (Tohidifar et al. 2016; UNESCO 2019). The isolation of Oriental beech forests (Fig. 3) in this region by mountains and deserts in part explains both why these forests are the oldest surviving temperate forests of Western Eurasia and their specific role in biodiversity.

A summary of our results on elaterids in beech forests from France to Iran together with a comparison with findings from other species groups provides clear evidence of the importance of biogeographically old beech forests in supporting a unique fauna. This is particularly the case for beech forests in the Caucasus Ecoregion, which host several very distinct species' communities. However, the critical role played by deadwood and decaying trees in old-growth features in maintaining biodiversity is often underappreciated by the public (Müller et al. 2017). This will need to be addressed if community efforts aimed at greater protection are to be intensified, especially in the beech forests of Georgia, Türkiye, Armenia, Azerbaijan and Iran, given their very large contribution to the biodiversity present within beech forests.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-025-00678-4.

Acknowledgements Our study was supported by the Bundesministerium für Bildung und Forschung (BMBF), as the BeechDIV project, and by the Federal Office of the Environment, Switzerland, as the Swiss project AMORE I (FOEN). We are grateful to everyone for their input during fieldwork and sampling.

Author contribution GM and JM: wrote the main manuscript text, AM identified most of the beetles on species level, part of the beetle species were identified by AB and MK. HA, VC, MC, VD, LD, JE, KG, TG, R,H, RJ, IK, GK, JK, ZK, TL, MM, PP, NR, LT and MV: managed the field works and collecting the beetle specimen CB, MG. and all authors reviewed the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. Project: BMBF -Biodiversity in deadwood,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,01DK21002,Federal Office of the Environment,Switzerland,as the Swiss project AMORE I (FOEN)

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interest The authors declare no competing interests.

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