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How does *Acer negundo* invasion shape plant species diversity in the understory of early oak-hornbeam forests in proximity to a primeval ecosystem?

Patryk Czortek [a], Michał Depczyński [b], Radosław Puchałka [c,d,*]

[a] University of Warsaw, Faculty of Biology, Białowieża Geobotanical Station, Sportowa 19, Białowieża 17–230, Poland
[b] Department of Plant Taxonomy and Nature Conservation, Faculty of Biology, University of Gdańsk, Wita Stwosza 59, Gdańsk 80-308, Poland
[c] Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Lwowska 1, Toruń 87-100, Poland
[d] Centre for Climate Change Research, Nicolaus Copernicus University in Toruń, Lwowska 1, Toruń 87-100, Poland

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ABSTRACT

The impacts of numerous non-native trees on temperate forest understories are still poorly quantified, despite growing interest in invasion ecology. *Acer negundo* exemplifies this gap as one of the most widespread invasive trees in Europe, with little evidence on how it alters understory diversity and composition. We examined how increasing *A. negundo* cover affects taxonomic diversity, phylogenetic relatedness structure and community assembly processes in the understory of early-successional oak-hornbeam forests embedded within the Białowieża Primeval Forest. Ordination and regression analyses revealed that *A. negundo* suppressed both taxonomic and functional diversity, while enhancing phylogenetic diversity in the understory. A decline in species richness was accompanied by a shift from niche differentiation and habitat filtering towards stronger interspecific competition, reflected in the loss of light-demanding species and an increase in nutrient-demanding taxa. A higher presence of competitive, phylogenetically distinct tall herbs may explain the observed high phylogenetic diversity beneath dense *A. negundo* canopy. However, from a successional perspective, this may hinder the colonization of understory by typical forest specialists and impair the native trees self-regeneration abilities. Our findings highlight the need for early intervention to control the spread of *A. negundo*, with a particular focus on early-successional forests, which are especially prone to invasion. Furthermore, quantifying the *per capita* impacts of *A. negundo* along its invasion gradient may support the identification of ecological thresholds beyond which natural recovery becomes increasingly limited.

1. Introduction

Boxelder maple (*Acer negundo* L., Sapindaceae) is native to the western and central-northern regions of North America, with its range extending southward into Central America (POWO, https://powo.science.kew.org/taxon/781412–1, accessed 25 Aug 2025). Although *A. negundo* tolerates a wide range of temperatures and soils, its optimum occurrence is in temperate climates and on alluvial soils. This short-lived, dioecious and wind-pollinated species has characteristics typical of pioneer river valley species, such as early entering the reproductive period, usually at 8–11 years of age. Nevertheless, under particularly favourable conditions, some individuals may start flowering and producing seeds as early as 2–3 years of age. *Acer negundo* spreads effectively into indigenous ecosystems due to its strong vegetative reproduction, with broken branches and twigs capable of long-distance dispersal via river water, similar to seeds (Säumel and Kowarik, 2013). Urban areas often act as starting points for *A. negundo* invasion in the river valleys, with artificial linear landscape structures serving as its additional migration corridors (DeWine and Cooper, 2007; Straigytė et al., 2015; Vykhor and Prots, 2013).

Acer negundo was introduced to Europe, to the United Kingdom, around 1688 (Bean, 1916), and to Poland in 1808 (Tokarska-Guzik, 2005). Due to its ease of cultivation, wide tolerance to meteorological conditions, and rapid growth, it became a popular tree planted in parks and roadside alleys in Central Europe (Hereźniak, 1992). The spread of *A. negundo* from cultivation in Poland was first documented in 1899 (Tokarska-Guzik, 2005). *Acer negundo* has so far been recorded in 16 European countries, where it is spreading from cultivation in eight and

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* Corresponding author at: Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Lwowska 1, Toruń 87-100, Poland.
E-mail address: puchalka@umk.pl (R. Puchałka).

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occurs exclusively as naturally regenerating populations in two (Brus et al., 2019). The most recent distribution of *A. negundo* in Europe, based on current data from the Global Biodiversity Information Facility (GBIF.org, 2025) and a review of scientific and grey literature from south-eastern and eastern Europe (Puchałka et al., 2023b), indicates a wide range of this non-native tree in these regions (Fig. 1; Online Resource 1). Currently, particularly abundant observations come from France, western Germany, Poland, the Czech Republic, southern Slovakia and Hungary, where its occurrence coincides with the area of oak-hornbeam forests of the *Carpinion betuli* association (Bohn et al., 2003, 2007; Preislerová et al., 2022). Numerous sites have also been recorded in southern France, western Russia, and eastern Ukraine, where *A. negundo* colonizes other habitat types (Fig. 1; Online Resource 1). As in other European countries (Hasenauer et al., 2016; Porté et al., 2011; Straigytė et al., 2015; Vykhor and Prots, 2013), in a region of the Białowieża Primeval Forest it is an invasive species rapidly colonizing ruderal sites, urbanized areas, post-agricultural grasslands, riparian and oak-hornbeam forests (Adamowski et al., 1998).

Its expansion in mature, highly shaded forests is often constrained by limited light availability (Saccone et al., 2013, 2010). However, within canopy gaps or during early stages of stand development, *A. negundo* can successfully establish and compete with native trees (Kołaczkowska and Mędrzycki, 2021). Once established, its control becomes highly challenging: mechanical cutting often stimulates vigorous resprouting, and only complete uprooting can prevent regeneration (Merceron et al., 2016; Nikolaeva et al., 2020). High propagule pressure and rapid re-establishment further make eradication labor-intensive and costly, contributing to *A. negundo* being recognized as one of the most invasive species in Europe (Brus et al., 2019; Puchałka et al., 2023b; Campagnaro et al., 2018; Weber and Gut, 2004). These regeneration strategies, combined with traits incuding faster growth than most trees native to Central Europe (Zajdler et al., 2019) and a wide tolerance to environmental factors, allow *A. negundo* to form monospecific stands (Sikorska et al., 2019; Veselkin et al., 2021). Understory of such forest patches is usually dominated by grasses and herbaceous ruderals (Porté et al., 2011; Marozas et al., 2015; Veselkin and Dubrovin, 2019).

Most studies on the influence of *A. negundo* on plant species diversity have been conducted in highly human-transformed ruderal and riparian ecosystems, and mainly focused on assessing species richness of the understory (Wohlgemuth et al., 2022). The results of these studies have limited extrapolation power to other ecosystems of similar character, making it difficult to assess the vulnerability of other habitats to the invasion risk of this species (Dyderski and Jagodziński, 2019; Olden et al., 2018). Moreover, our understanding of how *A. negundo* invasion in oak-hornbeam forests alters the processes structuring understory community assembly also remains limited. Furthermore, it is also unclear how the presence of *A. negundo* affects the phylogenetic structure of understory, i.e. the evolutionary similarity of co-occurring species, which reflects their adaptive capacity and may be crucial for long-term maintenance of both taxonomical and functional diversity of the understory. The answers to such questions may be provided by analyses that take into account not only classical measures of diversity, such as species richness and the Shannon index, but also metrics of plant functional composition and phylogenetic relatendness structure (Schleuter et al., 2010; Czortek, 2023).

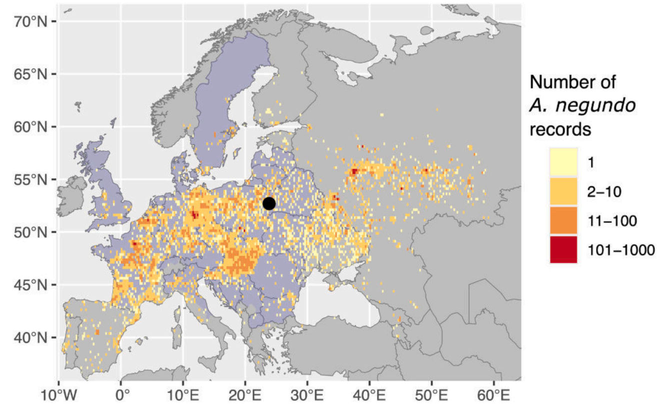

Fig. 1. Distribution and density of *Acer negundo* occurrence records (based on GBIF, 2025; supplemented with additional sources, see Online Resource 1) and the distribution of oak-hornbeam forests in Europe (marked in blue; Preislerová et al#, 2022). Black point is the study area.

The spread of *A. negundo* in post-agricultural open areas and its frequent occurrence in early successional stages of oak-hornbeam forests adjacent to the Strict Reserve of the Białowieża National Park may pose a threat to this primeval forest ecosystem. This raises concern for the preservation of naturalness in Europe's last primeval forest ecosystem, despite its presumed low susceptibility to plant invasions (Czortek et al., 2024; Jaroszewicz et al., 2019; Lapin et al., 2019; Łapok et al., 2018). A thorough understanding of the ecological effects of *A. negundo* invasion, especially during the initial stages of forest succession, is essential for developing effective strategies to mitigate its impact on biodiversity, community structure, trophic relationships, nutrient dynamics, ecosystem functioning, ecosystem services and mechanisms of secondary succession (Aerts et al., 2017; Blackburn et al., 2011). Incorporating multiple dimensions of understory diversity, including taxonomic, functional and phylogenetic diversity metrics, is therefore important for informing forest management practices and guiding conservation-oriented responses to invasion. One possible solution to achieve this goal can be assessment of *per capita* effects, which can be expressed through quantifying changes in vegetation diversity components in response to varying levels of invader dominance. These estimates have proven useful for drawing generalizations about non-native species impacts across ecosystems, as they enable standardized comparisons and enhance inference strength (Barney et al., 2015; Bury et al., 2024; Czortek et al., 2025; Kumschick et al., 2015; Parker et al., 1999). In this study, we applied this framework by establishing a gradient of *A. negundo* cover, allowing us to relate shifts in understory diversity directly to the increasing abundance of this species in the canopy layer.

Applying a *per capita* effects approach in oak-hornbeam forest patches of the Białowieża National Park's Strict Reserve foreland, where other invasive plants are largely absent (but see Czortek et al., 2025), establishes a robust baseline for evaluating the impact of *A. negundo* on early-successional forests in more transformed landscapes. This makes our research broadly applicable to Central European oak-hornbeam forests (Bohn et al., 2007, 2003). This relevance is further reinforced by the importance of oak-hornbeam forests in Europe, where they constitute a key Natura 2000 habitat and a backbone of continental biodiversity conservation (Preislerová et al., 2022). Despite being legally protected, these habitats are under threat from climate change, which is contributing to declining conditions for native tree species and herbaceous plants (Puchałka et al., 2023a; Dyderski et al., 2025). These processes may facilitate the invasion of non-native deciduous tree species, such as *A. negundo*, which is considered a 'winner of climate change' and may soon become common across numerous types of European deciduous forests (Puchałka et al., 2023b).

Our study investigated how increased *A. negundo* cover may affect understory diversity in early successional oak-hornbeam forests located in the proximity of the Białowieża Primeval Forest by exploring: (i) shifts in taxonomic, phylogenetic and functional diversity of plant species; and (ii) how invasion by this non-native tree may trigger changes in the importance of habitat filtering, interspecific competition and niche differentiation in shaping the co-occurrence patterns of understory plant species. We hypothesized that increasing *A. negundo* cover in the canopy will (H1) reduce understory taxonomic, phylogenetic and functional diversity. We further hypothesized that (H2) these changes will weaken the roles of niche differentiation and habitat filtering in shaping the community assembly processes, thereby increasing the importance of interspecific competition.

2. Materials and methods

2.1. Study site

The field work was carried out in an area covering the Białowieża Clearing and Grudki Clearing in the Białowieża Forest (north-eastern Poland), characterized by temperate transitional climate (Okołowicz and Martyn, 1979; Online Resource 2). Both clearings are located within the Natura 2000 area 'Białowieża Forest' (PLC200004). They are also recognized as hotspots of *A. negundo* invasion within the Białowieża Primeval Forest region. According to Adamowski et al. (2002), Mędrzycki (2002), and iNaturalist observations (accessed 28 Aug 2025 https://www.inaturalist.org/observations?place_id=18103&subview=map&taxon_id=47726), the highest densities of this species were reported within our study area, where it can form dense stands comprising dozens of individuals. Beyond these localities, *A. negundo* also occurrs in the western and northern parts of the Białowieża Forest, although these populations are markedly smaller, typically numbering fewer than about ten mature individuals each. Single trees are further recorded along the western boundary of the Białowieża National Park Strict Reserve and in scattered localities within its north-western part. For these reasons our study covered relatively small area of about 13 km^2, which provided an optimal context for detecting and quantifying the ecological consequences of *A. negundo* invasion under tightly controlled conditions. The high homogeneity of the study plots enabled us to standardize habitat conditions and isolate the effects of *A. negundo* cover on the understory vegetation with greater confidence, ensuring strong comparability among plots and reliable detection of invasion impacts.

Both clearings have been used for mowing, grazing and agriculture since the 17th–18th centuries, and these practices continued until the 1950s. A marked depopulation occurred in the early 1990s. The current human impact is limited to the occasional mowing of semi-natural meadows that are managed on an extensive basis. Large portions of both clearings are covered by early stages of subcontinental oak-hornbeam forest (*Tilio-Carpinetum*). Currently in abandoned settlements, fields, and meadows, secondary forest succession is taking place (Adamowski and Bomanowska, 2011; Czortek et al., 2025).

2.2. Field works

We conducted the fieldwork in July 2023, when early spring geophytes such as *Anemone nemorosa* (Puchałka et al., 2022) can still be found in the vegetative, fruiting or post-dispersal stages and most other species are flowering or fruiting (Faliński, 2001). This was the optimum time to obtain as complete a list of species as possible. The study area was divided into four sites of study plots, selected for the presence of subcontinental oak-hornbeam patches in the early stages of succession (Fig. 2). The maximum distance between study sites was approximately 5 km. The plots were characterised by young stands of *B. pendula*, *C. betulus*, *P. tremula*, *Q. robur*, *S. caprea*, and *T. cordata*, as well as invasive *A. negundo* with similar vertical structure and tree size. A total of 40 square study plots (25 m^2 each) were delineated, spanning a gradient from 0 % to 100 % canopy cover by *A. negundo*. To ensure a stratified sampling design, vegetation plots were established across four classes of *A. negundo* canopy cover: ten plots without *A. negundo*, ten with 5–25 % cover, ten with 26–50 %, and ten with 51–100 % cover. We carried out floristic inventories of vascular plants on the plots, assessing taxon cover according to the non-transformed, nine-degree Braun-Blanquet scale (Online Resource 3). Species names were taken from Euro+Med checklist (http://ww2.bgbm.org/EuroPlusMed/, accessed 1 Nov 2023).

2.3. Plant species diversity characteristics

Besides the traditional taxonomical diversity metrics (i.e. species richness and Shannon index), we accounted for the functional composition of plant species assemblages. For each plot, we compiled information on eight plant functional traits, obtained from the LEDA (Kleyer et al., 2008), BIEN (Enquist et al., 2016), BiolFlor (Kuhn et al., 2004), and Pladias databases (Chytrý et al., 2021). We focused on standard functional traits related to the leaf economic spectrum (i.e. specific leaf area, leaf dry matter content, and canopy height), describing the species' strategies of resource use and competition. In addition, we considered seed mass, the onset and duration of flowering, and pollination mechanisms (insect, wind, or self-pollination) as traits reflecting the species' reproductive strategies and responses to habitat filters (Díaz et al., 2016; Grime, 2006; Westoby, 1998).

Because our study lacked direct measurements of *A. negundo*-invasion driven shifts in abiotic habitat properties, we inferred habitat conditions from the species composition of the plots, using ecological indicator values (EIVs) for light (EIV-L), temperature (EIV-T), moisture (EIV-M), soil reaction (EIV-R), and soil fertility (EIV-N), following the approach of Leuschner and Ellenberg (2017). Despite limitations arising from their discontinuous and expert-based nature (Schaffers and Sýkora, 2000), this approach remains widely used in vegetation ecology (e.g. Ridding et al., 2020; Evangelista et al., 2016) and shows good

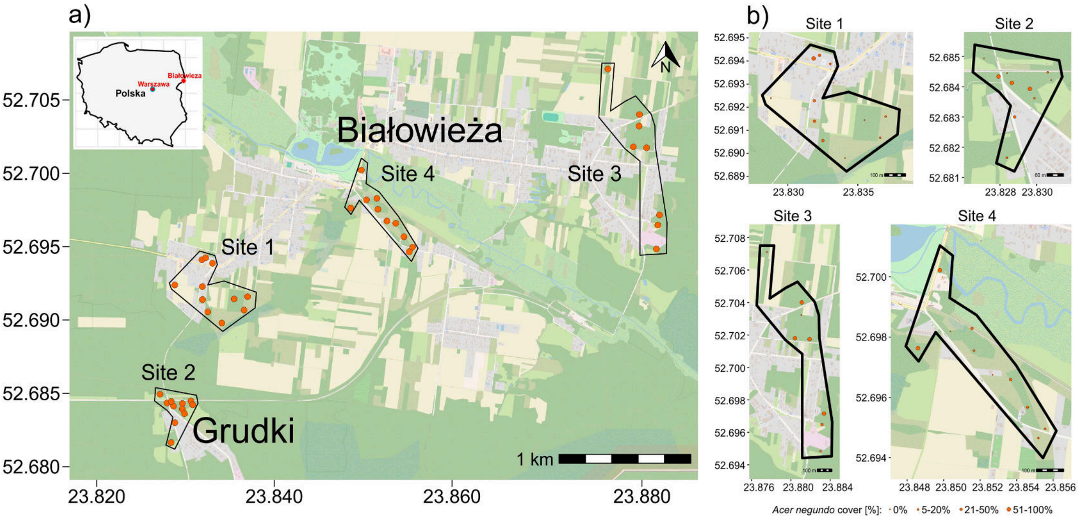

Fig. 2. Distribution of vegetation plots in the study area (a) comprising four study sites (b).

correspondence with direct soil measurements (e.g. Szymura et al., 2014; Dzwonko, 2001).

Information on functional traits and EIVs for some species was missing but instead of omitting them from analyses we imputed missing data through the employment of a phylogenetic imputation procedure (Online Resource 4). The first 15 phylogenetic eigenvectors explained 67.3 % of the variation in species' phylogenetic distances, and the imputation accuracy was satisfactory, with low error rates for continuous (NRMSE = 0.31) and categorical traits (misclassification = 0.32). Based on the imputed trait data, for each plot, we calculated the community-weighted means (weighted by the species abundance) of plant functional traits and EIVs.

Using the *FD* package (Laliberté and Legendre, 2010), for each plot we calculated five functional diversity metrics: functional richness, functional dispersion, functional divergence, functional evenness, and Rao quadratic entropy (Online Resource 5). Low values of these indices suggest a strong influence of environmental filtering or intense interspecific competition in shaping the community composition (Chesson, 2000). Conversely, high values can signify the dominant role of niche differentiation in shaping the community assembly processes – a mechanism through which species exhibiting divergent functional traits reduce interspecific competition allowing relatively stable co-existence of plants within an assemblage (Carroll et al., 2011; Czortek, 2023; Czortek et al., 2021). Employing the *PhyloMeasures* package (Tsirogiannis and Sandel, 2016), for each vegetation plot we computed the mean nearest taxon distance index. Low values indicate phylogenetic clustering, whereas high values reflect greater evolutionary divergence among species (Tsirogiannis and Sandel, 2016).

2.4. Data analysis

We characterized differences in the understory species composition amongst the plots varying in the percentage cover of *A. negundo* in the tree stand using the Detrended Correspondence Analysis (DCA; gradient length = 4.81 SD), implemented in the *vegan* package (Oksanen, 2015). Employing the passive projection of vegetation characteristics (i.e. taxonomical, functional, and phylogenetic diversity metrics, as well as CWMs of plant functional traits and EIVs), we fitted vegetation characteristics (Table 1) into the ordination space as passive vectors. We assessed the explanatory power of indirect correlations of vegetation characteristics with species composition through the computation of the coefficients of determination (R^2) and *P*-values using a permutation test with 999 iterations (provided by the *vegan* package; Oksanen, 2015). To assess whether the *A. negundo* invasion influence the species composition of the understory we performed the Canonical Correspondence Analysis (CCA) with *A. negundo* cover as an explanatory variable and tested for the significance of this impact using the PERMANOVA analysis (*vegan* package; Oksanen, 2015).

Table 1
Summary statistics of all variables included in the analyses. Abbreviation: CWM – community-weighted mean, EIV – ecological indicator value.

Variable	Min	Max	Mean	SD
Taxonomical diversity				
Species richness	6.000	32.000	21.600	6.250
Shannon index	0.855	2.714	2.046	0.402
Functional diversity				
Functional richness	0.238	0.598	0.412	0.069
Functional dispersion	0.066	0.213	0.160	0.035
Functional divergence	0.614	0.960	0.839	0.078
Functional evenness	0.112	0.764	0.378	0.214
Rao quadratic entropy	0.009	0.047	0.032	0.009
Phylogenetic diversity				
Mean nearest taxon distance	74.490	273.610	150.350	59.154
CWMs of plant functional traits				
Canopy height CWM [m]	0.545	2.291	1.153	0.311
Leaf dry matter content CWM [mg g^{-1}]	192.800	312.700	253.800	24.989
Specific leaf area CWM [cm^2 g^{-1}]	187.500	347.100	271.600	35.302
Seed mass CWM [mg]	0.806	3.188	1.890	0.533
CWMs of ecological indicator values				
Light EIV CWM	4.448	7.690	6.346	0.918
Temperature EIV CWM	4.990	6.291	5.415	0.283
Soil moisture EIV CWM	4.251	6.428	5.439	0.496
Soil fertility EIV CWM	3.417	7.900	5.979	1.116
Soil reaction EIV CWM	4.768	7.067	6.405	0.553
Acer negundo cover [%]	0.000	100.00	32.500	30.550

To assess how *A. negundo* invasion shapes the taxonomical, functional, and phylogenetic diversity of the understory, as well as CWMs of plant functional traits and CWMs of ecological indicator values (EIVs) describing species' ecological requirements in the study plots, for each vegetation characteristic we performed one mixed effect model, using the *glmmTMB* package (Brooks et al., 2017). In each model, we used *A. negundo* cover as a fixed predictor, and the study site identity as a random intercept to account for the effects of the vegetation survey design, local heterogeneity of abiotic conditions, and history of land-use. We modeled the species richness using a generalized mixed effect model with a Poisson distribution, chosen based on a relatively low value of the dispersion parameter (1.04; $P = 0.77$) as provided by the result of dispersion test implemented in the *DHARMa* package (Hartig, 2022). For each of the five functional diversity metrics, we performed one generalized mixed effect model with the beta distribution of the response variable. To account for the effects of *A. negundo* invasion on the Shannon index and CWMs of four plant functional traits and five EIVs, we built ten linear mixed effects assuming approximate normality of response variables. We used the *ggeffects* package (Lüdecke, 2018) to account for marginal responses of modeled variables to *A. negundo* invasion, allowing us an assessment of effect sizes and biological importance of the observed patterns instead of focusing on traditional methods of the statistical significance evaluation solely (Nakagawa and Cuthill, 2007; Wasserstein and Lazar, 2016). We performed all statistical analyses using R 4.3.1 software (R Core Team, 2024).

3. Results

The DCA ordination of understory species composition revealed two primary gradients in the ordination space (Fig. 3a; Table 2). Considering the gradient along the DCA axis 1 we explored that species composition of plots with high percentage cover of *A. negundo* in tree stand was described by high phylogenetic diversity of plant species (high values of mean nearest taxon distance index; MNTD), high functional evenness (FEve), as well as high contribution of species producing heavier seeds (seed mass CWM), and species of high soil fertility and reaction demands (nitrogen and reaction EIV CWMs), e.g. *Aegopodium podagraria*, *Alliaria petiolata*, *Anthriscus sylvestris*, *Lapsana communis*, and *Chelidonium majus* (left side of the gradient along DCA1 axis; Fig. 2a; Table 2; Online Resource 6). In plots with low *A. negundo* cover the species composition of the understory was characterized by high values of Shannon index (Shan), functional dispersion (FDis), Rao quadratic entropy (RaoQ), and a high proportion of species of higher leaf dry matter content (LDMC CWM), e.g. *Carex hirta*, *Dactylis glomerata* subsp. *glomerata*, *Leontodon hispidus*, *Phleum pretense*, and *Rumex acetosa* (right side of the gradient along DCA1 axis; Fig. 3a; Table 2; Online Resource 6). The gradient along the DCA axis 2 divided vegetation plots with high contribution of species with high specific leaf area (SLA CWM) and high temperature demands (EIV-T CWM; e.g. *Anemone nemorosa*, *Dactylis glomerata* subsp. *lobata*, *Lathyrus pratensis*, *Valeriana officinalis*, and *Veronica officinalis*; upper side of DCA ordination plot) from plots with high species and functional richness (Rich and FRic, respectively), high functional divergence (FDiv), as well as a high proportion of species of higher moisture demands (EIV-M CWM) and canopy height (C.height CWM), e.g. *Epipactis helleborine*, *Knautia arvensis*, *Rubus idaeus*, *Rumex crispus*, and *Tragopogon orientalis* (lower side of DCA ordination plot; Fig. 3a; Table 2; Online Resource 6).

Taking into account the result of the CCA ordination we found a

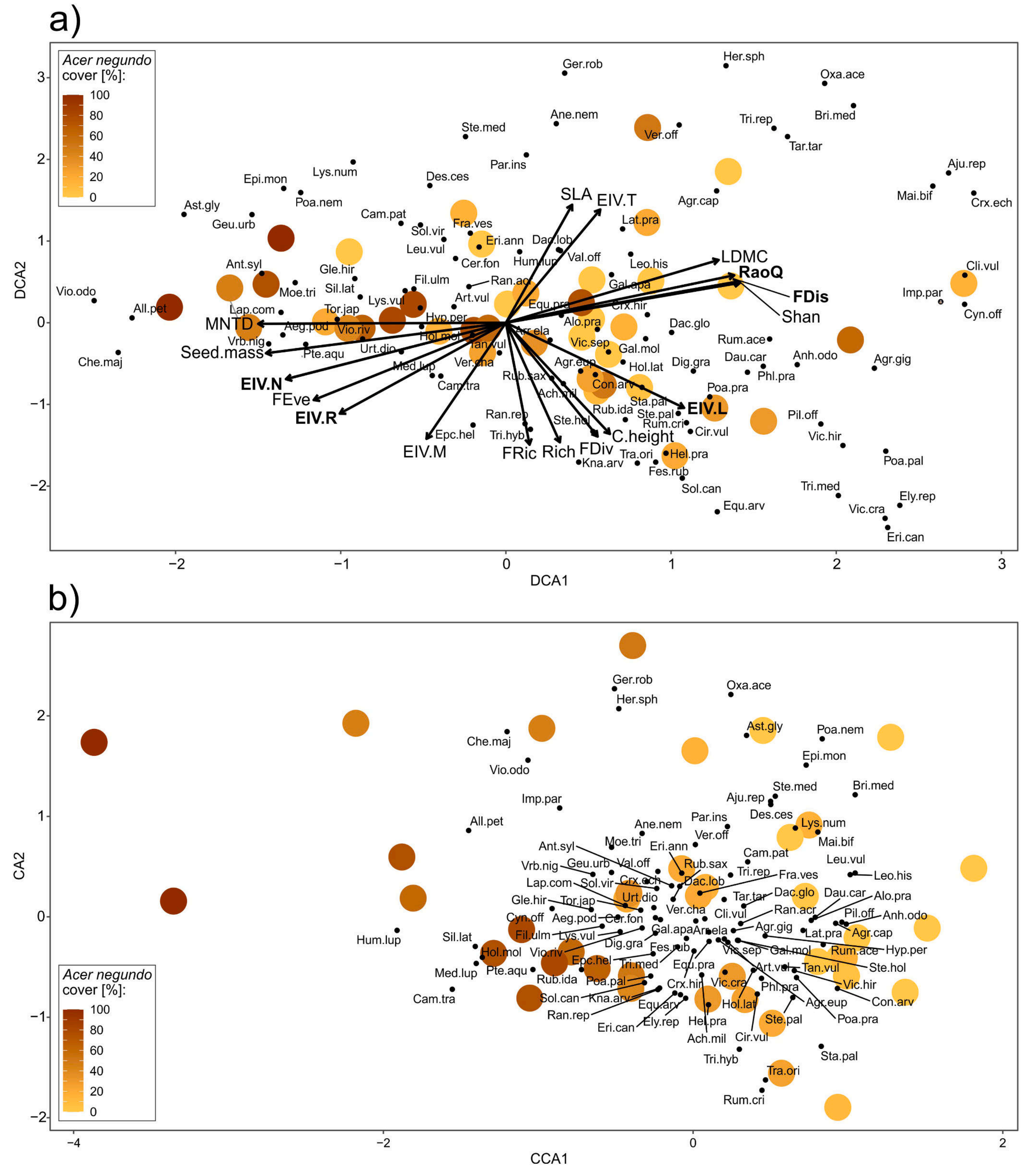

Fig. 3. Visualisation of DCA ordination showing dissimilarities in species composition of the understory along a gradient of *A. negundo* cover with passive projection of vegetation characteristics describing species composition of the understory; statistically significant results are marked in **bold**, (a) with result of CCA ordination illustrating relationship between *A. negundo* percentage cover and plant species composition of the study plots (b). For full variable names in (a) see Table 2. Seven-letter labels in (a) and (b) represent species acronyms. Seven-letter labels in (a) and (b) represent species acronyms. Only species recorded more than once in the study plots were included in (a), and those recorded more than twice were included in (b). For full species names in (a) and (b) see Online Resource 6.

Table 2

Passive projection of vegetation characteristics fitted to the results of the DCA ordination, illustrating dissimilarities in understory species composition along a gradient of *A. negundo* cover. Coefficients of determination (R^2) and associated P-values were obtained using permutation tests based on 999 iterations. Abbreviations: CWM – community weighted mean. Statistically significant results are marked in **bold**.

Variable	Acronym	NMDS1	NMDS2	R^2	P
Taxonomical diversity:					
Species richness	Rich	0.217	−0.975	0.031	0.561
Shannon index	Shan	0.945	0.326	0.135	0.106
Functional diversity:					
Functional richness	FRic	0.095	−0.995	0.065	0.336
Functional dispersion	FDis	0.940	0.338	0.322	**0.005**
Functional divergence	FDiv	0.370	−0.928	0.006	0.880
Functional evenness	FEve	−0.776	−0.630	0.031	0.601
Rao quadratic entropy	RaoQ	0.921	0.387	0.3868	**0.001**
Phylogenetic diversity:					
Mean nearest taxon distance	MNTD	−0.999	−0.008	0.056	0.381
CWMs of plant functional traits:					
Canopy height CWM [m]	C.height	0.419	−0.907	0.044	0.497
Leaf dry matter content CWM [mg g^{-1}]	LDMC	0.858	0.512	0.089	0.217
Specific leaf area CWM [cm^2 g^{-1}]	SLA	0.267	0.963	0.163	0.054
Seed mass CWM [mg]	S.mass	−0.887	−0.459	0.025	0.660
CWMs of ecological indicator values:					
Light EIV CWM	EIV.L	0.719	−0.694	0.455	**0.001**
Temperature EIV CWM	EIV.T	0.381	0.924	0.023	0.666
Soil moisture EIV CWM	EIV.M	−0.320	−0.947	0.118	0.133
Soil fertility EIV CWM	EIV.N	−0.887	−0.460	0.608	**0.001**
Soil reaction EIV CWM	EIV.R	−0.670	−0.741	0.392	**0.001**
Acer negundo cover [%]	-	−0.968	−0.248	0.254	**0.006**

significant effect of *A. negundo* cover in influencing the species composition of vegetation plots (ordering plots along the CCA1 axis; Fig. 3b), as confirmed by a result of the PERMANOVA analysis (χ^2=0.261; F=1.643; P = 0.001). While the vast majority of plant species revealed high affinity to plots with low *A. negundo* cover (e.g. *Alopecurus pratensis*, *Briza media*, *Lathyrus pratensis*, *Leucanthemum vulgare*, and *Ranunculus acris*; right side of the gradient along CCA1 axis; Fig. 3b; Online Resource 6), only a few species were highly associated with plots with high cover of *A. negundo* (e.g. *Alliaria petiolata*, *Campanula trachelium*, *Cynoglossum officinale*, *Humulus lupulus*, and *Silene latifolia*; left side of the gradient along CCA1 axis; Fig. 3b; Online Resource 6).

We observed the notable effects of *A. negundo* invasion on several metrics of plant species diversity analyzed (Fig. 4; Table 3). The differences between marginal (R^2_m) and conditional (R^2_C) R^2 values were generally low, indicating a limited contribution of the study site identity on the results obtained. We observed the largest random effect for species richness and CWMs of leaf traits, while it was negligible for most diversity indices and EIVs (Table 3). Focusing on taxonomical diversity indices we found that species richness of the understory decreased from ~24 species to ~16 species, and the Shannon index decreased from 2.23 to 1.67 at *A. negundo* cover in tree stand ranging from 0 % to 100 % (Fig. 4a,b; Table 3). Alongside increasing the cover of *A. negundo* from 0 % to 100 %, the values of mean nearest taxon distance index increased from 138.88 to 174.19 (Fig. 4c; Table 3). Four of the five analyzed metrics of functional diversity were negatively influenced by *A. negundo* invasion (Fig. 4d–g; Table 3). While functional richness and functional divergence decreased only slightly (from 0.43 to 0.37 and from 0.87 to 0.78, respectively; Fig. 4d,e; Table 3), Rao quadratic entropy and functional dispersion decreased substantially (from 0.04 to 0.02 and from 0.17 to 0.13, respectively; Fig. 4f,g; Table 3) at *A. negundo* cover ranging from 0 % to 100 %. Only functional evenness increased along with increasing the invasion intensity from 0.33 at 0 % to 0.49 at 100 % of *A. negundo* cover (Fig. 4h; Table 3).

Regarding the CWMs of plant functional traits, we reported gently positive effects of *A. negundo* invasion on canopy height (an increase from 1.08 to 1.30 m; Fig. 5a; Table 3), specific leaf area (an increase from 265.91 to 282.58 cm^2 g^{-1}; Fig. 5b; Table 3) and seed mass CWMs (an increase from 1.73 to 2.21 mg; Fig. 5c; Table 3), and negative impacts on leaf dry matter content CWM (a decrease from 261.44 to 239.53 mg g^{-1}; Fig. 5d; Table 3) at the cover of this nonnative tree

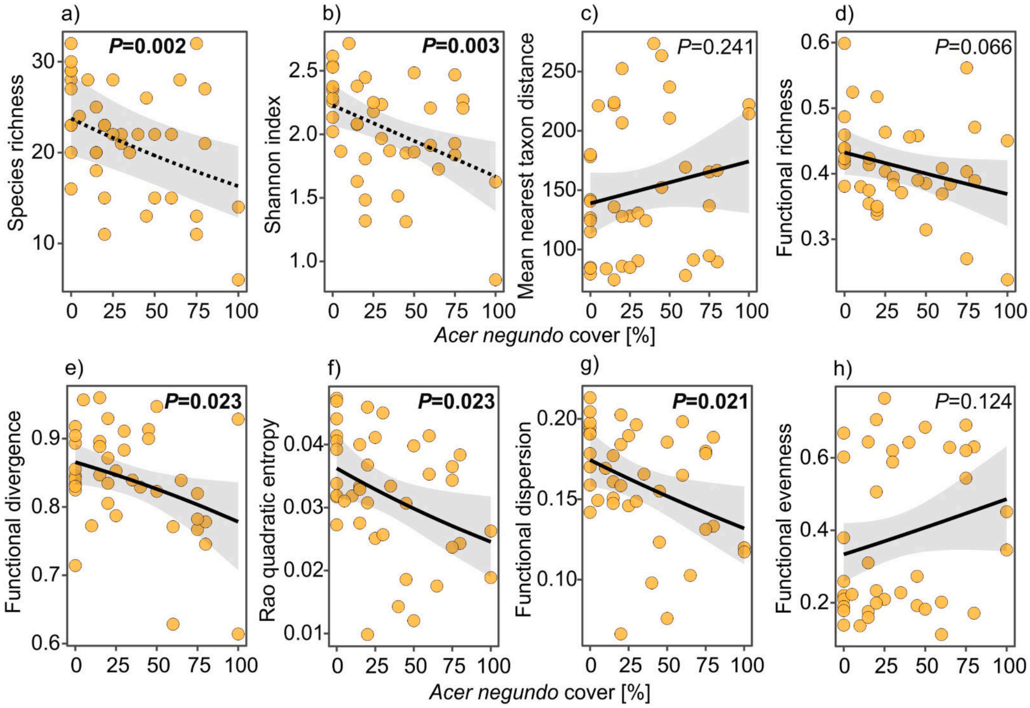

Fig. 4. Visualization of mixed effect models (with site identity adopted as random factor) predicting impacts of *A. negundo* percentage cover on: taxonomical diversity metrics (a-b), phylogenetic diversity (c), and functional diversity metrics (d-h) of the understory vegetation. For model parameters see Table 3. Statistically significant results are marked in **bold**.

Table 3
Parameters of mixed effect models (with site identity adopted as random factor) predicting impacts of *A. negundo* percentage cover on plant species diversity metrics and community weighted means (CWMs) of plants' functional traits and ecological indicator values (EIV). Abbreviations: RE SD – standard deviation of random effect. Statistically significant results are marked in **bold**.

Variable	Estimate	SE	*t/z*	*P*	RE SD	R^2_m	R^2_c
Taxonomical diversity:							
Species richness:							
(Intercept)	3.167	0.095	33.280	**< 0.001**	0.160	0.154	0.455
A. negundo cover	−0.004	0.001	−3.080	**0.002**	-	-	-
Shannon index:							
(Intercept)	2.228	0.083	26.669	**< 0.001**	< 0.001	0.184	0.184
A. negundo cover	−0.005	0.001	−2.974	**0.003**	-	-	-
Functional diversity:							
Functional richness:							
(Intercept)	−0.272	0.071	−3.814	**< 0.001**	0.066	0.186	0.311
A. negundo cover	−0.002	0.001	−1.834	0.066	-	-	-
Functional dispersion:							
(Intercept)	1.554	0.060	−25.765	**< 0.001**	< 0.001	0.174	0.174
A. negundo cover	−0.003	0.001	−2.314	**0.021**	-	-	-
Functional divergence:							
(Intercept)	1.862	0.128	14.497	**< 0.001**	< 0.001	0.824	0.824
A. negundo cover	−0.006	0.002	−2.269	**0.023**	-	-	-
Functional evenness:							
(Intercept)	−0.692	0.187	−3.682	**< 0.001**	< 0.001	0.144	0.144
A. negundo cover	0.006	0.004	1.536	0.124	-	-	-
Rao quadratic entropy:							
(Intercept)	−3.281	0.072	−45.240	**< 0.001**	< 0.001	0.139	0.139
A. negundo cover	−0.004	0.001	−2.270	**0.023**	-	-	-
Phylogenetic diversity:							
Mean nearest taxon distance index:							
(Intercept)	138.876	13.348	10.404	**< 0.001**	0.003	0.034	0.034
A. negundo cover	0.353	0.301	1.173	0.241	-	-	-
CWMs of plant functional traits:							
CWM of canopy height [m]:							
(Intercept)	1.081	0.076	14.172	**< 0.001**	0.061	0.046	0.086
A. negundo cover	0.002	0.001	1.377	0.169	-	-	-
CWM of leaf dry matter content [mg g^{-1}]:							
(Intercept)	261.441	6.793	38.48-	**< 0.001**	7.591	0.071	0.163
A. negundo cover	−0.219	0.126	−1.730	0.083	-	-	-
CWM of specific leaf area [cm^2 g^{-1}]:							
(Intercept)	265.905	8.899	29.878	**< 0.001**	7.981	0.021	0.073
A. negundo cover	0.166	0.178	0.932	0.351	-	-	-
CWM of seed mass [mg]:							
(Intercept)	1.734	0.119	14.510	**< 0.001**	0.033	0.076	0.081
A. negundo cover	0.004	0.002	1.792	0.073	-	-	-
CWMs of ecological indicator values (EIVs):							
CWM of light EIV:							
(Intercept)	6.705	0.233	28.704	**< 0.001**	0.280	0.147	0.244
A. negundo cover	−0.011	0.004	−2.667	**0.007**	-	-	-
CWM of temperature EIV:							
(Intercept)	5.431	0.064	83.720	**< 0.001**	< 0.001	0.003	0.003
A. negundo cover	< 0.001	0.001	−0.350	0.725	-	-	-
CWM of soil moisture EIV:							
(Intercept)	5.394	0.113	47.520	**< 0.001**	< 0.001	0.007	0.007
A. negundo cover	0.001	0.002	0.540	0.592	-	-	-
CWM of soil fertility EIV:							
(Intercept)	5.221	0.197	24.461	**< 0.001**	< 0.001	0.412	0.412
A. negundo cover	0.023	0.004	5.233	**< 0.001**	-	-	-
CWM of soil reaction EIV:							
(Intercept)	6.140	0.113	54.190	**< 0.001**	< 0.001	0.207	0.207
A. negundo cover	0.008	0.002	3.190	**0.001**	-	-	-

ranging from 0 % to 100 %. Considering the CWMs of ecological indicators values, *A. negundo* invasion exerted a strong negative effect on the occurrence of more light-demanding species (a decrease in light EIV CWM from 6.71 at 0 % to 5.58 at 100 % *A. negundo* cover; Fig. 5e; Table 3). Contrary, under conditions of the prevalence of this nonnative species in tree stand, the proportion of species with higher soil fertility and reaction requirements increased prominently from 5.22 at 0 % to 7.55 at 100 % in case of fertility EIV CWM (Fig. 5f; Table 3), and from 6.14 at 0 % to 6.96 at 100 % of *A. negundo* cover in case of reaction EIV CWM (Fig. 5g; Table 3). We did not identify impacts of *A. negundo* invasion on the contribution of species with different temperature and moisture requirements (Fig. 5h,i; Table 3).

4. Discussion

4.1. Invasion-driven effects on species composition and taxonomical diversity

Results of ordination analyses confirmed that the invasion of *A. negundo* in initial successional stages of oak-hornbeam forests was an important factor explaining differences in understory species composition. Similarly, previous studies focusing on other forest types, such as riparian, pine, or urban forests, reported declines in plant species diversity following the invasion of this species (Bottollier-Curtet et al., 2012; Lipikhina et al., 2022; Marozas et al., 2015; Saccone et al., 2010; Veselkin et al., 2021; Veselkin and Dubrovin, 2019). Negative impacts of

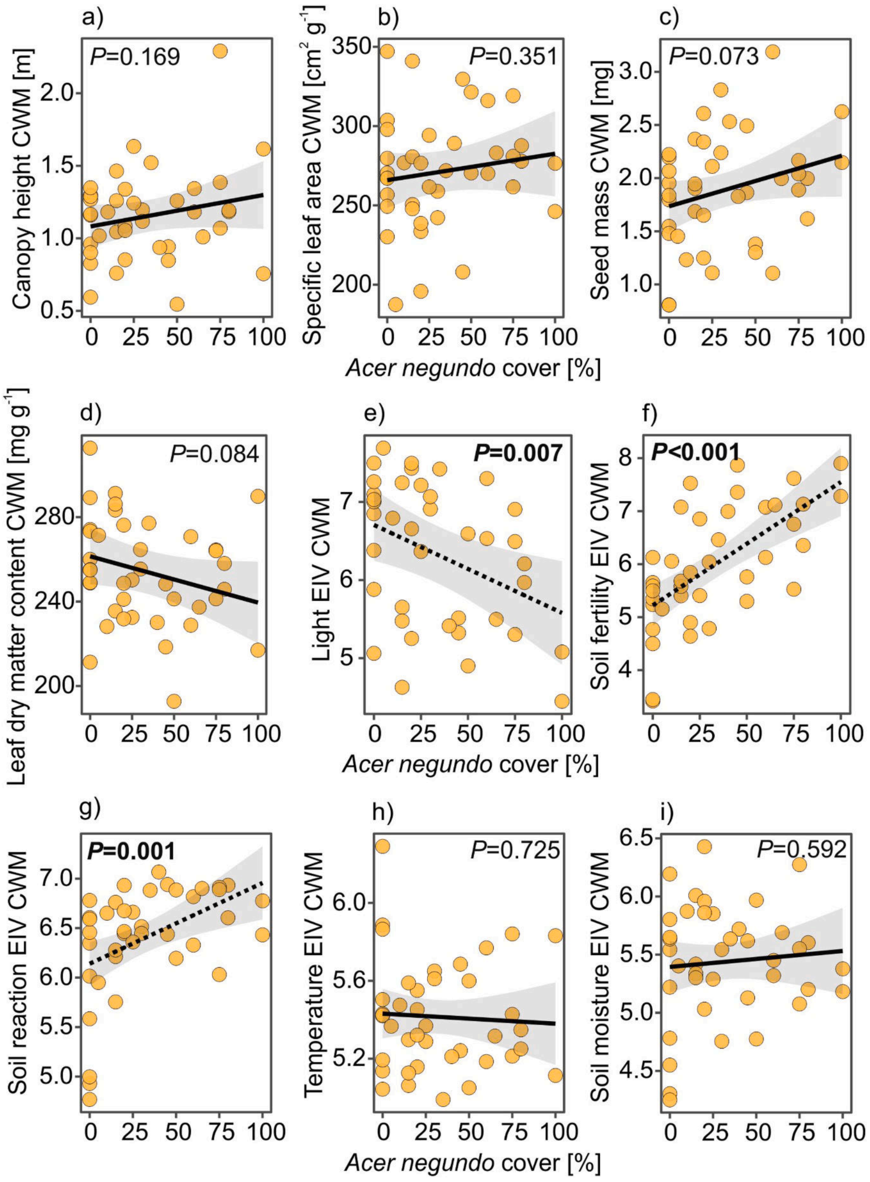

Fig. 5. Visualization of mixed effect models (with site identity adopted as random factor) predicting impacts of *A. negundo* percentage cover on: community weighted means (CWMs) of plant functional traits (a-d) and CWMs of ecological indicator values (e-i) of the understory vegetation. For model parameters see Table 3. Statistically significant results are marked in **bold**.

invasive trees on understory species composition have also been documented for other North American non-natives, such as *Prunus serotina* (Halarewicz and Pruchniewicz, 2015; Halarewicz and Zołnierz, 2014; Reinhart and Clay, 2009), *Quercus rubra* (Chmura, 2013; Woziwoda et al., 2014), and *Robinia pseudoacacia* (Šibíková et al., 2019; Slabejová et al., 2019; Vítková et al., 2020). The differences we observed were reflected in distinct patterns of species groups' occurrence across plots varying in *A. negundo* cover. These groups varied not only in their light and soil fertility requirements, but also in their interspecific competitive abilities and tolerance to environmental stress.

The observed decline in species richness and Shannon diversity index with increasing in *A. negundo* cover is consistent with previous findings on understory in riparian, urban, and pine forests invaded by this species (Dubrovin et al., 2023; Lipikhina et al., 2022; Saccone et al., 2010; Veselkin et al., 2021; Veselkin and Dubrovin, 2019). This pattern supports our Hypothesis 1. Reduced taxonomic diversity of the understory has also been documented in relation to other inasive trees, such as *Q. rubra* and *P. serotina* (Halarewicz and Zołnierz, 2014; Vanhellemont et al., 2010). These effects are most pronounced in nutrient-poor habitats where the understory is composed of species adapted to low light availability or a thinner litter layer. Nevertheless, most existing studies have not revealed a clear positive or negative effect of introduced trees on understory diversity (Wohlgemuth et al., 2022). This inconsistency suggests that the ecological impacts of tree invasions are highly context-dependent and influenced by site-specific factors (Dyderski and Jagodziński, 2020). However, although numerous studies have examined the effects of various non-native species on flora, fauna, and ecosystem functions in different habitats (e.g. Čerevková et al., 2020; Gentili et al., 2019; Lazzaro et al., 2017; Rusterholz et al., 2014), the broader consequences of non-native tree invasions for biodiversity in Central European forests remain insufficiently understood (especially oak-hornbeam forests). Existing research has largely focused on a narrow group of species, most notably *P. serotina, P. menziesii, Q. rubra* and *R. pseudoacacia* (Carboneras et al., 2018; Roy et al., 2024; Vilà et al., 2024). Thus, our study represents a necessary step in building the empirical foundation for broader syntheses of invasion impacts.To summarize, invasion of *A. negundo* significantly reduces understory species richness and taxonomic diversity, with effects comparable to other invasive trees.

4.2. Interspecific competition lowers the importance of niche differentiation

Our study revealed that increasing cover of *A. negundo* was associated with decreases in four out of five analyzed metrics of functional diversity, with the exception of functional evenness. This pattern is in line with our Hypothesis 1. These negative invasion-driven effects suggest that *A. negundo* may substantially influence community assembly processes during early successional stages of oak-hornbeam forests. Similar declines in functional diversity have been reported following invasions by other non-native tree species, such as *R. pseudoacacia* (Hejda et al., 2017) and *Q. rubra* (Chmura, 2020). However, the effects of invasive trees on forest functional diversity in temperate Europe remain poorly understood. Current knowledge is largely based on case-specific studies, underscoring the need for further systematic research (Dimitrova et al., 2022; Wohlgemuth et al., 2022).

Alongside the decrease in functional richness, increasing *A. negundo* cover was associated with declines in functional dispersion and Rao quadratic entropy. This may indicate a progressive homogenization of plant functional trait composition in determining the species co-occurrence patterns along the invasion gradient. This trend reflects the competitive exclusion of functionally diverse understory species by a limited subset of taxa revealing high niche similarity and convergence in functional traits. Accordingly, with increasing *A. negundo* cover, the role of niche differentiation in shaping community structure could be diminished, giving way to a higher importance of interspecific competition, thus confirming Hypothesis 2. A similar effect of invasive trees on understory vegetation has been observed in nutrient-poor pine forests, where invasions by *P. serotina* and *Q. rubra* were shown to promote the occurrence of competitive species (Dyderski and Jagodziński, 2020). However, the negative impact of *Q. rubra* is more plausibly attributed to its adverse effects on soil properties and increased shading (Stanek et al., 2020). Other studies, in turn, have demonstrated that the invasion of *R. pseudoacacia* not only alters species composition, but also promotes competitive and disturbance-tolerant species (Hejda et al., 2017). Nevertheless, it is important to recognize that invasion-driven effects on functional diversity of the understory may be ambiguous, either positive or negative, depending on tree species identity, vegetation type, or soil fertility (Hejda et al., 2017; Wohlgemuth et al., 2022). Accordingly, our results should be viewed in light of the successional dynamics of early oak-hornbeam forest stages. Pioneer and meadow species (relicts of former agricultural, mowing, and grazing practices) remained relatively abundant in plots experiencing low levels of *A. negundo* invasion. This may suggest that, with increasing invasion intensity of this tree species, not only did the role of niche differentiation decline. Habitat filtering also gradually lost its significance in shaping the community assembly, in line with expectations formulated in Hypothesis 2. Overall, increasing *A. negundo* cover reduced functional diversity and promoted trait convergence, with interspecific competition prevailing over niche differentiation in the understory of early successional oak-hornbeam forests.

4.3. Higher competition decreases the role of habitat filtering

Surprisingly, functional evenness increased with *A. negundo* cover, which contrasts with our Hypothesis 1. This pattern likely reflects shifts in the dominant functional strategies along the invasion gradient. In plots with low *A. negundo* cover, the understory contained a high proportion of meadow species (e.g., *Tragopogon orientalis*, *Alopecurus pratensis*, *Arrhenatherum elatius*, *Galium mollugo*, or *Leontodon hispidus*). This dominance pattern contributed to a less regular occupation of the trait hyperspace, as only a few functionally similar types associated with high light availability prevailed. In contrast, in plots with high *A. negundo* cover, these light-demanding species were partly replaced by taxa possessing trait combinations associated with more efficient resource acquisition or greater shade tolerance. This replacement led to a more even distribution of realized niches across the available trait space, thereby increasing functional evenness (Clark et al., 2012; Le Bagousse-Pinguet et al., 2021). To our knowledge, no previous studies have documented a positive effect of non-native tree invasion on functional evenness. For instance, in *Q. rubra*-dominated forests, functional evenness decreases, likely due to stronger habitat filtering and a reduced role of niche differentiation in shaping understory species co-occurrence (Chmura, 2020). By contrast, Gentili et al. (2019) found no significant effect of *Q. rubra* on functional evenness. Lower functional evenness in *R. pseudoacacia*-dominated forests has been attributed to intensified environmental filtering caused by overshading and dominance of a few species with similar traits, especially high nitrogen-use efficiency. This dominance can lead to the exclusion of specialist species and result in an uneven representation of low number of functionally similar species within the community (Gentili et al., 2019).

On the other hand, the lower regularity in realized niche distribution in plots less occupied by *A. negundo* suggests that some parts of trait hyperspace could be inaccessible, reflecting a strong role of habitat filtering (Li et al., 2018). This pattern is supported by the negative relationship between *A. negundo* invasion and functional divergence (consistent with Hypothesis 1), indicating that plots with lower cover hosted more species with niches varying substantially from the majority of understory species. Legacy effects of former agricultural, mowing, and grazing practices on the studied plots (Adamowski and Bomanowska, 2011) may explain these patterns, as high proportions of pioneer species (e.g., *Agrostis capillaris*, *Convolvulus arvensis*, *Equisetum arvense*, *Elymus repens*, or *Pilosella officinalis*) were found in plots with low *A. negundo* cover.

The negative relationship between *A. negundo* invasion and functional divergence, consistent with Hypothesis 1, aligns with the detrimental effect of this non-native tree on leaf dry matter content CWM. High values of this functional trait are typical for plants adapted to occur in stressful conditions such as intense insolation, drought, and nutrient limitation (Cornelissen et al., 2003; Grime, 2006; Wright et al., 2004). This suggests that under low *A. negundo* cover, the understory structure was shaped by strong habitat filtering. During forest succession, light-demanding and fast-growing pioneer species are gradually replaced by more shade-tolerant forest species adapted to reduced light availability and more stable moisture conditions (Adamowski and Bomanowska, 2011). These latter species often reveal lower LDMC values, which may reflect their adaptation to limited light conditions and a resource-acquisitive strategy under shading (Poorter et al., 2009; Wright et al., 2004). To our knowledge, no studies to date have examined the impact of other invasive tree species on LDMC.

One might expect that the negative impact of *A. negundo* invasion on CWM of light EIV reflects the colonization of shade-tolerant species into the understory of plots with canopy dominated by this non-native tree. These species, associated with more advanced stages of the forest succession, included, for instance, *Viola riviniana*, *Campanula trachelium*, *Poa nemoralis*, *Lapsana communis*, *Moehringia trinervia*, or *Glechoma hirsuta*. This trend is supported by the positive effect of *A. negundo* invasion on species with higher seed mass, typically associated with mature forest understories (Hermy et al., 1999). Since forest species were mostly single occurrences in the study plots, the negative relationship between CWM of light EIV-L and *A. negundo* cover mainly reflects a decline of light-demanding species rather than colonization by shade-tolerant ones. These early-successional taxa may have been competitively excluded under the influence of invasion by nitrophilous tall-herbs with high soil fertility and reaction demands. This pattern confirms Hypothesis 2. Initially, these species may have colonized available niches previously unused or inaccessible to vascular plants, and subsequently dominate the understory, e.g., *Alliaria petiolata*, *Aegopodium podagraria*, *Anthriscus sylvestris*, *Urtica dioica*, or *Filipendula ulmaria* (Kuhn et al., 2004). These patterns are supported by the positive effect of *A. negundo* invasion on the CWMs of soil nitrogen and reaction EIVs. Moreover, the aforementioned species are also characterized by relatively high canopy height and specific leaf area, which is reflected in a slight but consistent increase in CWMs of these traits' values along the *A. negundo* invasion gradient.

In essence, invasion by *A. negundo* was associated with higher functional evenness but lower functional divergence, reflecting the decline of light-demanding pioneers and the spread of nitrophilous tall-herb species. Together, these trends suggest that stronger interspecific competition progressively diminished the role of habitat filtering in shaping the understory structure.

4.4. Invasion-driven effects on phylogenetic diversity

In plots with low *A. negundo* cover, phylogenetic clustering (indicated by reduced values of mean nearest taxon distance index) was high despite high taxonomic diversity in the herb layer. This suggests that in species-rich plots, the majority of observed plants belonged to closely related clades, reflected in the high representation of species from the Poaceae and Asteraceae families. In contrast, under *R. pseudoacacia* invasion in acidophilous oak forests, the increasing representation of these two groups has been attributed to low shading and high nitrogen availability, which favour ruderal species (Piwczyński et al., 2016). Conversely, in plots with high *A. negundo* cover, phylogenetic relatedness among species was heterogeneous (as indicated by elevated values of mean nearest taxon distance index), resulting from the supplementation of taxa representing more distantly related clades. This pattern partially contradicts Hypothesis 1 and reflects the presence of phylogenetically distant forest species and abundant nitrophilous tall herbs in plots with *A. negundo*-dominated canopy, effectively outcompeting more closely related taxa. While the colonization by competitors may lead to profound shifts in taxonomic diversity, a subset of species associated with open habitats could still persist under conditions of high *A. negundo* abundance, albeit at lower frequencies than in understory of less-invaded plots. These patterns may help explain not only the persistence of relatively high phylogenetic diversity in plots with dense canopy of this non-native but also its increase along the *A. negundo* invasion gradient. Altogether, *A. negundo* invasion was linked to a shift from phylogenetic clustering in less-invaded plots to greater phylogenetic diversity under its dense canopy, driven by the coexistence of open-habitat species, distantly related forest specialists and nitrophilous tall herbs.

4.5. Study limitations

The focus on a small, homogeneous study area minimally affected by other non-native plant species enabled a clear assessment of *A. negundo* impacts. However, this design constrains the study to a case-based investigation and limits its transferability to forest types other than oak-hornbeam. However, oak-hornbeam forests occupy a large part of Central Europe (Bohn et al., 2003, 2007; Preislerová et al., 2022) and overlap geographically with the distribution of *A. negundo* (Puchałka et al., 2023a). Our findings therefore provide an important regional baseline for assessing invasion impacts, suggesting that the processes identified here are likely to be relevant across Central European oak-hornbeam forests. Nevertheless, validation in a wider range of *A. negundo*-invaded forests across Europe is required to confirm the generality of the observed patterns.

To evaluate the effects of *A. negundo* on understory diversity, we relied on EIVs as indirect proxies of habitat conditions, due to the lack of direct measurements of abiotic factors. However, EIVs impose important constraints. Because they are based on realized niches rather than direct measurements, they reflect multiple influences and may obscure whether patterns arise from biotic interactions or abiotic constraints, complicating the identification of individual drivers (Schaffers and Sýkora, 2000). This limitation is particularly important for soil fertility and reaction, which are strongly influenced by microsite heterogeneity and nutrient cycling dynamics, and direct measurements would provide clearer evidence of *A. negundo* impacts and the mechanisms structuring understory assembly. Accordingly, our findings should be interpreted with caution. Therefore, future research should complement vegetation surveys with direct measurements of key abiotic parameters. Such integrative approaches will be essential to disentangle the relative importance of different drivers and refine our understanding of how *A. negundo* reshapes ecosystem functioning through its ecosystem-engineering effects.

5. Conclusions

We demonstrated that *A. negundo* invasion not only alters species composition and taxonomic diversity but also reshapes community assembly processes and influences the phylogenetic structure of the understory of oak-hornbeam forests. Moreover, *A. negundo* facilitates the establishment of nitrophilous tall herb species with high competitive abilities. At the same time, the importance of niche differentiation and habitat filtering in structuring understory assemblages markedly declined with increasing *A. negundo* cover. Nitrophilous tall herbs are widely recognized as succession inhibitors. Their increasing abundance in the understory may significantly reduce the survival and recruitment of late-successional tree seedlings and hinder colonization by forest specialist species. Accordingly, our results suggest that *A. negundo* may significantly slow both the trajectories and mechanisms of succession in oak-hornbeam forests. In the long term perspective, *A. negundo* invasion can therefore erode the resilience and functioning of these ecosystems, diminishing their overall conservation value. The invasion-driven mechanisms uncovered here are likely to extend beyond the studied sites, affecting not only other oak-hornbeam forests but also habitats with the potential to regenerate into this community type, underscoring their broad applicability for these ecosystems in Central Europe. This relevance is amplified by the fact that oak-hornbeam forests constitute one of the common forest types in Central Europe. Consequently, our results offer a robust evidence base for guiding management in Central European oak-hornbeam forests developing in more transformed landscapes, including unmanaged patches embedded in monoculture-dominated areas, as well as in ruderal, urban, rural, post-agricultural, and post-industrial ecosystems. Our findings underscore the critical importance of systematic monitoring and early control of *A. negundo* spread. This is particularly crucial during the initial stages of forest succession, when ecosystems are most susceptible to invasion-driven shifts. Furthermore, evaluating the *per capita* impacts of *A. negundo* along its invasion gradient can facilitate the identification of thresholds beyond which natural recovery may become limited. This approach supports the development of targeted intervention strategies aimed at mitigating the risk of irreversible regime shifts and preserving the functional integrity of both managed and unmanaged forests.

CRediT authorship contribution statement

Puchalka Radoslaw: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Conceptualization. **Michał Depczyński:** Writing – review & editing, Resources, Investigation. **Patryk Czortek:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123164.

Data availability

The data supporting the findings of this study have been deposited in the FigShare repository and are publicly available at https://doi.org/10.6084/m9.figshare.29596499.

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