High Canopy Cover of Invasive Acer Negundo L. Affects Ground Vegetation Diversity

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Abstract

We assessed the link between canopy cover degree and ground vegetation diversity under alien the ash-leaved maple (Acer negundo) and other (native or alien) tree species. We investigated urban and suburban forests in the large city of Yekaterinburg, Russia. Forests were evaluated on two spatial scales. Through an inter-habitat comparison completed over three years, we recorded canopy cover and plant diversity among 13 sample plots of 20 × 20 m where A . negundo dominated and 13 plots where other tree species dominated. In an intra-habitat comparison, we recorded canopy cover and ground vegetation diversity among 800 sample plots measuring 1 m2 in the extended urbanised forest, which featured abundant alien (308 plots) and native trees (492 plots). We observed decreased diversity among vascular ground plant species by 40% (inter-habitat) and 20% (intra-habitat) in areas dominated by the A. negundo compared to areas dominated by native tree and shrub species. An abundance of A . negundo was accompanied by increased canopy cover. We found a negative relationship between canopy cover and the number of understory herbaceous species. Thus, the interception of light and the restriction of its amount for other species is a main factor supporting the negative influence of A . negundo on native plant communities.

Introduction

Ash-leaved maple (*Acer negundo* L.) is an invasive tree in the territory of Northern Eurasia that is currently colonising disturbed and semi-natural territories (Vinogradova et al. 2010; Straigytė et al. 2015; Merceron et al. 2016; Gusev et al. 2017). *A. negundo* actively renews itself in the urbanised forests of the Middle Urals (Veselkin and Korzhinevskaya 2018; Veselkin et al. 2018), but the invasion of *ash-leaved maple* is dangerous for some types of plant communities (Emelyanov and Frolova 2011; Saccone et al. 2013). In communities dominated by *A. negundo*, the diversity of native plants decreases (Emelyanov and Frolova 2011; Kostina et al. 2016; Veselkin and Dubrovin 2019). Invasion of the European *Acer platanoides* L. (Reinhart et al. 2005) and the Far Eastern *Acer ginnala* Maxim produce a similarly negative effect on the diversity of native plant communities in North America (Schuster and Reich 2018).

The ash-leaved maple is not only an alien and invasive species but also a transformer species. Transforming species significantly change the conditions in the invaded ecosystems (Richardson et al. 2000). The impact of transformer species is realised by influences on the light regime of communities (Gorchov and Trisel 2003; Knight et al. 2008; Niinemets 2010; Schuster and Reich 2018), nutrient cycles (Allison and Vitousek 2004; Gioria and Osborne 2014; Bonifacio et al. 2015; Horodecki and Jagodzinski 2017; Schuster and Reich 2018; Zhang et al. 2019) and different components of the biota (Callaway et al. 2004; Stinson et al. 2006; Suding et al. 2013; Brouwer et al. 2015; Mueller 2016; Kamczyc 2019; Veselkin et al. 2019b).

In this study, we focused on testing the hypothesis of whether the associated effects of the canopy cover of *A. negundo* can explain its effect on living ground vegetation, namely shrubs and herbs. In general, light availability determines the productivity of the ground vegetation (Gilliam and Roberts 2014; Landuyt

et al. 2019; Czapiewska et al. 2019) and its species composition (Canham 1994; Knight et al. 2008; Barbier et al. 2008). Competition for light or specialisation in its use is the leading determinant in the organisation of plant communities. Therefore, we assumed that the main direction of the relationship between canopy cover and ground cover diversity is negative; that is, with an increase in canopy cover, the number of ground cover species decreases.

The reduced richness of ground cover under *A. negundo* due to its influence on illumination levels can be explained in several ways. Firstly, it can be assumed that the ash-leaved maple shades the soil surface more completely than trees of other species (Fig. 1 a), implying that the canopy cover in thickets of *A. negundo* is denser than in thickets of other trees. However, at the same time, similarly dense canopy cover decreases the richness of ground cover in the same way regardless of the tree species forming the canopy. This assumption seems easy to understand but has no definitive experimental confirmation, while there is much evidence that invasive plants create a denser canopy than native plants (Reinhart et al. 2006; Nilsson et al. 2008; Cusack and McCleery 2014; Berg et al. 2017). Often conclude that the shading is an active mechanism of the impact of invasive plants in native plant communities (Reinhart et al. 2006; Nilsson et al. 2008; Bravo-Monasterio et al. 2016). However, sometimes higher shading under alien plants has not been empirically confirmed (Lanta et al. 2013; Dyderski and Jagodzi'nski 2019). The estimates of the shading effect in the secondary range of the ash-leaved maple are not evident: the effect may not differ (Berg et al. 2017) or may be stronger than that of native trees (Saccone et al. 2010; Bottollier-Curtet et al. 2012).

In addition to the hypothesis about the strong shading of *A. negundo*, it is possible that even with the same canopy cover, the ash-leaved maple has a stronger effect on ground cover than other trees (Fig. 1 b – c). This suggestion implies that the reduced richness of the ground cover under *A. negundo* is associated not only with shading but also with certain other mechanisms. The reasons for this are potentially very diverse and may include increased litter formation (Nilsson et al. 2008), the different chemical composition of litter (Cusack and McCleery 2014) and soils (Bottollier-Curtet et al. 2012) as well as slower (Hladyz et al. 2011) or accelerated (Bottollier-Curtet et al. 2012) litter decomposition. Furthermore, direct allelopathic effects of invasive plants on native plants are possible (Call and Nilsen 2005; Dorning and Cipollini 2006; Kumar and Bais 2010; Cipollini et al. 2012; Nielsen et al. 2015; Gruntman et al. 2017), as is the effect of invasive plants on soil organisms (Callaway et al. 2004; Stinson et al. 2006; Brouwer et al. 2015).

Fig. 1 Hypothetical mechanisms of the generation of reduced diversity of the ground cover throughout shading in communities with *Acer negundo* (dark-grey circle) in comparison with other trees (white circle); rhombus– average rates

We emphasise the need for further research, including in new geographic regions, to identify the mechanisms of *A. negundo* invasion and the impact of this invasion on native plant communities. In this study, we conducted two field investigations to estimate the impacts of ash-leaved maple invasion on

native plant communities. This paper analyses whether the ability of *A. negundo* to create a dense canopy explains its influence on ground cover.

We tested two hypotheses. First, we assumed that *A. negundo* trees create a denser (closed) leaf canopy than other tree species of the southern taiga.

Second, we assumed that the angles of linear regression describing the relationship between the density of the canopy and the species richness of the ground cover are the same in both *A. negundo* thickets and those of other tree species.

Materials And Methods

Study area. The data was collected in urbanised habitats in the southern taiga subzone of the boreal zone of the Middle Urals, located in the territory of the Yekaterinburg urban agglomeration. The average annual temperature is +3°C, which has shown an upward trend (1°C increase in the last 25 years). The average annual precipitation is 542 mm. The average height of snow cover in February is 20–25 cm, and the average duration of snow cover is 160–180 days. Yekaterinburg is a large city with a population of 1.5 million people. The surrounding territories are dominated by pine forests of natural origin on sod-podzolic soils and brown soils. The territory of Yekaterinburg is heavily polluted (Sturman, 2008) due to a large number of industrial enterprises and the high density of the transport network. The climate is moderately continental with cold winters and warm summers. *A. negundo* actively renews itself in the urbanised forests of the Middle Urals (Veselkin and Korzhinevskaya 2018; Veselkin et al. 2018).

General design. To test our working hypotheses, we executed two studies: the first was an inter-habitat comparison, while the second was carried out as an intra-habitat comparison.

Inter-habitat comparison.

Sample plots. The inter-habitat comparison was carried out using 13 sites of intra-urban vegetation located in the city of Yekaterinburg and its suburbs in the Middle Urals, Russia. The area of the site allowed the placement of at least two plots measuring 20 × 20 m. At each site, we selected two plots, the first in the thickets of ash-leaved maple and the second in thickets of other tree species. Two plots in one area formed a linked pair of one plot with the studied impact of *A. negundo*; (An+) and one without its impact, (An–; factor 'plot type'). Paired plots were located as close together as possible and no further than 0.4 km from each other. Moreover, they were similar by a relievo and location relative to human housing and infrastructure, and they had close values in terms of canopy cover. The level of moisture was normal (10 sites) or increased (three sites). According to the European nature information system (EUNIS) habitat classification, 10 sites were classified as small green spaces completely or almost surrounded by buildings (X22) or roads (X23), three sites as large parks (X11) and one site as low forest or shrubs in wetlands (F9) (Hill et al. 2004). In total, we laid 26 plots. An– plots were dominated by *Ulmus laevis* Huds. (three plots), *Pinus sylvestris* L. (three), *Malus baccata* (L.) Borkh (two), *Prunus padus* Mill. (one), *Salix fragilis* L. (one), *Tilia cordata* Mill. (one), *Sorbus aucuparia* L. (one), *Salix alba* L. (one).

Geographical coordinates of sample plots and generalised data of their characteristics are given in the supplementary material.

Descriptions of vegetation. We performed descriptions of vegetation every year from 2017–2019. In 2018, the vegetation on one of the sites was destroyed. We therefore laid an extra couple of plots at the another site in 2018. We performed 72 descriptions covering the period from June to August in 2017, 2018 and 2019 (24 descriptions per year). We recorded species richness and the total cover of the aboveground organs of plants in the herbaceous layer (in %). The species richness was measured as the number of species per 400 m^2.

Estimation of canopy cover. Every year in mid-July, we took 10 colour photos of the canopy at each plot. We took the photos in randomly selected places, pointing the camera straight up to a height of 0.8–1.2 m. We used a Lumix DMC-FP2 digital camera (CCD sensor: 1/2.5”/10.3 million pixels/primary colour filter; photo resolution: 3648 × 2736 pixels). In total, we took 720 photos. To prepare images for analysis, we used Adobe Photoshop 11.0 (Adobe System Inc., 2008). Each photo was converted into binary so that crowns, tree trunks and other obstacles to natural sunlight were rendered as black pixels. The open sky was displayed as white pixels. The analysis of canopy cover was performed in Matlab R2018b (9.5.0.944444, The MathWorks Inc., 2018) using the original code. The code and an example of a pre- and post-processing photo of canopies are published in the supplementary material.

Intra-habitat comparison.

Site. The second study was performed in June 2018 in the Yugo-Zapadnyi Forest Park in the city of Yekaterinburg. According to the EUNIS classification, a forest park is an X11 habitat type (large parks) (Hill et al. 2004). We laid the site measuring 795 × 20 m on the 7°-northerly slope from the top of a small ridge to the middle of the slope. The site was generally populated by nettle pine forests with an undergrowth of *Rubus idaeus* L., forb-grass and small-grass. The pine stand was strongly disrupted by selective felling, and derivative communities with *Populus balsamifera* L. and *A. negundo* in the tree layer were formed at certain places. On a 795 × 20 m site, we laid five parallel transects 795 m in length on each of which 160 plots were marked at 5 m intervals. As a result, we formed a square grid with a step of 5 m and 800 plots in its nodes. Situation of the study site and generalised data of its characteristics are given in the supplementary material.

Characteristics of plant communities and the estimation of canopy cover. We took two photos with the Lumix DMC-FP2 digital camera at each of the 800 plots. The first photo was taken straight up from a height of 0.8–1.2 m, while the second was taken straight down from a height of 1.5–2 m. At the same time, a 1 × 1 m frame was laid on the ground.

In each photo of the canopies, we visually estimated the total canopy cover as a percentage of the field of view with an accuracy of 5%. We also identified the species or at minimum the genus of trees and shrubs which fell into the frame of each photo. The proportion of coverage of each taxon was estimated by eye. In each photo of the ground cover, we identified the species, the genus or at minimum the family of low

shrubs, herbs and individual trees less than 1.5 m in height. We counted only the number of taxa that were located within a 1 × 1 m frame.

During plant identification, we used a list including 131 species based on 27 preliminary geobotanical descriptions of this section of the forest park (Veselkin et al. 2018). We were able to identify some of the plants in the photos only to the family or genus level. At the same time, plants we were unable to identify to the species level were considered as different conditional species if we could distinguish their morphological features. This made it possible to sufficiently fully calculate the total number of vascular plant species on each plot. We used the term 'species richness' when evaluating alpha diversity.

At each site, we identified a dominant taxon of woody plants without dividing their life forms (shrubs, undergrowth trees or trees of the second and first layers). The taxon which occupied the largest share of the total canopy cover in the image was considered dominant.

All woody plant species encountered were assigned to one of two groups: native () or alien ().

Data analysis. We used different versions of GLM (general linear models) to carry out analysis of effects that may influence on ground cover diversity. The values of the canopy cover and species richness of the ground cover were analysed for study 1 in a two-way ANOVA (factors: 'plot type' and 'year of observation') and for study 2 in a one-way ANOVA (factor: 'woody dominant'). The relationship between canopy cover and the species number of vascular plants for ground cover were assessed using three-way (study 1) and two-way (study 2) GLMs with the discrete factors 'plot type' and 'year' and the continual factor of 'canopy cover'. Values of canopy cover expressed in percentages were previously transformed by arcsine. Data analysis was performed using the JMP 10.0.0 (SAS Institute Inc., USA, 2012) and STATISTICA 8.0 (StatSoft Inc., USA, 1984–2007) packages. The values given in the text are the mean values of the features ± standard errors.

Results

Canopy cover. In both the inter-habitat and intra-habitat comparisons, higher canopy cover was observed for *A. negundo* in comparison with other species of woody plants in urban pine forests.

Inter-habitat comparison. We observed a slightly higher canopy cover in communities dominated by the ash-leaved maple compared to communities with other woody dominants. In a two-way ANOVA, the differences between plots An+ and An– in canopy cover were significant ($F\text{plot type}_{(1;\,66)} = 6.06$; $P = 0.0165$), while the effect of the year ($F\text{year}_{(2;\,66)} = 1.91$; $P = 0.1555$) and the interaction between option and year were insignificant ($F\text{plot type} \times \text{year}_{(2;\,66)} = 0.18$; $P = 0.8344$). The absolute differences in the mean values of canopy cover between the plots were small (Fig. 2): 90 ± 1% in the An+ plots and 86 ± 1% in the An– plots.

Fig. 2 Average rates (±SE, ±95CI) of canopy cover in communities dominated by *Acer negundo* (An+; dark-grey plots) and other tree species (An-; white plots)

Intra-habitat comparison. We found a higher canopy cover in areas dominated by *A. negundo* compared to areas with other tree dominants. In the one-way ANOVA, the differences in canopy cover between the plots dominated by native and alien tree species versus *A. negundo* were significant ($F\text{plot type}_{(2;\,797)}$ = 4.21; P = 0.0151). The absolute differences in the mean values of canopy cover between the options were small (Fig. 3): areas with native dominants showed 66 ± 1%, with *A. negundo* 70 ± 1% and with other alien dominants 70 ± 2%.

Fig. 3 Average rates (±SE, ±95CI) of canopy cover in areas dominated by native (white plots), alien, excluding *Acer negundo* (white plots) species and individually – *Acer negundo* (dark-grey plots)

We found that native and alien woody species resulted in heterogeneous canopy cover (Fig. 4). Some alien species, such as *Populus balsamifera*, had thin canopies, while some native species, such as *Prunus padus* and *Sorbus aucuparia*, had dense canopies. Moreover, among the alien species, the canopies of *A. negundo* were not the densest. Some alien woody plants (namely *Ulmus laevis*, *Acer tataricum*, and *Malus baccata*) had higher average canopy cover than *A. negundo*.

Fig. 4. Average rates (±SE, ±95CI) of canopy cover of different species of native (white plots) and alien (white and dark-grey plots) tree species; rare species – the indication for a group of plots dominated by species rarely found in the studied site (*Amelanchier spicata*, *Caragana arborescens*, *Cotoneaster lucidus*, *Crataegus sanguinea*, *Larix sibirica*, *Lonicera xylostella*, *Tilia cordata*)

Richness of ground cover. In both inter-habitat and intra-habitat comparisons, we observed reduced species richness of the ground cover on plots with a tree layer formed by the ash-leaved maple.

Inter-habitat comparison. We observed reduced species richness of the ground cover in communities dominated by *A. negundo* compared to communities with other dominant trees. In a two-way ANOVA, the differences in the number of species per 400 m^2 were significant between plots An+ and An– ($F\text{plot type}_{(1;\,66)}$ = 23.44; P < 0.0001). The observation year ($F\text{year}_{(2;\,66)}$ = 0.50; P = 0.6079) and the interaction between the factors were not significant ($F\text{plot type} \times \text{year}_{(2;\,66)}$ = 0.45; P = 0.6401). The absolute differences in average values of species richness of the ground cover between the plot types were significant (Fig. 5): 17.1 ± 1.7 species per 400 m^2 in the An+ plots and 28.8 ± 1.7 species per 400 m^2 in the An– plots.

Fig. 5 Average rates (±SE, ±95CI) of species' number per 400 m^2 in communities dominated by *Acer negundo* (An+; dark-grey plots) and other tree species (An-; white plots)

Intra-habitat comparison. We found that on the plots with alien woody dominants, including *A. negundo*, the number of ground cover species was lower in comparison to sites with native dominants ($F\text{plot type}_{(2;\,797)}$ = 28.58; P < 0.0001). We observed that absolute differences in average values of species richness between the plots with native woody dominants were 6.6 ± 0.1 species per m^2; with alien woody

dominants, excluding *A. negundo*, - 5.2 ± 0.2 species per m^2; and with *A. negundo* - 5.3 ± 0.2 species per m^2 (Fig. 6).

Fig. 6 Average number (±SE, ±95CI) of observed ground cover species per m^2 on plots dominated by native (white plots), alien, excluding *Acer negundo* (light-grey plots) species, and individually – on plots dominated by *Acer negundo* (dark-grey plots)

Plots were relatively homogeneous in terms of richness of the ground layer under the canopy regardless of whether the dominant species was native or alien (Fig. 7). Areas dominated by different species of alien plants did not differ in terms of ground richness. Among the native plants, two groups of species were distinguished according to the richness of ground cover communities: 1) underbrush shrubs *Prunus padus* and *Sorbus aucuparia* and 2) trees of the first and second tiers of *Pinus sylvestris*, *Salix* sp., *Betula* sp., *Populus tremula*.

Relationship between canopy cover and species richness of ground cover. In both the inter-habitat and intra-habitat comparisons, a negative correlation was found between canopy cover and the number of vascular plant species comprising ground cover.

Fig. 7 Average number (±SE, ±95CI) of observed ground cover species per m^2 on plots under the canopies of different native (white plots) and alien (light-grey and dark-grey plots) tree species; rare species – the indication for a group of plots dominated by species rarely found in the studied site (*Amelanchier spicata*, *Caragana arborescens*, *Cotoneaster lucidus*, *Crataegus sanguinea*, *Larix sibirica*, *Lonicera xylostella*, *Tilia cordata*)

Inter-habitat comparison. In the three-way GLM using the factors ‘plot type’, ‘canopy cover’ and ‘year’, the species richness of the ground cover significantly depended on the main effects ‘plot type’ ($F\text{plot type}_{(1;\,60)}$ = 13.61; P = 0.0005) and ‘canopy cover’ ($F\text{cover}_{(1;\,60)}$ = 6.02; P = 0.0170). No other effects, including interaction effects, were significant. This means that the angle of inclination of the lines (coefficients b in the equation y = a + bx) describing the relationship between canopy cover and the number of species of ground cover on plots dominated by the ash-leaved maple and other tree species did not differ (Fig. 8, b - d). An increase of 10% in canopy cover induces a decrease in the number of ground cover species by 5.82 ± 3.30 species per 400 m^2 (P = 0.0866) in the An+ plots and by 4.77 ± 2.66 species per 400 m^2 (P = 0.0820) in the An– plots. The estimates for species richness of the ground cover in the absence of the shading effect of trees (coefficient a in the equation y = a + bx) in the plots An– and An+ were similar: in the An– plots a = 70.05 ± 23.09 species (P = 0.0046) and in the An+ plots a = 69.29 ± 29.60 species (P = 0.0252).

Fig. 8 Relationship between the average canopy cover and the number of ground cover species per 400 m^2 (inter-habitat comparison) (a) and per 1 m^2 (intra-habitat comparison) at plots dominated by native tree species (white circles) (b), alien tree species, excluding *Acer negundo* (light-grey circles) (c), and

individually – *Acer negundo* (dark-grey circles) (d). The points are slightly jittered to avoid overlapping on Figures b-d

Intra-habitat comparison. In the second study's two-way GLM with the factors 'plot type' and 'canopy cover', the number of ground cover species on the site significantly depended only on the main effects $F\text{plot type}_{(2;\,794)} = 25.73$ ($P < 0.0001$) and $F\text{cover}_{(1;\,794)} = 12.43$ ($P = 0.0004$). The 'plot type × canopy cover' interaction was not significant: $F\text{plot type × cover}_{(2;\,794)} = 1.69$; $P = 0.1855$; this indicates that we did not establish a difference in the angle of inclination of the lines describing the relationship between the canopy cover and the number of ground cover species per m^2 on plots with different woody dominants (Fig. 8, a). However, the species richness of the ground cover changed with the growth of the canopy cover depending on the dominant plants. A significant decrease in species richness with an increase of canopy cover was observed in plots with a dominance of both native (with a 10% increase in canopy cover by 0.27 ± 0.07 species per m^2; $P < 0.0001$) and alien plants (with a 10% increase in canopy cover by 0.38 ± 0.13 species per m^2; $P = 0.0035$). On plots dominated by *A. negundo*, the number of ground cover species did not change significantly with an increase in canopy cover (with an increase in canopy cover of 10%, the number of ground cover species per m^2 decreased only by 0.04 ± 0.11; $P = 0.7465$).

In the plots dominated by *A. negundo*, the species richness of the ground cover was reduced even at the lowest shading levels: in the equation y = a + bx, a = 5.51 ± 0.79 species per m^2 ($P < 0.0001$). On plots dominated by native or alien plants—excluding *A. negundo*—initial levels of ground cover richness were higher: under native plants, a = 8.40 ± 0.46 species per m^2 ($P < 0.0001$); under alien plants, a = 7.92 ± 0.93 species per m^2 ($P < 0.0001$).

Discussion

Our results show the general consistency of the appearance at the two spatial scales we observed. In both inter-habitat and intra-habitat comparisons, we registered a reduced ground cover species richness under canopies of ash-leaved maple. This result confirms the generally accepted idea that alien plants produce a negative impact on the diversity of native communities. Our earlier inter-habitat comparison showed a decrease in alpha diversity influenced by *A. negundo* of about 40% (Veselkin and Dubrovin 2019). However, unlike the conclusions reached through inter-habitat comparison (Maron and Marler 2008; Hejda et al. 2009; Emelyanov and Frolova 2011; Lanta et al. 2013; Kostina et al. 2016; Veselkin and Dubrovin 2019), the 20% decrease in the diversity of ground cover in our intra-habitat comparison can be linked with the traits of the alien plants rather than with the traits of the habitats they invade.

Additionally, we found that the results regarding the transformation of the light regime correspond between inter-habitat and intra-habitat comparisons. In both studies, we confirmed that the canopy cover of *A. negundo* is higher than the canopy covers of other tree species. Additionally, we observed a decrease in ground layer species richness linked with an increase in canopy cover. In the inter-habitat

comparison, this effect was detected both in thickets of ash-leaved maple and in thickets of other tree species. In our intra-habitat comparison, this effect was traced under the canopies of native and alien trees but not under the canopies of *A. negundo*.

Our first working hypothesis was that *A. negundo* can create strong shading. The ash-leaved maple seems to produce a denser canopy than many other woody species. This thesis cannot be strictly proven by the inter-habitat comparison because we purposefully selected plots in pairs of communities An+ and An– with high and equal canopy cover. However, the intra-habitat comparison also clearly shows that the average cover of *A. negundo* is greater. In intra-habitat comparison, estimates of canopy cover under different types of trees and shrubs were gathered randomly. However, the ash-leaved maple does not form the highest canopy cover of leaves present in this study. There are several native and alien plants that form denser canopies. Therefore, it is more correct to summarise our results as the following: *A. negundo* creates a canopy of leaves which is equally as dense as the canopy of other alien trees but denser than that of native trees.

This fact could have several explanations. For example, the ability to show varying levels of shading is connected with the different heights of the lower canopy edge. According to our estimates, the higher canopies shade the soil surface at the vertical projection point less than lower canopies: trees of the first layer (n = 218) yielded shading of 55 ± 1%; of the second layer (*A. negundo* [n = 194] yielded shading of 70 ± 1%; other species (n = 131) yielded shading of 67 ± 1%); and shrubs (n = 257) yielded shading of 77%. Furthermore, we suggest that high canopy cover formed by alien plants may have a different structure for leaf canopy, with different degrees of leaf overlap or of damage to leaves by phytophages (Cincotta et al. 2009; Adams et al. 2009; Veselkin et al. 2019a).

The conclusion that the ash-leaved maple forms a denser canopy of leaves than native trees is consistent with most of the published data about this species (Saccone et al. 2010; Bottollier-Curtet et al. 2012). This conclusion is relative to some other invasive plants (Reinhart et al. 2006; Nilsson et al. 2008; Cusack and McCleery 2014; Berg et al. 2017).

Our second hypothesis assumed that with an increase in shading level, the number of grass species equally decreases both under *A. negundo* and under other tree species. In our inter-habitat comparison, an increase in canopy cover was linked with a decrease in plant diversity both under ash-leaved maple shading and that of other trees. However, the intra-habitat comparison illustrated an increase in the canopy cover of *A. negundo* that was not accompanied by a decrease in plant diversity.

However, on both spatial scales, the number of grass species under crowns of *A. negundo* was less than under crowns of native trees over the whole range of canopy cover. Consequently, the transformation of the light regime of communities does not explain the decrease in plant richness in *A. negundo* thickets (Fig. 9). We cannot confirm that our results describe all possible effects of light regime transformation under an ash-leaved maple canopy. Notably, in the Middle Urals, the maximum sun height above the horizon during the summer season is 43–56°. Although the photos shot vertically upward show the canopy cover at the point the camera was located, they do not fully describe the lighting conditions for

each plot because they ignore the intensity of side light flux. The difference between the estimates of canopy cover and illumination may be especially large for the intra-habitat comparison, but this difference is smaller for the inter-habitat comparison. One more possible consequence of the transformation of light conditions under the canopy of *A. negundo* is a specific change in the spectral composition of light.

Fig. 9 A probable mechanism of the generation of reduced diversity of the ground cover throughout canopy shading in communities dominated by *Acer negundo* (dark-grey circle) in comparison with other trees (white circle); rhombus – average rates

Along with a decrease in illumination, the mechanisms of the suppression of ground cover under the influence of the ash-leaved maple may be different, depending on spatial canopy structure. For example, the fact that *A. negundo* has a dense and low crown may not only decrease illumination in *A. negundo* thickets but also blocks the flow of seeds or other plant diaspores. It is known that the diversity and pool of seed banks may decrease in native communities invaded by alien plants (Gioria et al. 2012; Gioria and Osborne 2014), including ash-leaved maple (Veselkin et al. 2018).

In addition, the ability of alien species to reduce diversity via allelopathic effects is often discussed (Call and Nilsen 2005; Gruntman et al. 2017), and allelopathic activity has been confirmed for the water extracts from *A. negundo* leaves (Csiszár 2009; Csiszár et al. 2013) and for the soil from its thickets (Yeryomenko 2014). However, in another experiment, the allelopathic activity of the soil from the thickets of *A. negundo* was not confirmed (Veselkin et al. 2019b). Accompanying the direct allelopathic effects on plants of substances secreted by *A. negundo*, indirect allelopathy is possible and is a probable effect of *A. negundo* on native plants through its primary effect on soil microorganisms. In this experiment, though we did not confirm the effect of soil from ash-leaved maple thickets on seed germination, we observed suppression of mycorrhiza in model grasses (Veselkin et al. 2019b). Consequently, direct and indirect allelopathy are possible mechanisms for the influence of *A. negundo* on native plants, although their ecological impact requires further evaluation.

Conclusion

We observed decreased ground cover plant species in large (inter-habitat comparison) and small (intra-habitat comparison) vegetation areas dominated by the alien maple *Acer negundo* compared to areas dominated by native tree and shrub species. At the same time, the dominance of the ash-leaved maple was accompanied by a recorded higher canopy cover of a height of 1–1.2 m. Additionally, in both studies, we established a negative correlation between the canopy cover of trees and the number of vascular plant species of ground cover. Thus, the capture of light and restriction of its amount for other species is a central mechanism that causes several of the negative effects of *A. negundo* on native communities. Similar to other studies (Lanta et al. 2013), we found that high canopy cover, which produces high shading, is not the only mechanism by which *A. negundo* realises its potential as a transformer species. Most likely, the ash-leaved maple affects native plants and the structure of communities via additional

factors. We believe that further studies are needed to understand which of these mechanisms (influence on the seed bank; direct allelopathy; influence on soil microorganisms; transformation of the physicochemical properties of soil) can explain the impact of *Acer negundo* on the diversity and composition of plant communities.

Declarations

DATA AVAILABILITY

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

CODE AVAILABILITY

The script for estimating the canopy cover is given in supplementary material.

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CONTRIBUTION

DVV conceived the ideas, designed the research, and analyzed data. DID collected the field data. DID and LAP performed processing and prepared data for analysis. DVV wrote the text of the paper. DDV, DID, and LAP corrected and discussed the text.

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ETHICS DECLARATIONS

Conflict of interest

The authors declare that they have no conflicts of interest.

Ethics approval

Not relevant.

Consent to participate

The authors declare that they gave their consent to participate in the investigation.

Consent for publication

The authors declare that they consent to the publication.

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Figures

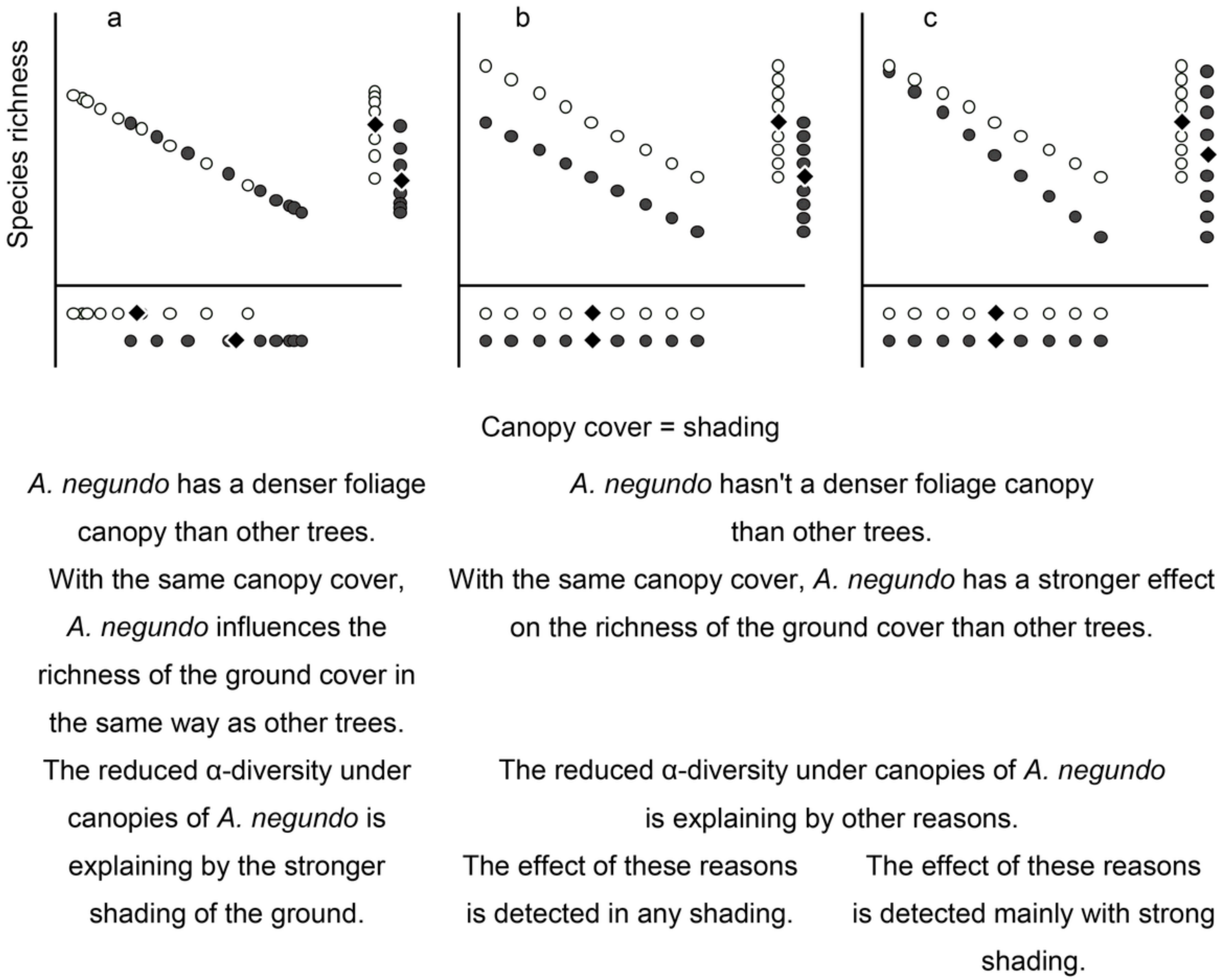

Figure 1

Hypothetical mechanisms of the generation of reduced diversity of the ground cover throughout shading in communities with Acer negundo (dark-grey circle) in comparison with other trees (white circle); rhombus– average rates

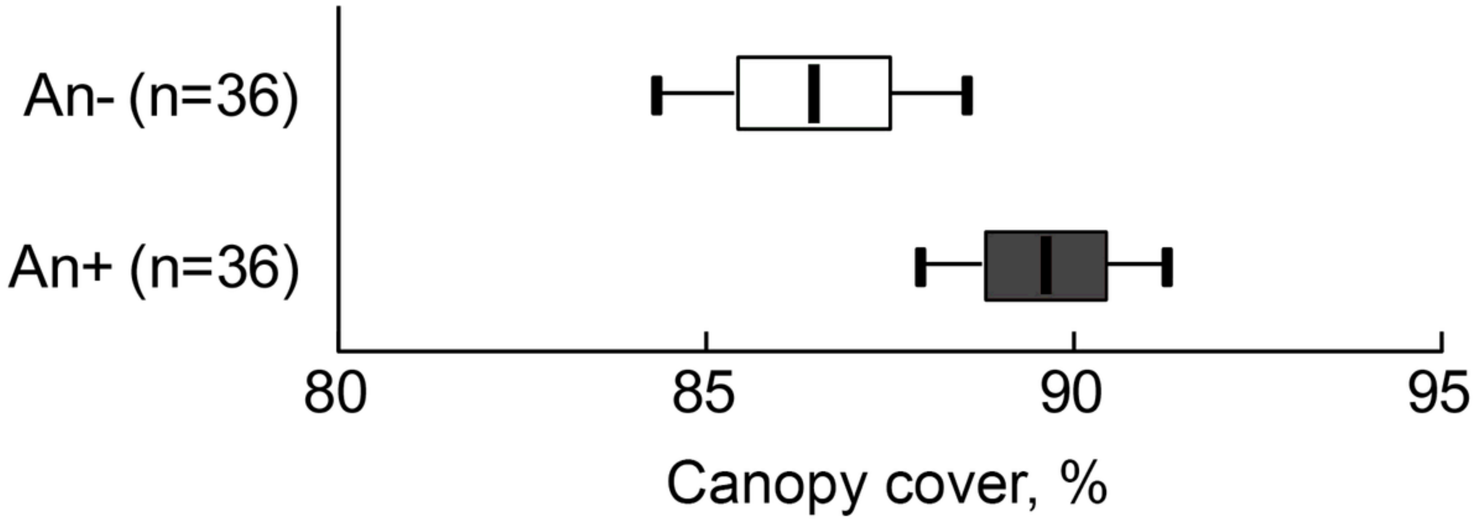

Figure 2

Average rates (±SE, ±95CI) of canopy cover in communities dominated by Acer negundo (An+; dark-grey plots) and other tree species (An-; white plots)

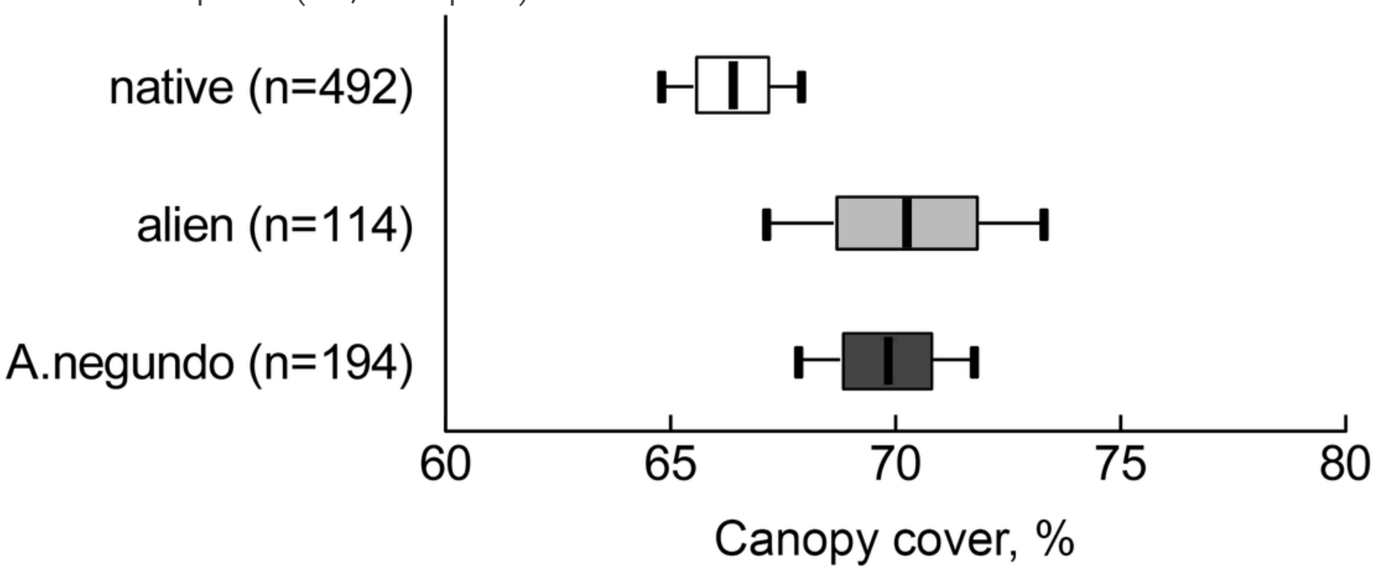

Figure 3

Average rates (±SE, ±95CI) of canopy cover in areas dominated by native (white plots), alien, excluding Acer negundo (white plots) species and individually –Acer negundo (dark-grey plots)

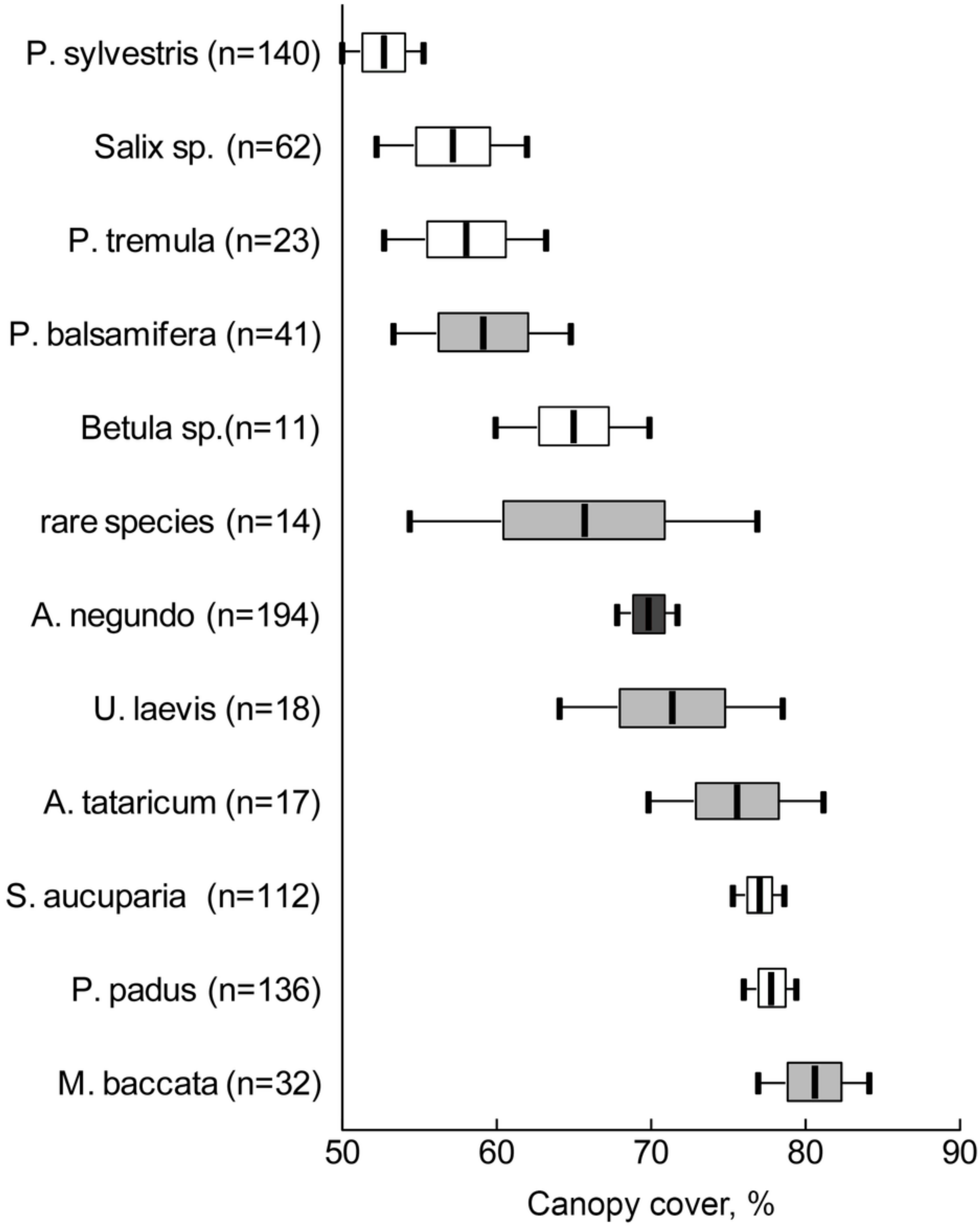

Figure 4

Average rates (±SE, ±95CI) of canopy cover of different species of native (white plots) and alien (white and dark-grey plots) tree species; rare species – the indication for a group of plots dominated by species rarely found in the studied site (Amelanchier spicata, Caragana arborescens, Cotoneaster lucidus, Crataegus sanguinea, Larix sibirica, Lonicera xylostella, Tilia cordata)

Figure 5

Average rates (±SE, ±95CI) of species' number per 400 m2 in communities dominated by Acer negundo (An+; dark-grey plots) and other tree species (An-; white plots)

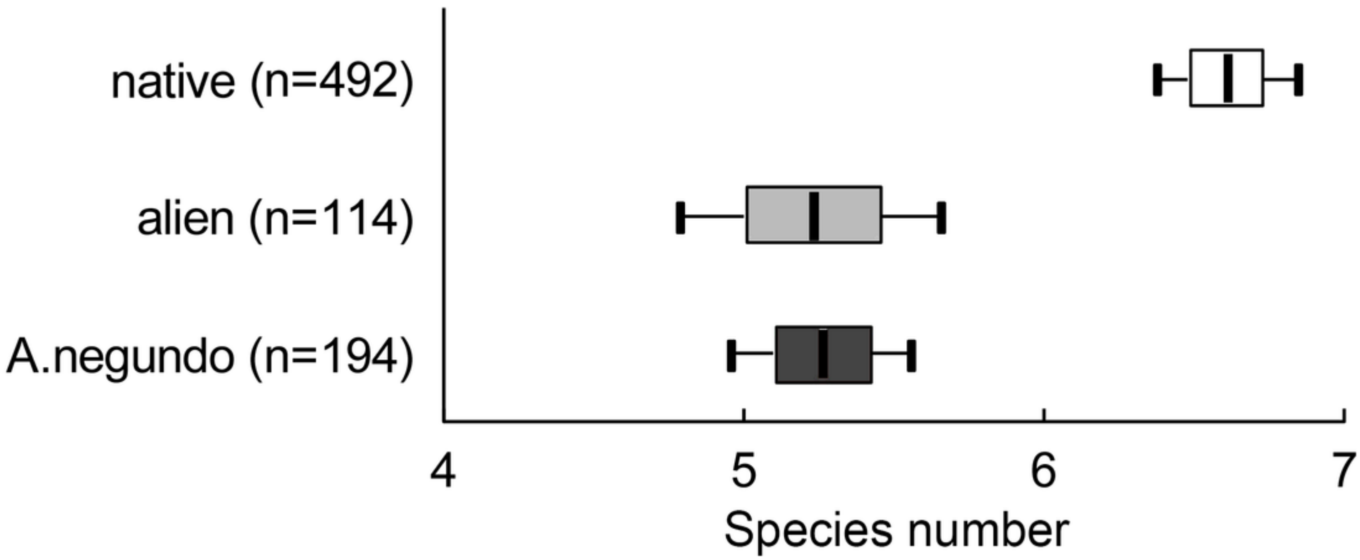

Figure 6

Average number (±SE, ±95CI) of observed ground cover species per m2 on plots dominated by native (white plots), alien, excluding Acer negundo (light-grey plots) species, and individually – on plots dominated by Acer negundo (dark-grey plots)

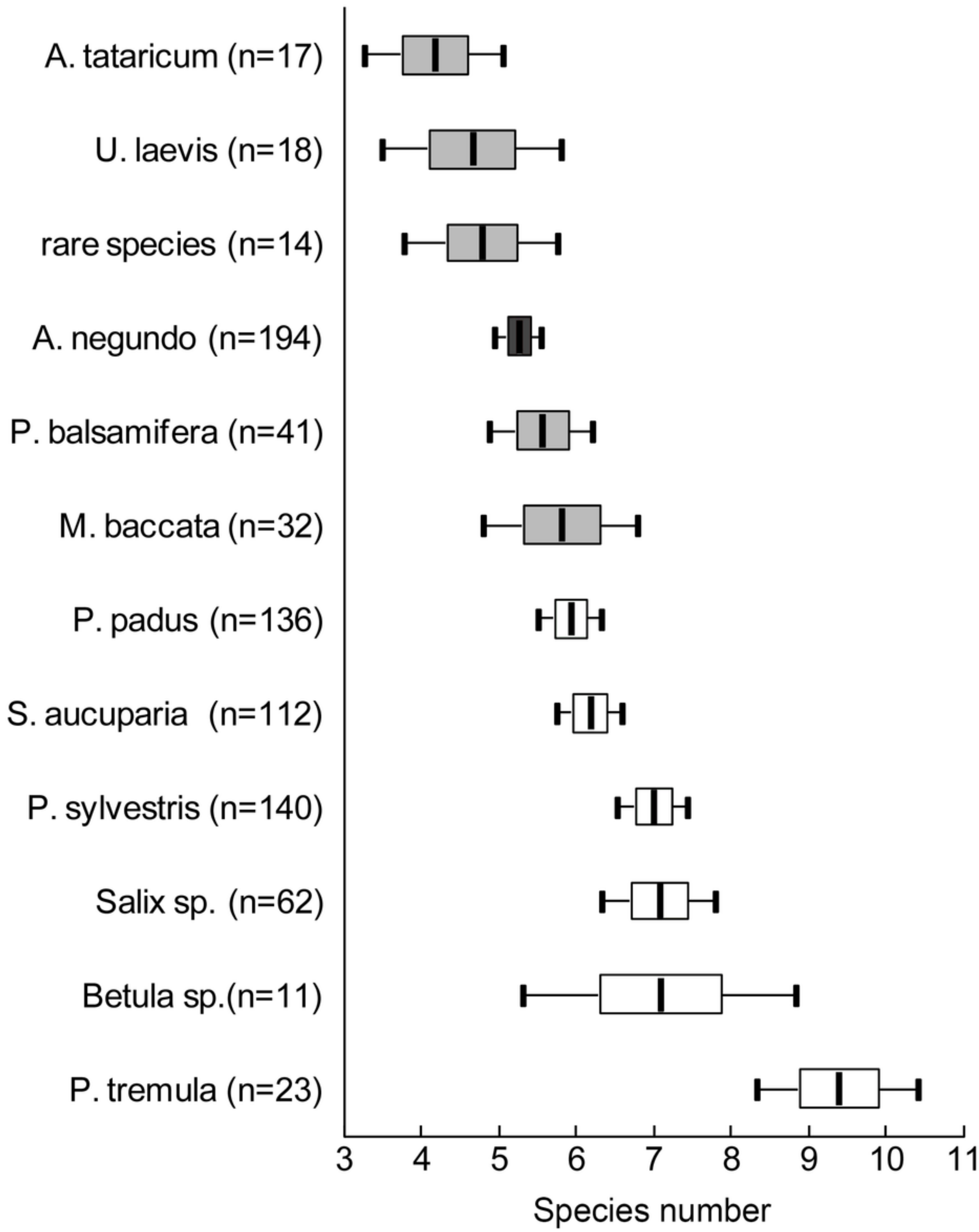

Figure 7

Average number (±SE, ±95CI) of observed ground cover species per m2 on plots under the canopies of different native (white plots) and alien (light-grey and dark-grey plots) tree species; rare species – the indication for a group of plots dominated by species rarely found in the studied site (Amelanchier spicata, Caragana arborescens, Cotoneaster lucidus, Crataegus sanguinea, Larix sibirica, Lonicera xylostella, Tilia cordata)

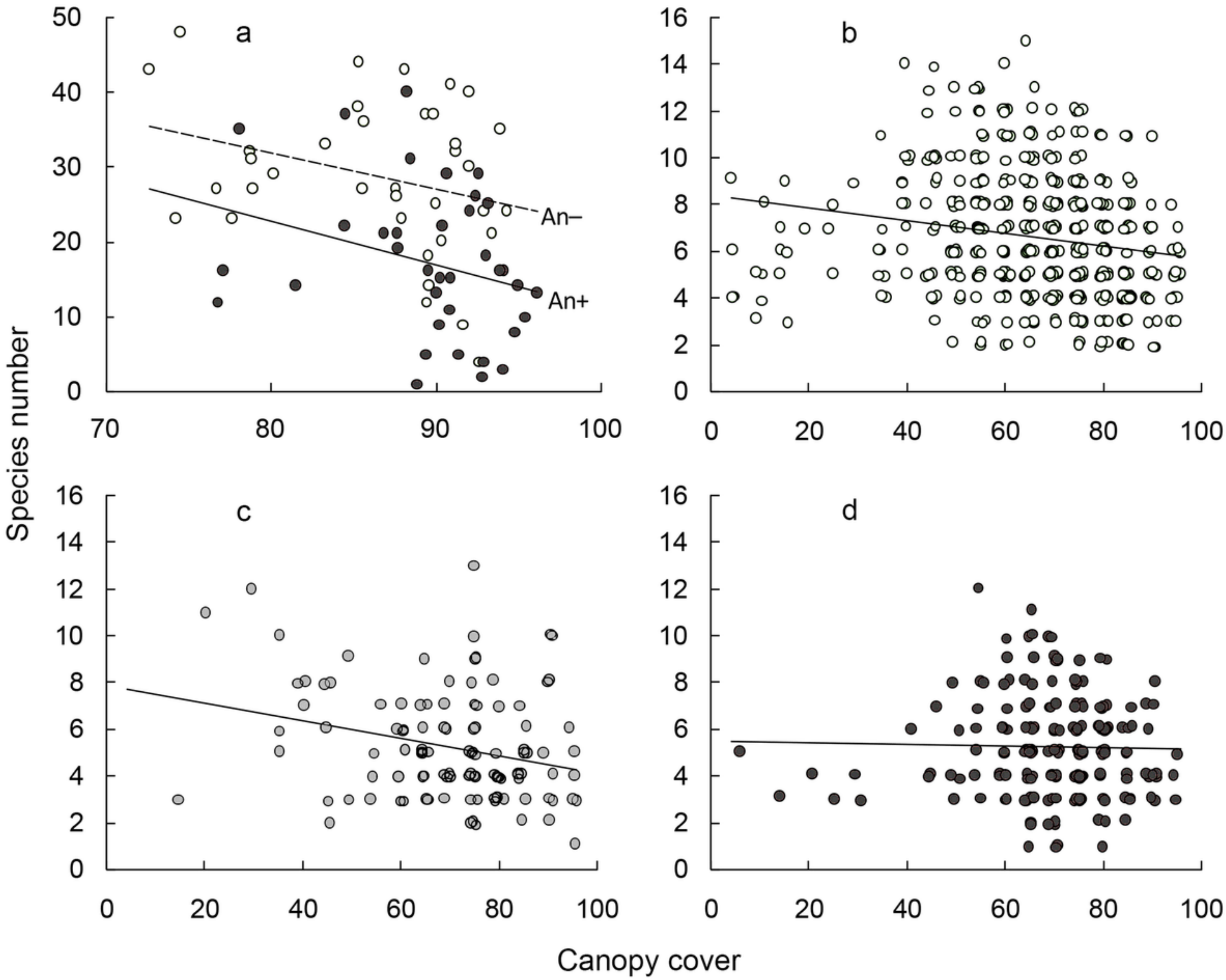

Figure 8

Relationship between the average canopy cover and the number of ground cover species per 400 m2 (inter-habitat comparison) (a) and per 1 m2 (intra-habitat comparison) at plots dominated by native tree species (white circles) (b), alien tree species, excluding Acer negundo (light-grey circles) (c), and individually –Acer negundo (dark-grey circles) (d). The points are slightly jittered to avoid overlapping on Figures b-d

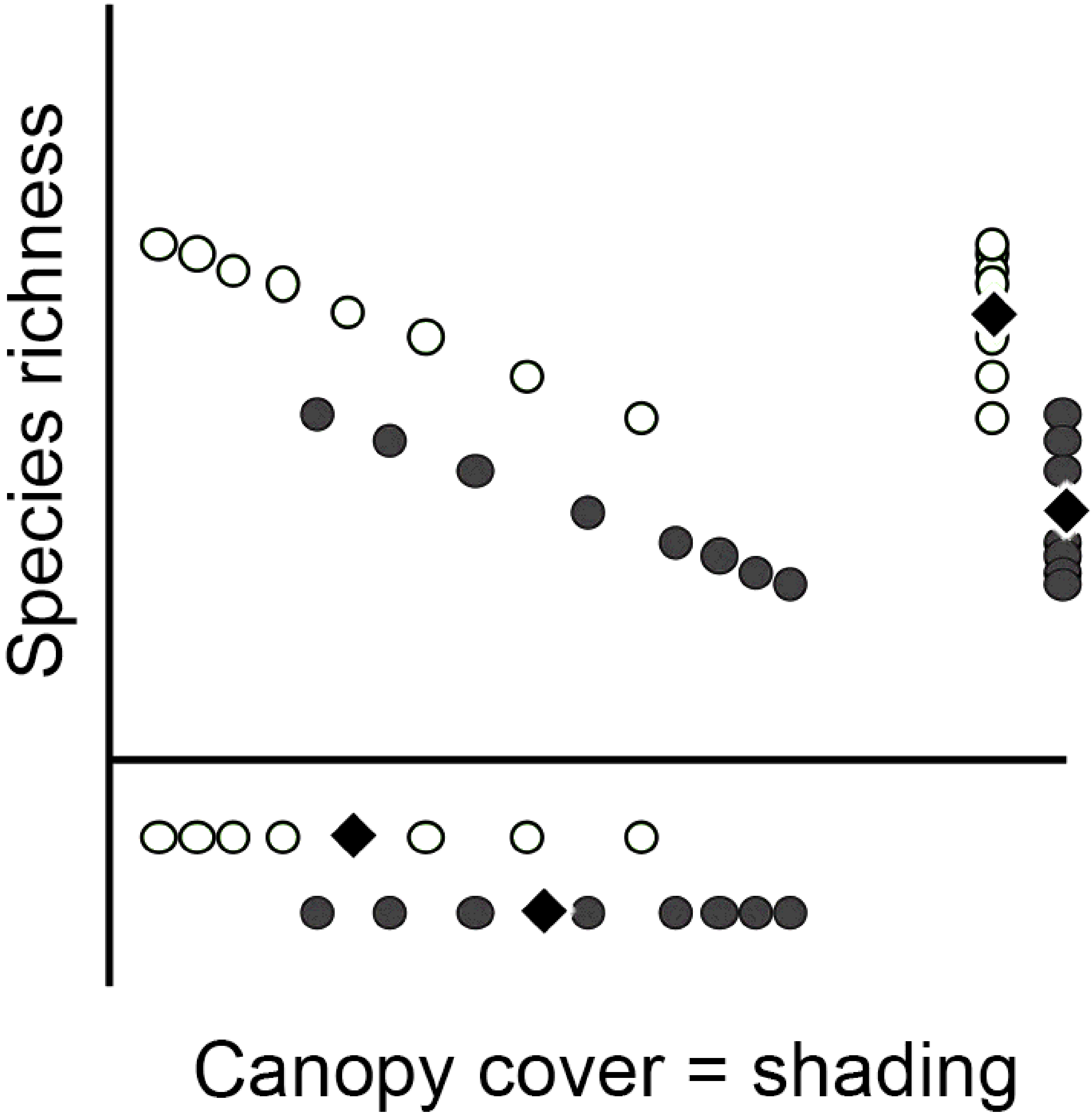

Figure 9

A probable mechanism of the generation of reduced diversity of the ground cover throughout canopy shading in communities dominated by Acer negundo (dark-grey circle) in comparison with other trees (white circle); rhombus – average rates