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MASTERARBEIT

Titel der Masterarbeit

**„Comparison of herbivore communities on the native Field Maple
Acer campestre (L.) and the neophyte Box Elder *Acer negundo* (L.)“**

Verfasserin

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Zusammenfassung

Der Eschenahorn, *Acer negundo* (L.), wurde vor über 300 Jahren als Zierpflanze aus Nord-Amerika eingeführt und wurde mit der Zeit ein invasiver Neophyt in Auwäldern entlang der europäischen Flüsse. Die mit dem Eschenahorn in Europa assoziierte Arthropodenfauna ist noch wenig bekannt. Ziel der Arbeit war es zu untersuchen, ob *A. negundo* (1) eine geringere Herbivorenabundanz aufweist; (2) eine andere Herbivorengemeinschaft beherbergt, die (3) durch Generalisten dominiert wird; und (4) weniger durch Blattfraß herbivorer Wirbelloser geschädigt wird, im Vergleich zu dem einheimischen *A. campestre*. Ich habe mittels Klopfmethodik herbivore Invertebraten von 42 Baumindividuen des einheimischen Feldahorns *A. campestre* und des invasiven Eschenahorns *A. negundo* gesammelt. Die Probennahmen erfolgten alle zwei Wochen über vier Monate (Mai bis August 2011) in einem Auwald des Nationalparks Donau-Auen in der Nähe von Orth an der Donau. Zusätzlich wurden verschiedene Baum- und Habitatparameter aufgenommen, wie z.B. Baumhöhe, Brusthöhendurchmesser oder die Distanz zum nächsten Waldrand bzw. Gewässer. Insgesamt wurden 4342 herbivore Invertebraten aus 100 Arten gesammelt und analysiert, um Abundanz, Artenreichtum, Diversität, Wirtspflanzenspezifität und Artenzusammensetzung zu beschreiben. Um den Blattfraß durch Herbivorie zu quantifizieren, wurden 630 Blätter (15 per Baumindividuum) markiert und über die gesamte Vegetationsperiode fotografiert. *Acer negundo* zeigte trotz geringerer Herbivorenabundanz in den Klopfproben einen ähnlich hohen relativen Blattflächenverlust wie *A. campestre*. Ich beobachtete sechs Mal mehr spezialisierte Herbivore an *A. campestre* (19 Arten, 281 Individuen) als an *A. negundo* (7 Arten, 40 Individuen). Die Artengemeinschaften von Insekten an *A. negundo* wurden größtenteils von Generalisten dominiert. Zudem konnte ich zeigen, dass die Artenzusammensetzung auf den beiden Baumarten in unterschiedlicher Weise durch Umweltfaktoren beeinflusst wurde. Monophage Arten wurden demnach am Stärksten durch die Ahornart beeinflusst, wohingegen die Artenspektren polyphager Herbivorer stärker von der Größe der Bäume und deren Standorteigenschaften (Risiko von Überschwemmungsereignissen, Bestandesstruktur) beeinflusst waren. Meine Ergebnisse weisen darauf hin, dass die Integration

des invasiven Neophyten *Acer negundo* in das Nahrungsnetz des Auwaldes der Donauauen noch nicht vollständig abgeschlossen ist.

Schlüsselwörter: Neophyt; invasive Art; herbivore Insekten; Donau-Auen; Generalisten; Spezialisten; Blattflächenverlust; "enemy release"; *Acer negundo*; *Acer campestre*

Abstract

Box elder, *Acer negundo* (L.), was introduced from North America to Europe more than 300 years ago as an ornamental and later became an invasive tree, mainly in riverine forests. The invertebrate fauna associated with *A. negundo* in its European range remains largely unknown. The aims of this study were to assess whether *Acer negundo* (1) may profit from a lower herbivore load; (2) has a different herbivore community structure, (3) which is dominated by generalist feeders; and (4) may be overall less damaged by herbivores than the co-occurring native *A. campestre*. I collected herbivore invertebrates from 42 trees of the invasive alien *A. negundo* and its native congeneric species *A. campestre*. Sampling occurred every two weeks by means of the beating method over four months (May to August 2011) in the Danube floodplain forest near the village Orth an der Donau. Furthermore different tree and habitat descriptors (e.g. tree height, diameter at breast height, distance to the nearest forest edge and water body) were measured. In total I recorded 4,342 herbivore invertebrates (100 species) and analyzed them to describe the herbivore load, species richness, diversity, host specificity and composition of the herbivore communities on each tree species. I also recorded the leaf area loss on 630 leaves (15 leaves per tree individual) over the whole vegetation period by means of digital photographs to quantify the magnitude of herbivore damage. In spite of its lower herbivore numbers *Acer negundo* showed a similar proportional leaf damage as the native *A. campestre*. The proportion of specialized herbivores was six times higher on the native tree (19 species, 281 individuals) than on the invasive one (7 species, 40 individuals). Insect assemblages on *A. negundo* were dominated by generalist feeders. Herbivore species composition on the two tree species responded differentially to habitat descriptors. For specialized species the most influencing factor

was the maple species. For polyphagous species tree species rather unimportant but tree and site characters affected species composition (i.e. likelihood of flooding events, forest structure). This study suggests that the integration into the food web of the invasive alien *Acer negundo* in the Danube floodplain forest is not yet complete.

Keywords: alien plants; invasive species; insect herbivores; Danube floodplain forest; generalists; specialists; leaf area loss; enemy release; *Acer negundo*; *Acer campestre*

Introduction

Neobiota are one of the main reasons of biodiversity decline in the world (e.g. Kowarik & Starfinger, 2001; Kowarik, 2003; Hulme, 2007). They cause high financial costs for monitoring, management and control measures and thereby also represent a significant socioeconomic challenge (Colautti et al., 2006; Olson, 2006). In Austria there occur at least 225 well established alien plants (Essl & Rabitsch, 2002), of which 112 species (76 neophytes and 26 archeophytes) have thus far been found in the National Park "Donau-Auen" (Drescher & Magnes, 2002). Hence, alien plants nowadays comprise about 13% of vascular plant biodiversity in this nature reserve (Drescher & Magnes, 2002). One of these non-native plant species is the North American box elder tree *Acer negundo* which was introduced as an ornamental garden, road-side and park tree in Europe in 1688 (Wein, 1931; Kowarik, 1992). Since the beginning of the 19th century this tree species has spread mainly in anthropogenically disturbed areas, including softwood floodplain forests along rivers. Box elder were rated in Austria as an invasive species first in 2002 (Drescher & Magnes, 2002; Essl & Rabitsch, 2002; Walter et al., 2005). Therefore, management plans are now implemented to control its further distribution, for example in the national parks "Thayatal" and "Donau-Auen" (Drescher & Magnes, 2002; Essl & Hauser, 2002).

The Danube east of Vienna is one of the last near-natural, extensive and free-flowing rivers in the middle of Europe (Lazowski, 1997). Its associated floodplain forest is characterized by dynamic processes triggered through the annual high water

in summer, caused by alpine snow-melt (Lazowski, 1997). Such disturbance regimes support the formation and persistence of open gravel and sand banks, where specialized flooding-tolerant pioneer plant communities can establish (Lazowski, 1997; Gepp, 1986). In these dynamic open habitats box elder *Acer negundo* can establish highly efficiently. In its native range this very fast growing pioneer tree utilizes a broad range of habitat types (Mędrzycki, 2011).

The fast spread of an alien plant frequently has a negative impact on autochthonous ecosystems, i.e. biodiversity decline or loss (via hybridization), competitive displacement of native species, changes in (abiotic and biotic) habitat conditions, including the deprivation of the nutrition basis for a certain specialist fraction of the native fauna (Schuldes & Kübler, 1991; Kowarik, 1995, 1996), and other ecosystem functions (e.g. Olden & Poff, 2003; Sax & Gaines, 2003; Hulme, 2007; Pyšek et al., 2009; Winter et al., 2009; Vilà et al., 2000, 2009, 2011). However, in some rare cases the invaders apparently do not cause any detectable ecological and economic threats (Kendle & Rose, 2000; Tecco et al., 2006; Gozlan, 2008) or even have beneficial effects (D'Antonio & Meyerson, 2002; Davis et al., 2011; Schlaepfer et al., 2011). In the case of the Danube floodplain forests, *Acer negundo* has a negative influence on the silver willow floodplain in open and disturbed habitats (Drescher et al., 2005). Due to its fast germination and growth rate (Mędrzycki, 2011; Porté et al., 2011) it can rapidly build a second lower tree layer which is increasing canopy cover and consequently reduces the growth and establishment of light-demanding young willows and other pioneer plants (Essl & Rabitsch, 2002; Porté et al., 2011).

In the last decades, several studies attempted to explain the exceptional and undesirable success of introduced non-indigenous plants, which spread very fast and often invasively into a new ecosystem. The enemy release hypothesis predicts that natural enemies of an invading organism do not yet exist in a just recently colonized habitat due to the absence of a common co-evolutionary history between the invader and native enemies (Darwin, 1859; reviewed in e.g. Keane & Crawley, 2002; Torchin et al., 2002, 2003; Mitchell & Power, 2003). Accordingly, lower infestation by phytophagous insects, parasites and diseases may confer a competitive advantage to aliens, fostering their success and survival in comparison to native plant species.

However, it can be expected that taxonomically related plant species with a similar architecture and phytochemistry can be integrated more easily in the dietary range of herbivores than taxonomically unrelated species (Neuvonen & Niemelä, 1983; Frenzel & Brandl 2001; Novotný et al. 2002a, 2002b). In fact, no single hypothesis may exclusively explain the structure of herbivore communities on invasive plants, but rather several factors may act in concert.

The identification of invaders' traits and different establishment mechanisms has been one of the main topics in invasion ecology (Davis et al., 2000; Daehler, 2003; Seastedt & Pyšek, 2011). Most studies on introduced alien plants in Europe are concerned with the role of biotic interactions of an invader with the community of native herbivorous insects (Brändle et al., 2008; Saccone et al., 2010), the first appearance of an invasive alien species in the adventive area, or why certain ecosystems are more susceptible to alien plants than others (Kolar & Lodge, 2001; Keane & Crawley, 2002). So far, only few studies compared abundance, species richness and species composition of insect communities between invasive alien plants and native congeners (Goßner, 2004; Frenzel et al., 2000). Such studies revealed differences as well as similarities, depending on the focal plant pairs. Schmitz (1995, 1998b) compared insects associated with alien species of the herbaceous genus *Impatiens* with those on the native *Impatiens noli-tangere* in Central Europe and found no differences between the alien and the native plant species. Later, Schmitz (2007) recorded for the first time a host plant range extension of two monophagous species towards the invasive *Impatiens* plant. Frenzel and Brandl (2003) studied species richness and abundance of ecto- and endophagous herbivore insects on native and alien herbaceous Brassicaceae plants in Germany and also found no differences in herbivore load and species richness.

In the present study I examined the invertebrate herbivore communities (ectophages and endophages) of two syntopic maple tree species, the invasive *Acer negundo* and the native *A. campestre*, in a floodplain forest in eastern Austria. The invasive *A. negundo* (1) may profit from a lower herbivore load; (2) is expected to have a different herbivore community structure, (3) which is dominated by generalist feeders; and (4) may be overall less damaged by herbivores than the co-occurring native *A. campestre*. Besides allowing for testing these hypotheses, my data will

provide evidence to what extent *A. negundo* is integrated into the food-web of the Danube floodplain forest and if the species has a competitive advantage, compared to a native tree species, due to a lower infestation by herbivores.

Material and Methods

Study area and sites

The study area was situated on the left bank of the river Danube, near the village Orth an der Donau (48°9' N, 16°42' E) in Lower Austria (Fig. 1). The area stretched more than 2 km along the floodplain forest of the Danube side arms "Kleine Binn" and "Große Binn", between the flood protection dam and the main river bed. The area is characterized by near-natural flood dynamics (periodic flooding of various intensity, which occurs most of the time in late spring and early summer induced by the snowmelt) (http://www.doris.bmvit.gv.at/pegel_und_seichtstellen/jahresverlauf/; Tockner & Stanford, 2002; Tockner et al. 1998) and shows a well preserved floodplain forest with many flooding-tolerant trees, e.g. white poplar and willow stocks (Margl, 1972; Margl, 1973). Herbivore insect faunas (e.g. moths) of the area are known to differ substantially between regions with or without regular risk of flooding events (Truxa & Fiedler, 2012).

In 1983 the floodplains of the rivers Danube and March were designated by the RAMSAR Convention as protected wetland area (BGBl. Nr. 225/1983). Around ten years later, in 1996, the area was declared as National Park "Donau-Auen" (BGBl. Nr. 653/1996), and some parts of the region were designated according to the European Flora and Fauna directive as Natura 2000 sites (Teufelbauer & Frank, 2009).

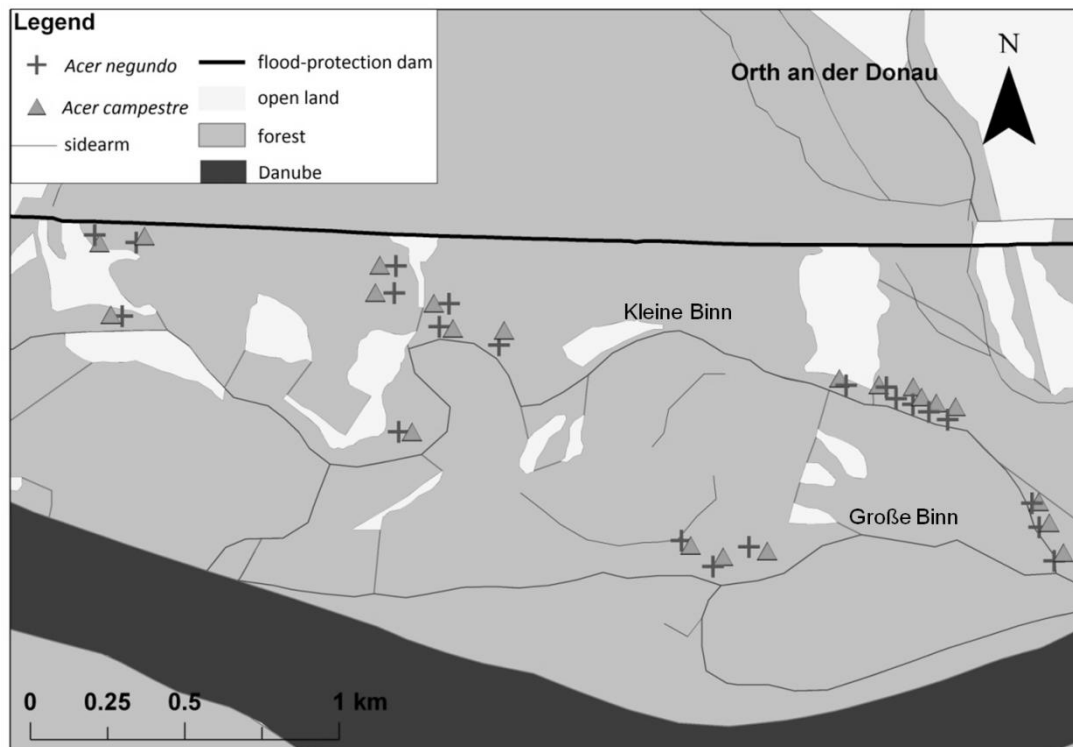


Figure 1. Study area (situated about 15 km east of Vienna in the NP Donau-Auen) indicating the location of the 21 sampled *Acer campestre* (triangles) and 21 sampled *Acer negundo* (crosses) trees.

Field work started in April 2011 with the selection of 21 trees of *Acer campestre* (AC) and *A. negundo* (AN), respectively. Selected trees were <5 m tall, with an approximately equal crown size. Sampling sites were selected to comprise of one tree of each *Acer* species located at a distance of <50 m to each other (N = 21 pairs) to minimize possible site effects. The distance between sampling sites was >50 m. All selected tree individuals were marked with an ID number and their location was measured with a Garmin GPSmap 60 CSx device. The selected 21 tree pairs were periodically sampled every two weeks from early May 2011 to late August 2011. This period represented the main vegetation and growing season.

Study species

Field maple *Acer campestre* (L.) (Sapindaceae) is a monoecious (Fischer et al., 2005) and predominantly insect pollinated tree (Knuth, 1898; Hesse, 1979) native to hardwood floodplain forests of Eurasia and Northwestern Africa (Hoffmann, 1960).

Field maple can be found at a broad range of sites, can reach a height up to 20 m and may reproduce from an age of 15-25 years onwards (Hoffmann, 1960; Fischer et al., 2005). *A. campestre* grows as a tree or shrub in hedgerows and the understory of forests.

Box elder *Acer negundo* (L.) (Sapindaceae) is a dioecious (Fryxell, 1957; Schütt et al., 2000) and wind pollinated tree (Daumann, 1972). It represents an invasive neophyte (from North America) in Austrian softwood floodplain forests (Fischer et al., 2005). Box elder also can establish at a broad range of sites, reaches a height up to 20 m and is able to reproduce from a young age of 5 years onwards (Rosario, 1988; Mędrzycki, 2011). *A. negundo* often grows as a multi-stemmed tree in the understory of alluvial forests. Both *Acer* species are frequently found in close proximity to each other in the softwood and hardwood floodplain forests of the Danube. However, due to its invasive status, recently implemented management measures aim to reduce the density of *A. negundo* within the national park borders (Drescher & Magnes, 2002).

Tree and habitat descriptors

For each selected tree, various parameters were measured (Table 1) to describe its status and the site conditions around each sampled tree individual.

Table 1. Tree and habitat descriptors measured for each individual of *Acer campestre* (AC) and *A. negundo* (AN).

Parameter	Measure unit
Tree height	m
Diameter at breast height (DBH)	m
Canopy closure	%
Distance to nearest forest edge	m
Distance to nearest permanent waterbody	m
Other AN specimens	number of individuals
Other AC specimens	number of individuals
Tree vitality	rank scale 1 to 5
Herb layer cover	%

Tree height, tree vitality (ranked on a scale from 1 (very good condition) to 5 (single dead branches, some twigs without leaves)) and herb layer cover below the tree crown (after the foliation of the study species) were visually estimated. The tree diameter at breast height (DBH) was measured with a tapeline. Other individuals of

both *Acer* species (with a minimum DBH = 4 cm) were counted within a radius of 5 meters around sampled trees. Canopy closure was measured using one digital photograph of the canopy above each sampled tree taken with a Canon Powershot SX100IS and analyzed with the program ImageJ 1.44p (Rasband, 1997-2005). For this, photographs were converted into 8-bit pictures and the contrast was set higher. Subsequently the files were converted into binary pictures and the percentage of black pixels was calculated as measure for canopy closure. The distance to the nearest forest edge and waterbody, respectively, was extracted from digital maps with the geographic information system program ArcGis 9.0 (ESRI, 2008).

Insect sampling and analysis

Herbivore insects were collected with the beating method after Bodner et al. (2010) using a beating tray (1 m²) lined with a white cloth attached to the frame of an umbrella drop net. To standardize the beating procedure and sampling effort, I sampled only reachable branches (up to 2 m above ground) with a similar leaf area. Every selected branch was beaten 2-5 times (conditional on the thickness of the branch). All insects were immediately collected with an exhaustor from the beating tray and stored in 90% ethanol, except for larval stages of the order Lepidoptera. These larvae were collected alive in plastic containers to rear them to the adult stage. After beating, all tree individuals were visually searched for plant galls, leaf miners and snails for 10 minutes per each sampling round.

All sampled insects and gastropods were first sorted to order, family, sub-family, and herbivores finally to species level using a Nikon SMZ645 stereomicroscope. Coleoptera were identified using Freude et al. (1966-1983), Hemiptera using Wagner (1966, 1967), Kunz et al. (2011) and Biedermann & Niedringhaus (2004), and Lepidoptera using Ebert et al. (1994-2005), Razowski (2002, 2003) and Huemer & Karsholt (1999). Specimens which I could not identify to species level were sent to specialists of the relevant taxonomic groups.

All arthropods and gastropods were classified by their feeding mode as herbivores (phytophagous or zoo-phytophagous) or non-herbivores (zoophagous or other nutrition). Non-herbivores (1,553 individuals) were not further considered and

not determined to species level. In a second step, herbivores were categorized as monophagous (feeding only on the plant genus *Acer*), or polyphagous (feeding on *Acer* and more host-plants) using various sources (Freude et al., 1966-1983; Ebert et al., 1994-2005; Reiter, 1916; Razowski, 2002-2003; Nickel & Remane, 2002; Wagner, 1966-1967; Urban, 2010; Parenti, 2000). All sampled herbivore arthropods which specifically feed on plants other than *Acer* (according to literature) were classified as 'tourists' (altogether 440 individuals, 63 species) and were not considered in the further analyses.

To quantify infestation by plant galls and leaf miners, infested leaves (only those visible from the ground) were counted on each tree. Leaf miners were identified using Hering (1953) and Bradley et al. (1970). Plant galls were identified using Bellmann (2012).

In order to quantify the leaf area loss of the two *Acer* species, 15 leaves were marked per tree with a green colored tape and were digitally photographed at every sampling round. In total 315 leaves per *Acer* species were marked. Leaf area loss was quantified with the program Adobe Photoshop CS4 Extended (Adobe Systems, 2008) by measuring the total leaf area and the leaf area loss for each tree individual of both *Acer* species. For every sampling round the following variables were calculated from these data: total leaf area (cm²), total leaf area loss (cm²), and relative leaf area loss (%). All leaves which could not be recovered in the field, fell off the tree, or became withered during the sampling period were excluded of the data set at this time and not considered in the further analyses.

Data analysis

Data was checked for normal distribution with the Kolmogorov-Smirnov test and transformed using \sqrt{x} or $\arcsin \sqrt{x}$ transformations, if required to meet normality assumptions.

Taxonomic groups which had enough species for separate analyses were the Coleoptera, Hemiptera, Lepidoptera and Pulmonata. Ensifera, of which I found but one species on both trees, were considered only for calculations with the total

number of herbivore arthropods. For abundance comparisons I considered all herbivores (adult and larval), which are either specific *Acer* feeders (according to the literature) or are polyphagous species (viz. including all species that I could not reliably assign to the group 'tourists'). For diversity analyses, all taxa (adults as well as larvae) were used which I could identify to species level. 'Tourists' were not considered in any analyses.

A repeated-measures ANOVA was calculated to compare herbivore abundance and relative leaf area loss over time (7 sampling rounds) between both *Acer* species. To compare species richness on the two *Acer* species individual-based rarefaction curves were calculated with the program Past 2.14 (PALSTAT, Oslo; <http://folk.uio.no/ohammer/past/>), together with 95% confidence boundaries (CI). Species diversity of all herbivore arthropods on *Acer campestre* and *A. negundo* was expressed through the exponential bias-corrected Shannon diversity and Fisher's α index, both calculated with the program SPADE (Chao & Shen, 2010). These two measures are recommended for diversity analysis in incompletely sampled arthropod communities (Beck & Schwanghart, 2010). Differences between *Acer* species with regard to herbivore abundances, or their feeding impact, were assessed through GLMs using the package Statistica 7.1 (StatSoft, Inc. 2005). In these models I included tree condition as categorical predictor, and tree height, distance to the nearest forest edge (\sqrt{x} transformed) and canopy closure ($\arcsin \sqrt{x}$ transformed) as continuous predictors. Habitat and tree descriptors were tested for multicollinearity before use in multivariate analyses. For continuous predictors the standardized regression coefficients (beta) were used to evaluate the sign of relationships. Differences between tree species were visualized using least-squares means adjusted for covariates.

The relative contribution of host plant specialists to the invertebrate herbivore assemblages of the two *Acer* species was compared with a Mann-Whitney U-test. The incidence of these plant enemies was compared between the two tree species with Fisher's exact test.

Species composition of herbivore arthropods and gastropods on each tree individual of *Acer campestre* and *A. negundo* (i.e. aggregated over the seven

sampling rounds per tree) was compared with multivariate unconstrained and constrained ordination techniques using the program Primer 6 (Clarke & Gorley, 2006). For each insect order and the gastropods I first calculated the Bray-Curtis similarity matrix (analysis between tree individuals, abundance data square-root transformed) and subjected these matrices to non-metric multidimensional scaling (NMDS; 100 restarts, two dimensional ordinations). If collection data was very sparse (i.e., most entries were zero), I introduced a dummy species (with an abundance of $N=1$) at all trees. This procedure stabilizes similarity relations and avoids the elimination of thinly occupied trees from the data which otherwise may lead to erratic results (Clarke et al., 2006). This addition of a dummy species was done for all orders, except for the matrix of all herbivore arthropods (which was sufficiently rich in data). These matrices were also used for the distance-based linear models (described below). Differences of herbivore communities between both *Acer* species were examined for statistical significance using a one-way analysis of similarities (ANOSIM). Subsequently a multivariate dispersion index (MVDISP routine in Primer 6) was calculated for the herbivore arthropods and gastropods of the two *Acer* species, to assess variability (i.e. relative dispersion) among trees. The resulting pair wise "index of multivariate dispersion" (IMD) measures if invertebrate communities on one *Acer* species were less variable among trees than on the other species. Spearman matrix rank correlations were computed (999 permutations) between the Bray-Curtis similarity matrices for the major insect orders (Lepidoptera vs. Hemiptera, Lepidoptera vs. Coleoptera, and Coleoptera vs. Hemiptera) to compare the degree of faunal concordance.

Distance-based linear models (dbRDA: Anderson et al., 2006) were calculated to determine the relative importance of several tree and habitat descriptors for the assemblage composition of insects and gastropods on individual trees of both *Acer* species. Variables were evaluated according to their contribution to adjusted multivariate R^2 in step-wise forward model selections. In all cases, I had observed some very frequent species, so abundances were square-root transformed before calculating the Bray-Curtis matrices. For all data sets (except the matrix of all herbivore arthropods) I also inserted a dummy species (as described above). For

clarity, only those variables included in the best models with a multiple partial correlation coefficient of $r \geq 0.2$ were plotted in the ordination diagrams.

Statistical significance for all tests was set to $p \leq 0.05$. Where appropriate with multiple tests, a table-wide false-discovery rate approach was followed to control for the risk of inflated error rates (Waite & Campbell, 2006).

Results

Herbivore abundance, richness and species diversity

In total 2,453 individuals of herbivore arthropods and 1,889 individuals of gastropods were collected from the 42 trees during seven sampling rounds (Table 2). Of these invertebrates, I sampled 765 larval herbivore individuals on *Acer campestre* of which I was able to identify 241 to species level, and 176 arthropod larvae on *A. negundo* of which I identified 99 individuals to species level. Most of these larvae belonged to the order Hemiptera (AC: 71.8% of total larvae; AN: 58.5%). On *A. campestre* I found 31 tourists individuals (representing 42 species), and on *A. negundo* 205 tourists (belonging to 44 species; 24 shared tourist species). On both tree species these tourists were predominantly comprised of beetles (AC: 86.6% of tourist individuals; AN: 78.5%). I identified 100 different herbivore species (without tourists), 83 on *Acer campestre* and 68 on *A. negundo* (shared species: 51; see Appendix Table A1).

Table 2. Total numbers of collected herbivore invertebrates.

	Species	Individuals	% Larvae
<i>Acer campestre</i>	83	2,768	27.6
<i>Acer negundo</i>	68	1,574	11.8
Sum	100	4,342	21.7

The number of herbivore arthropods per tree was affected significantly by the sampled tree species (ANOVA: $F_{1,40} = 7.55$, $p < 0.01$) and sampling time ($F_{6,240} = 8.26$, $p < 0.001$). There was no significant tree species \times time interaction term ($F_{6,240} = 1.79$, $p = 0.102$). The average number of herbivore arthropods per tree was consistently higher on *Acer campestre*, and seasonal changes of herbivore abundance were similar on both *Acer* species (Fig. 2).

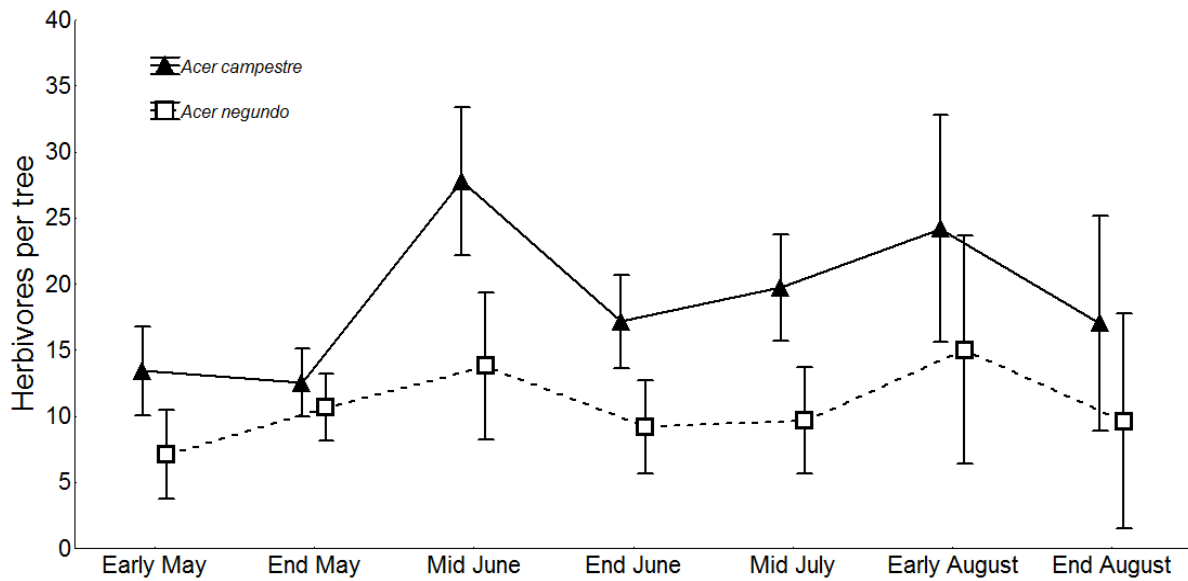


Figure 2. Least square mean numbers of herbivore arthropods \pm 95% CI per tree sample at different times of the season on two *Acer* species.

Individual-based rarefaction curves had a similar shape indicating a nearly identical richness of herbivore arthropods on both *Acer* species after controlling for abundance differences (Fig. 3).

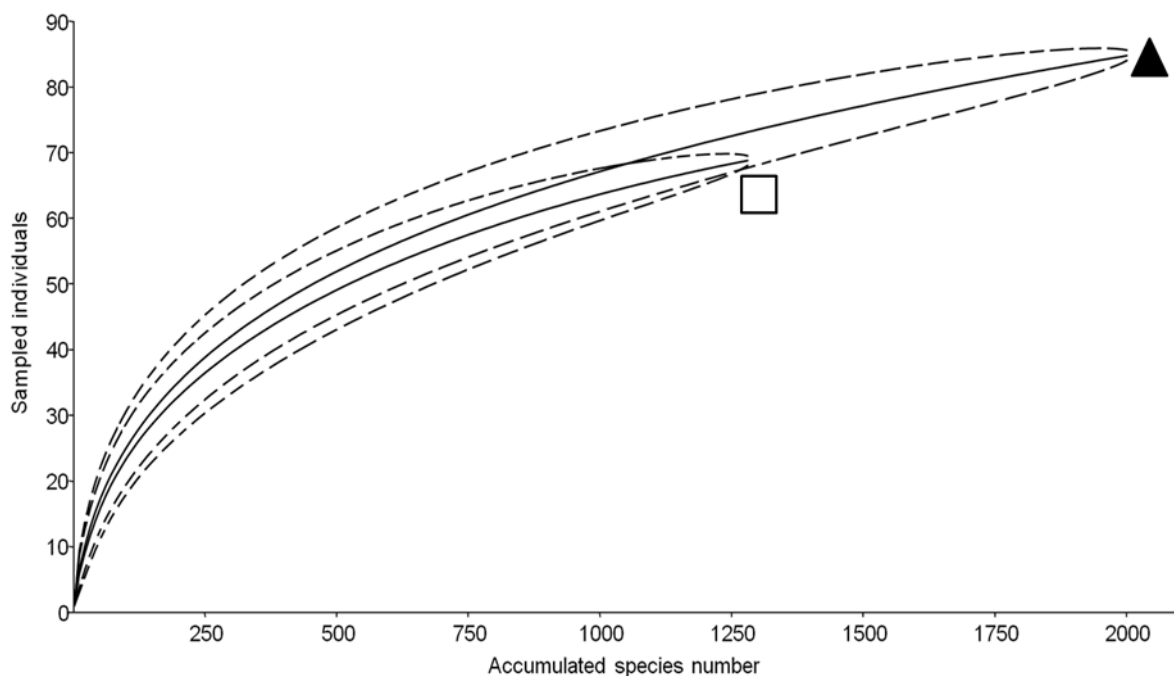


Figure 3. Individual-based rarefaction curves (solid lines) \pm 95% CI (dashed lines) for herbivorous arthropods on *Acer campestre* (filled triangle) and *A. negundo* (open square).

In line with rarefaction results on species richness, alpha diversity of herbivorous arthropods at the tree species level did not differ greatly between *A. campestre* and *A. negundo* (Table 3). Hence, species-abundance distributions of invertebrate herbivores were essentially the same on both tree species. The exponential bias-corrected Shannon diversity calculated for each tree individual also did not differ significantly between the two *Acer* species (t-Test: $t_{40} = 0.419$, $p = 0.677$).

Table 3. Overall abundance, species richness and diversity (Fisher's α , exponential bias-corrected Shannon diversity) of herbivore arthropods (excluding tourists and unidentified larvae) sampled on *Acer campestre* and *A. negundo*.

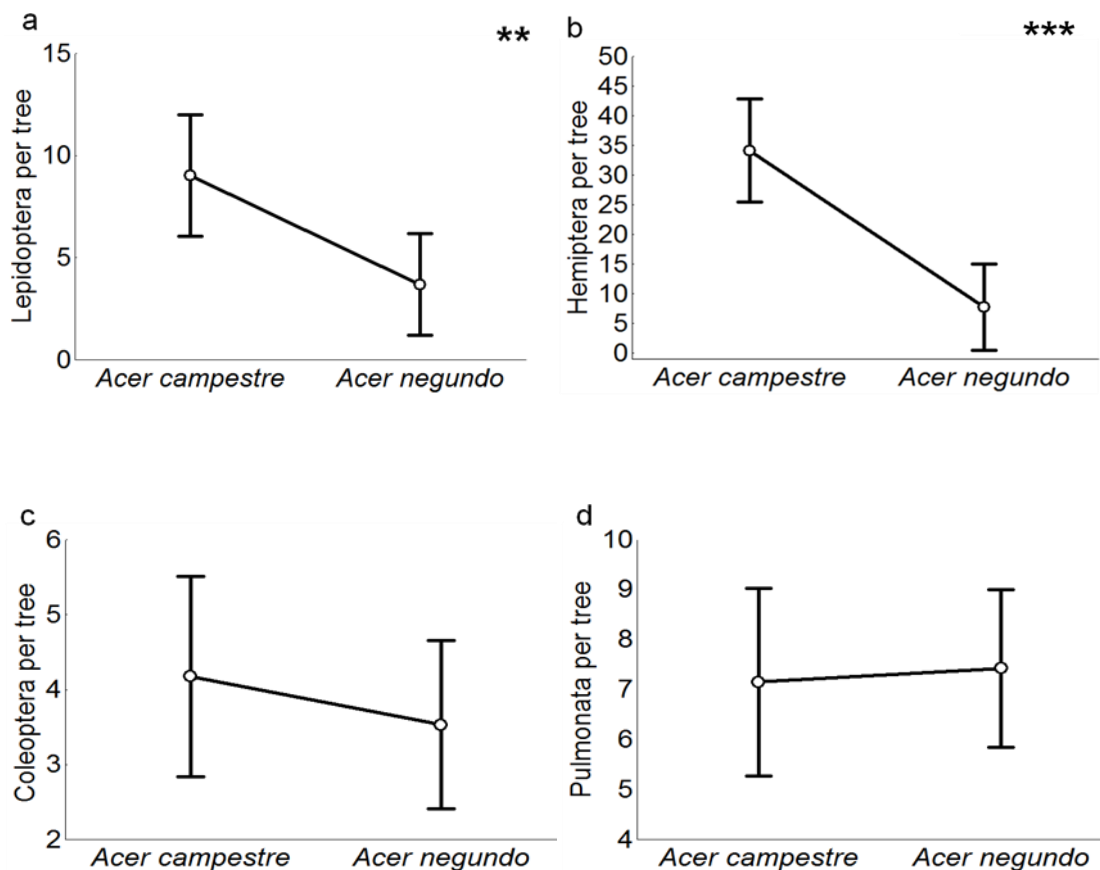
Tree species	Individuals	Species	Fisher's α (\pm SE)	Shannon diversity (\pm SE)
<i>A. campestre</i>	989	80	20.99 (\pm 2.33)	31.92 (\pm 6.12)
<i>A. negundo</i>	441	63	21.04 (\pm 2.61)	33.71 (\pm 3.86)
combined	1430	95	23.61 (\pm 2.39)	37.40 (\pm 3.88)

Herbivore abundance and specificity related to tree and site characters

The results of GLMs testing for effects of various tree and habitat parameters on the abundance of different insect orders, herbivore gastropods, herbivore arthropods, the relative abundance of specialists and the relative leaf area loss are shown in Table 4. Tree species had a significant effect on the abundance of Lepidoptera, Hemiptera, all herbivore arthropods, and the relative abundance of specialists (Table 4). The number of Lepidoptera, Hemiptera and total herbivore arthropods was higher on AC than on AN. Also the relative abundance of specialists was higher on AC. The abundance of beetles or snails and slugs did not differ significantly between both tree species, and also leaf area loss proved to be rather similar in both *Acer* species (Fig. 4). Tree vitality only affected the abundance of herbivore Pulmonata, which showed a prominent increase in abundance on trees classified as being in a very bad condition, even though this effect was just marginally significant (Appendix Fig. A1). Furthermore, the distance of sampled trees to the nearest forest edge was positively (but weakly) related to the abundance of Hemiptera (standardized regression coefficient: $\beta = 0.287$), Pulmonata ($\beta = 0.422$), and leaf area loss ($\beta = 0.438$). Tree height and canopy closure were not identified as significant predictors in any of the calculated GLMs (Table 4).

Table 4. Results of general linear models testing for effects of tree species, tree vitality, tree height, canopy closure and distance to the nearest forest edge on the abundance, relative contribution and feeding impact of herbivores for all 42 *Acer* trees. Nominally significant effects are printed in bold, those persisting after controlling for a table-wide false-discovery rate (Waite & Campbell, 2006) at $p < 0.05$ are printed in red.

Variable	Tree species	Tree vitality	Tree height	Canopy closure	Forest edge
Lepidoptera	$F = 11.26$, $p < 0.01$	$F = 0.12$, $p = 0.977$	$F = 0.03$, $p = 0.858$	$F = 0.01$, $p = 0.916$	$F = 1.64$, $p = 0.209$
Hemiptera	$F = 32.61$, $p < 0.001$	$F = 2.43$, $p = 0.067$	$F = 3.72$, $p = 0.067$	$F = 0.64$, $p = 0.428$	$F = 4.91$, $p < 0.05$
Coleoptera	$F = 0.82$, $p = 0.372$	$F = 0.45$, $p = 0.769$	$F = 0.19$, $p = 0.663$	$F = 0.01$, $p = 0.906$	$F = 0.05$, $p = 0.833$
Pulmonata	$F = 0.08$, $p = 0.786$	$F = 3.24$, $p < 0.05$	$F = 0.28$, $p = 0.599$	$F = 0.01$, $p = 0.939$	$F = 5.36$, $p < 0.05$
Herbivore arthropods	$F = 19.97$, $p < 0.001$	$F = 1.44$, $p = 0.242$	$F = 2.01$, $p = 0.166$	$F = 0.01$, $p = 0.927$	$F = 1.6$, $p = 0.214$
Fraction of specialists	$F = 12.73$, $p < 0.001$	$F = 1.08$, $p = 0.382$	$F = 0.70$, $p = 0.408$	$F = 0.07$, $p = 0.799$	$F = 0.002$, $p = 0.964$
Leaf area loss	$F = 0.36$, $p = 0.551$	$F = 0.76$, $p = 0.558$	$F = 1.39$, $p = 0.246$	$F = 1.21$, $p = 0.279$	$F = 4.97$, $p < 0.05$



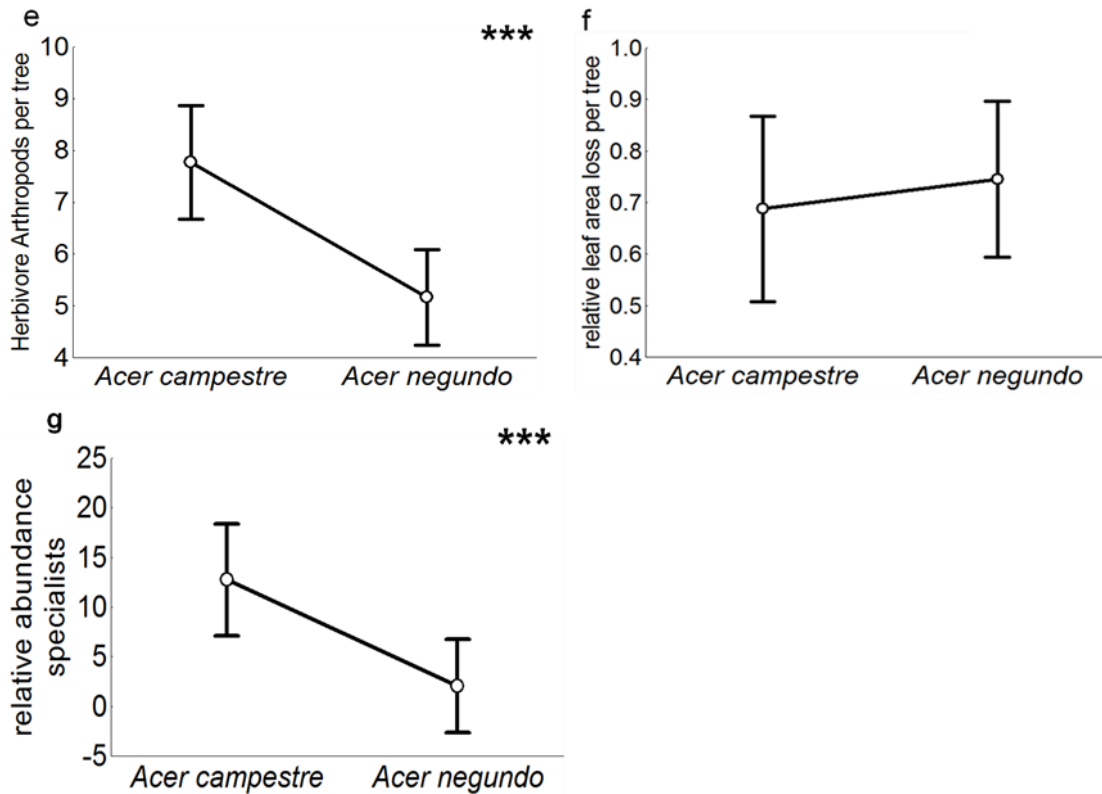


Figure 4. Least square mean (\pm 95% CI) of (a) sum of Lepidoptera individuals, (b) Hemiptera individuals (c) Coleoptera individuals (\sqrt{x} transformed), (d) Pulmonata individuals (\sqrt{x} transformed), (e) herbivore arthropods (\sqrt{x} transformed), (f) relative leaf area loss (arcsin \sqrt{x} transformed) and (g) relative abundance of specialists (%) per tree shown for both *Acer* species. Significant effects of tree species according to GLMs are indicated by asterisks (***) $p < 0.001$, ** $p < 0.01$).

Host specific herbivores

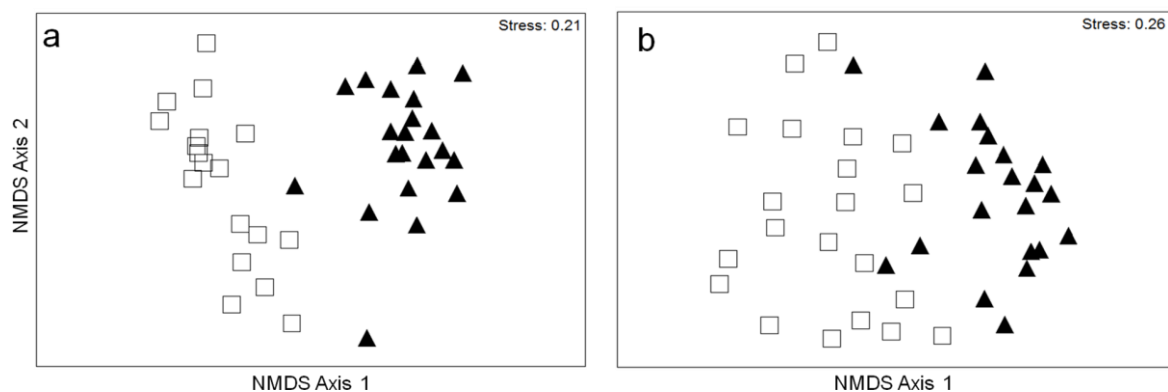
On average about one in six herbivore invertebrates encountered on *A. campestre* was a host-plant specialist, as opposed to less than one in thirty on *A. negundo*. The three most abundant herbivores on *A. campestre* were *Cyclophora annularia* (Geometridae) (69.7% of 176 Lepidoptera individuals), *Drepanosiphum platanoides* (Drepanosiphidae) (9.3%) and *Acericerus ribauti* (Cicadellidae) (8.4% of 416 adult Hemiptera individuals) which are all monophagous on the genus *Acer*. On *A. negundo* I found only one abundant species, *Rhinocola aceris* (Psyllidae) (10.8% of 186 adult Hemiptera individuals).

Infections of trees with plant galls were found significantly more often on *A. campestre* (100% of sampled trees infected) than on *A. negundo* (14.3%; Fisher's exact test: $p < 0.001$). The only plant gall building mite found on *Acer negundo* was 17

Aceria cephaloneus (Arachnida: Acari) which is specialized on the genus *Acer*. A similar result was found for lepidopteran leaf miners. Sixteen *A. campestre* trees (76.2% of 21 trees) were infested, while leaf miners were never found on *A. negundo* trees (Fisher's exact test: $p < 0.001$). *Stigmella aceris* and *S. speciosa* (Lepidoptera: Nepticulidae) were the only two leaf miners found on *A. campestre*.

Species composition of herbivore communities

As indicated by the NMDS ordinations based on Bray-Curtis similarities, the herbivore species composition differed prominently between both *Acer* species. The clusters of native maple trees were clearly more compact than those of the invasive maple (Fig. 5 a-e). For example, the Lepidoptera (Fig. 5a) or Pulmonata (Fig. 5d) on *A. campestre* formed a more homogeneous community, whereas on *A. negundo* the fauna of individual trees was more scattered. The results of ANOSIM tests for effects of *Acer* species on invertebrate species composition indicated significant differences for all orders as well as for the total community of herbivore arthropods. The by far highest value of the test statistic R (0.754) was found for Lepidoptera (Table 5) and the lowest for Coleoptera ($R = 0.117$) and Pulmonata ($R = 0.179$).



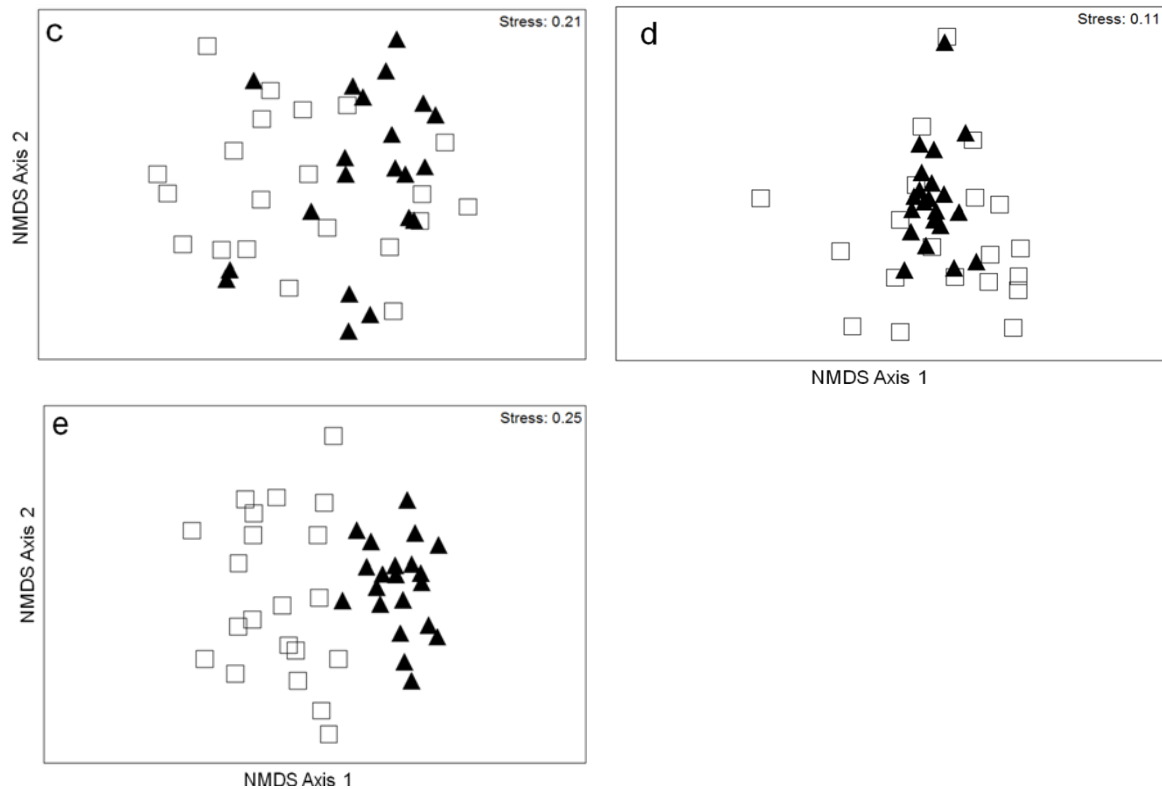


Figure 5. Non-metric two-dimensional scaling plots of herbivore invertebrates based on Bray-Curtis similarities for (a) Lepidoptera (242 individuals; 36 species), (b) Hemiptera (621 individuals, 36 species), (c) Coleoptera (525 individuals, 22 species), (d) Pulmonata (1,757 individuals, 5 species), and (e) the entire assemblage of herbivorous arthropods (1,438 individuals; 95 species) collected on individual *Acer campestre* (filled triangles) and *A. negundo* (open squares) trees.

Table 5. Results of analysis of similarities (one-way ANOSIM) testing for differences in species composition (quantified by Bray-Curtis similarities) of herbivore arthropods and gastropods (999 permutations) between *Acer campestre* and *A. negundo* trees.

	<i>R</i>	<i>p</i>
Lepidoptera	0.754	< 0.001
Hemiptera	0.471	< 0.001
Coleoptera	0.117	< 0.05
Pulmonata	0.179	< 0.001
All herbivore arthropods	0.534	< 0.001

An index of multivariate dispersion (MVDISP) was calculated to quantify how homogeneous the herbivore communities of individual trees are within either of the two *Acer* species. A value below 1 (as on AC) indicates a higher homogeneity of the species composition, and a value above 1 (as on AN) a greater dispersion of communities associated with tree individuals. The dispersion index for *A. campestre* was consistently lower than that for *A. negundo* (as indicated by the negative sign of IMD: Table 6), which fits to the more compact data clouds representing *A. campestre*

in the respective ordination plots (Fig. 5). Accordingly, herbivore assemblages on individual *A. negundo* trees showed far more intraspecific variation than in *A. campestre*.

Table 6. Results of multivariate dispersion (MVDISP) analyses showing the dispersion of herbivore arthropod and gastropod assemblages on *Acer campestre* and *A. negundo* based on Bray-Curtis similarities.

	Relative dispersion		
	<i>Acer campestre</i>	<i>Acer negundo</i>	Pair wise IMD
Lepidoptera	0.945	1.076	-0.131
Coleoptera	0.961	1.039	-0.079
Hemiptera	0.829	1.171	-0.343
Pulmonata	0.697	1.335	-0.639
All herbivore arthropods	0.687	1.313	-0.627

Spearman matrix rank correlations among different taxonomic insect groups indicated a significant relationship only between the Lepidoptera and Hemiptera assemblages collected at individual *Acer* trees. All other combinations were not significantly related (Table 7). Hence, herbivore species turnover between individual trees was reasonably concordant between leaf-chewing caterpillars and sap-sucking hemipterans, which both comprise a high fraction of host-plant specialists (Lepidoptera: 51.5% of 241 individuals; Hemiptera: 32.2% of 602 individuals). Correlations of both these insect groups with less host-specific beetles (0% host plant specialists!), in contrast, were weak and non-significant. In these comparisons sample size was not important, because there were about as many Coleoptera as Hemiptera individuals, and clearly more of both than Lepidoptera.

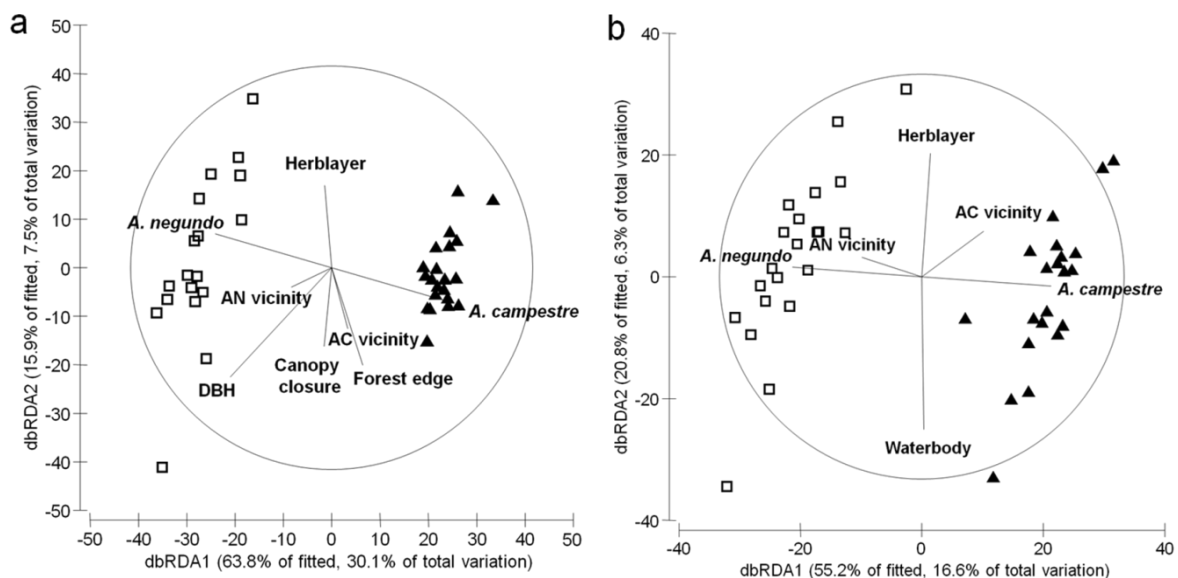
Table 7. Spearman matrix rank correlation coefficients (999 permutations) relating Bray-Curtis similarities of herbivore species assemblages of different insect orders across individual *Acer* trees.

Order	r_s	p -value
Lepidoptera – Hemiptera	0.346	0.001
Lepidoptera – Coleoptera	0.048	0.202
Coleoptera – Hemiptera	0.056	0.148

Species composition related to tree and habitat descriptors

The dbRDA ordination plots (Figure 6) and stepwise distance-based linear models (Table 8) show that species composition of herbivore assemblages of individual trees did not only segregate between the two tree species, but was also influenced by other site or tree characters. Importantly, the identity as well as hierarchy of factors

with significant explanatory power differed strongly between herbivore taxa. Tree species identity was important for all groups tested except for the Pulmonata. Yet, tree identity was the most important factor for the Lepidoptera, Hemiptera and all herbivore arthropods together, whereas for beetles the distance to the nearest waterbody entered first into the model. Caterpillar assemblages (Fig. 6a) were, in addition, significantly shaped by tree size and canopy closure above trees. For hemipterans (Fig. 6b), the distance to the nearest waterbody and the extent of the herb layer beneath the *Acer* trees were important. Total arthropod assemblages (Fig. 6e) were related to these same factors as in the Hemiptera, with very similar relative contributions of individual predictors. For beetles (Fig. 6c), the sequence of these same three factors entering the stepwise model was different, since distance to the nearest waterbody took precedence over tree species. Snail and slug assemblages, in contrast, revealed a different set of significant predictors (Fig. 6d), including tree size, distance to the nearest forest edge, herb layer cover, and distance to water. Tree vitality and the number of conspecific trees in a radius of 10m around a focal tree never entered significantly into the step-wise statistical models.



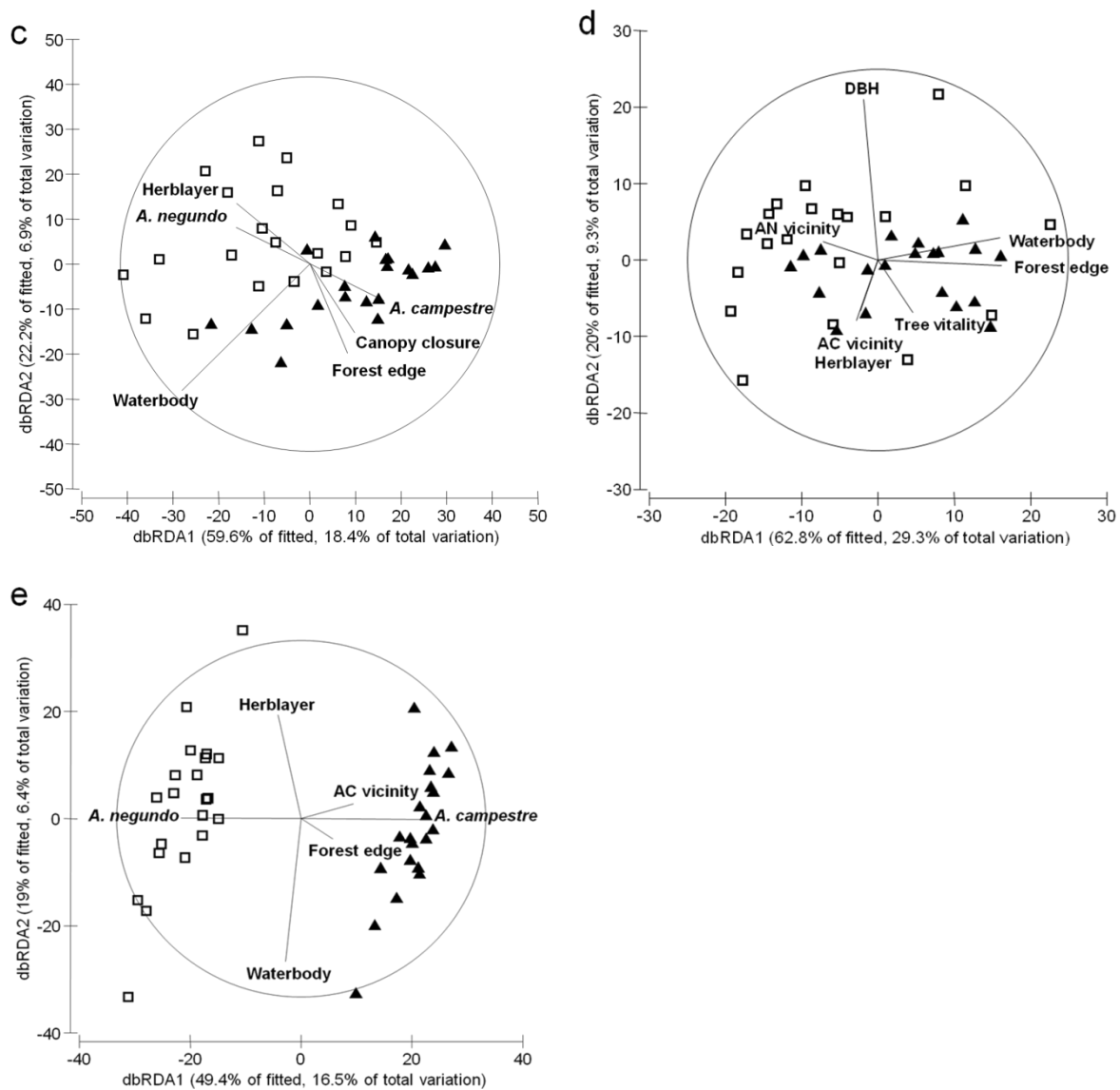


Figure 6. Distance-based redundancy analysis (dbRDA) ordination plots displaying the relationships between herbivore assemblages of individual trees relative to tree species identity and a variety of tree and site descriptors a. Lepidoptera, b. Hemiptera, c. Coleoptera, d. Pulmonata, e. All herbivore arthropods. The vectors within the circle show the effect of each predictor variable included in the model; the longer the vector from the center the larger the effect. Tree individuals of *Acer campestre* represented by black filled triangles, *A. negundo* by empty squares. For visual clarity only parameters included in the best models with a multiple partial correlation coefficient $r \geq 0.2$ are plotted (for details compare Table 8). DBH: Diameter at breast height. AC vicinity: number of other *A. campestre* individuals within a radius of 5 m. AN vicinity: number of other *A. negundo* individuals within a radius of 5 m.

Table 8. Results of step-wise distance-based linear models (selection criterion: adjusted R^2 , basis: Bray-Curtis similarity matrix, 9999 permutations) relating community composition of the three major insect orders, gastropods, and all herbivore arthropods to tree and habitat descriptors. n.i. = not included in the model. Given are adjusted multiple cumulative coefficients of determination R^2 plus their associated probability values p . Printed **in bold** are variables that increased significantly ($p < 0.05$) the explained proportion of variance.

	Group	Adj. R^2	p
Lepidoptera	Acer species	0.274	< 0.001
	DBH	0.303	< 0.01
	Canopy closure	0.322	< 0.05
	AN vicinity	0.333	0.102
	Forest edge	0.340	0.229
	Herblayer	0.347	0.216
	AC vicinity	0.353	0.242
	Waterbody	n.i.	n.i.
Hemiptera	Acer species	0.135	< 0.001
	Waterbody	0.165	< 0.01
	Herblayer	0.189	< 0.01
	AC vicinity	0.197	0.151
	AN vicinity	0.204	0.226
	Forest edge	n.i.	n.i.
	Tree vitality	n.i.	n.i.
	DBH	n.i.	n.i.
Coleoptera	Waterbody	0.086	< 0.001
	Acer species	0.169	< 0.001
	Herblayer	0.196	< 0.05
	Forest edge	0.201	0.305
	Canopy closure	0.208	0.273
	AC vicinity	n.i.	n.i.
	DBH	n.i.	n.i.
	Tree vitality	n.i.	n.i.
Pulmonata	Forest edge	0.187	< 0.001
	DBH	0.243	< 0.01
	Waterbody	0.279	< 0.05
	Herblayer	0.311	< 0.05
	AC vicinity	0.316	0.305
	AN vicinity	0.329	0.171
	<i>Acer</i> species	0.332	0.345
	Tree vitality	0.333	0.372
Herbivore arthropods	Acer species	0.138	< 0.001
	Waterbody	0.178	< 0.001
	Herblayer	0.207	< 0.001
	Forest edge	0.216	0.107
	Canopy closure	0.221	0.286
	AC vicinity	0.221	0.449
	DBH	n.i.	n.i.
	Tree vitality	n.i.	n.i.
	AN vicinity	n.i.	n.i.

Leaf area loss over the season

The time curve, across the 6 sampling rounds, of relative leaf area loss related to herbivory (Fig. 7) did not differ significantly between the two *Acer* species (repeated-

measures ANOVA: $F_{1,40} = 0.45$, $p = 0.506$). However, the timing of herbivore damage differed, with more leaf loss to herbivory occurring later in the season on *A. campestre* than on *A. negundo* (time: $F_{5,200} = 159.49$, $p < 0.001$; time \times tree species interaction: $F_{5,200} = 3.19$, $p < 0.01$). The cumulative relative leaf area loss through herbivore invertebrates on each tree individual did not differ significantly between both *Acer* species near the end of the vegetation period in late August (Fig. 7).

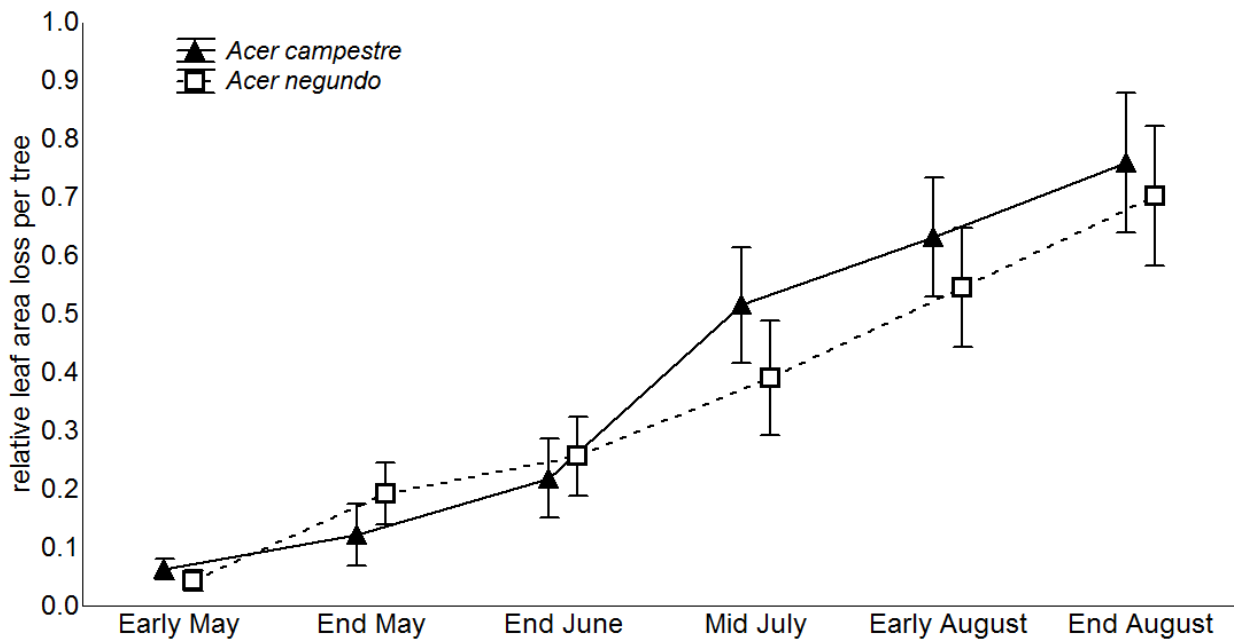


Figure 7. Least square means of relative leaf area loss (arcsin \sqrt{x} transformed) (\pm 95% CI) of the two *Acer* species over the growing season. Overall, herbivore damage was almost equal between the two tree species, but the timing of herbivory differed significantly, with more damage accumulating later in the season on *A. campestre*.

The total measured leaf area amounted to 10,389.3 cm² for *Acer campestre* (N°= 315 leaves) and 20,137.9 cm² for *Acer negundo* (N°= 315 leaves). At the end of August (last sampling round) the measurable leaf area (still remaining and not completely withered leaves) was 5,211.4 cm² on *Acer campestre*, and 9,148.1 cm² on *Acer negundo* (overall leaf area loss, AC: 44.9%; AN: 36.6%).

Discussion

Herbivore abundance, richness and diversity

On the native *Acer* tree I found nearly twice as many herbivore individuals as on the invasive alien species, but herbivore species richness on both tree species was very similar after controlling for sample size effects. Fisher's alpha and Shannon's diversity of herbivores also show no clear differences between both *Acer* species. Similar results were found for the species richness of herbivores on native and alien Brassicaceae species in Europe (Frenzel & Brandl, 2003). These authors found that similar abundance of insect species attack alien as well as native cabbage plant species. However, in contradiction to this latter study, in my surveys the abundance of herbivores of all orders except Coleoptera was significantly higher on the native *Acer* compared to the invasive species. Also insects which were common on the native maple tree were not the same that were common on the non-native one. This was particularly pronounced for specialist herbivores which were rarely encountered on *A. negundo*. Possibly, the pronounced chemical defense of Brassicaceae plants through glucosinolates (Frohne & Jensen, 1985) acts as a filter to allow only relatively host-specific pre-adapted herbivores to colonize aliens. In contrast, *A. negundo* apparently provides a more open resource for colonization through generalist foliage feeders of deciduous forest trees. Hartley et al. (2010) compared the herbivore abundance and species richness on the invasive Chinese tallow tree (*Triadica sebifera*) and three native tree species in Texas. They found out, that the herbivore abundance was significant lower as on the three native trees. The species richness of herbivorous was similar to the native ones. These results supported also my study.

Species composition and the effect of tree or site characters

With regard to species composition of the herbivores I noted profound differences among the taxa. Leaf-chewing caterpillar and sap-sucking hemipteran assemblages were particularly clearly separated between the native and the alien tree, in contrast to beetles or slugs and snails. Also the homogeneity of the herbivore communities differed distinctly among the two maple species. Communities on the native maple

were far more homogeneous across tree individuals, which is in line with the expectation of a co-evolutionary equilibrium between the plant and its herbivores. In contrast, the communities on the non-native maple tree were more heterogeneous. This indicates a higher degree of stochasticity and thus lower predictability, because these assemblages are mostly recruited from opportunistic polyphagous herbivores in the regional species pool. The arthropod herbivore community of the Chinese tallow tree show similar patterns (Hartley et al., 2010). The community was distinctly different to the communities of the other three compared native trees. Many studies detected that herbivore richness may strongly depend on the time of introduction of an invasive alien plant species because the formation of assemblages of insects on these plants needs considerable time (time hypothesis: Southwood, 1961; Brändle et al., 2008). In my study the less homogeneous communities on *Acer negundo* could be explained by the not yet completed co-evolutionary process.

Assemblages of polyphagous herbivores, represented in my samples by gastropods and the order Coleoptera, were more strongly shaped by habitat characteristics (i.e. distance to the nearest forest edge and waterbody, canopy closure, herb layer, tree vitality and tree size) than by tree species identity. Apparently, for these herbivores the microclimate of the habitat and the condition of the tree individual are more decisive in regulating colonization than the host tree's species identity.

Monophagous herbivores, represented in my study mostly by species in the orders Lepidoptera and Hemiptera, showed exactly the opposite pattern. Here, tree species identity governed assemblage structure, while other tree or site descriptors had only minor modulating influence on species composition. Leaf-chewing and sap-sucking herbivores differed markedly as to what site characters affected their species composition. For specialized species the primary factor is the host plant (Komonen et al., 2004; Quinn et al., 1998), as food resource and breeding ground. For polyphagous species the identity of the food plant may be less important (Müller et al., 2011), as long as the nutritional quality is sufficient. In a floodplain forest where my study take place, I found a large range of alternative food plants that serve as sources for such generalist feeders to occasionally colonize *A. negundo*. More important for such species are tree and site characters, i.e. the distance to the

nearest waterbody (indicating the likelihood of flooding events), the distance to the nearest forest edge (related to microclimate and hiding places) or the forest canopy closure (another correlate of microclimate). Since overall host specialists play a prominent role in herbivore communities, for the entirety of all herbivorous arthropods the maple species emerged again as the most decisive factor. Communities were further modulated by the proximity to the nearest waterbody or forest edge and the extent of the herb layer cover which may serve as a source of polyphagous herbivores.

As with species composition, tree species identity had the strongest significant influence also on herbivore abundance and relative abundance of specialists. Again, tree species effects were distinct for the more host-specific caterpillars and sap-sucking hemipterans, but absent for predominantly polyphagous beetles or snails and slugs. Other site and tree characters had no or only a weak influence on herbivore abundance.

In summary these results show that, in line with expectations, (1) the native field maple harbors a herbivore community comprising many specialists, which is relatively predictable and compact; (2) herbivore communities on the invasive alien box elder are dominated by opportunists and less predictable; (3) faunal differentiation between the native and neophyte tree depends on whether in a focal herbivore taxon specialists or generalists prevail; (4) these patterns are rather similar with regard to herbivore species composition and abundance, whereas herbivore species richness and diversity do not show noticeable differences. Accordingly, *Acer negundo* is colonized from the meta-community of regionally available herbivorous invertebrates by basically the same rules as every other tree, but turns out to be rather unattractive (or impossible to colonize) for most of the *Acer campestre* host specialists.

Host plant specificity of endophagous and ectophagous herbivores

I did not detect an extension of host ranges of endophagous herbivore species from the native to the invasive alien *Acer* species. Only two of the inspected leaves of the

invasive alien tree bore some plant galls, and none was attacked by leaf miners. Similarly, the ratio between specialized and generalist ectophagous herbivores which was on average six times higher on the native tree. This result supported a numerous studies which found also a lower ratio of specialists to generalists on non-native plants (Strong et al., 1984; Zwölfer, 1988; Fraser & Lawton, 1994). Hence, in the Danube floodplain *A. negundo* has thus far been colonized by host plant specialists of other *Acer* species only to a very marginal extent. Contrarily to my results, Frenzel & Brandl (2003) found no significant difference in the ratio of endo- and ectophagous on their study plants. Goßner and Ammer (2006) found a similar herbivore community on the native European spruce and on the non-native Douglas fir. These composition of dominating polyphagous species, would explain due to the existing low ratio of specialists to generalists on the native spruce (Niemelä & Mattson, 1996). Another study compared the herbivore arthropod fauna on introduced conifers with and without a native congener and detected a higher ratio of ectophagous to endophagous native insects (5.9 times numerous) on the exotic conifers which had native congeners in their new range (Roques et al., 2006). Endophagous living species are typically more host-specific and are incapable of leaving the plant in contrast to ectophagous species (Cornell & Kahn, 1989; Gaston et al., 1992). Furthermore endophagous species are more strongly linked to their hosts and interact more intimately with them, e.g. by manipulating the plant to build up galls (Frenzel & Brandl, 2003). The few monophagous species I found on *Acer negundo*, like certain aphids specialized to the genus *Acer*, are not causing leaf area loss. Rather they are dangerous for the plant because they are vectors of phytophagogenics like viruses (Sutakova, 1984). Polyphagous herbivores are in most cases the first insects who utilize a new host plant (Hansen et al., 2006). Young herbivore insect assemblages are, therefore, characterized by a small proportion of endophagous herbivores, because these need to be better adapted to the phytochemistry and structure of the new host plant (Strong et al., 1984, Frenzel & Brandl, 1998). This could explain the lower abundance and species richness of specialized endo- and ectophagous species on the invasive box elder.

Insect host-plant theory implies that taxonomically related plant species often share a similar phytochemistry and would thereby more easily be integrated into the

food web than invasive plants without allies in the native flora (e.g. Frenzel & Brandl, 2001; Novotný et al., 2002a, 2002b). My study supported this idea for the ectophagous herbivores, since these herbivores caused nearly the same leaf area loss on invasive box elder. However the integration into the food web of the Danube floodplain forest is not yet completed in view of the species composition. There dominating generalist feeders. Novotný et al. (2003) compared caterpillars feeding on two alien *Piper* species in New Guinea. They detected that the probability to colonize the alien species increased with the host range of the herbivores. Caterpillars which are strictly bounded on only one plant family were rare, whereas species which have a large host range (>10 plant families) prevailed among the herbivores on the invasive shrubs. Same results found for the Douglas fir and three other non-native Cupressaceae species in Europe (Roques et al., 2006). Goßner (2004) compared the arthropod abundance, species richness and the ratio of specialists to generalists on the native *Quercus robur* and the non-native *Q. rubra* in Europe. He found a lower ratio of specialists to generalists, a lower abundance and also lower species richness on the non-native oak species. These results are very similar to my observations on *Acer* species.

All available studies revealed a higher proportion of specialist herbivores in the native ranges of invasive plants compared to the invaded range (Jobin et al., 1996; Memmott et al., 2000; Imura, 2003; Hansen et al., 2006). These results are in line with the first assumption of the enemy release hypothesis, viz. in their native range these plants experience a substantial selection pressure through specialized herbivores. In addition, however, this hypothesis implies that the alien species is to a lesser extent down-regulated by predators, parasites and pathogens in the invaded range. I could not support this postulate in my study. Rather, *Acer negundo* experiences a similar herbivore pressure as its native congener (leaf area loss is nearly the same on AC and AN). Moreover, caterpillars found on both trees had similar parasitism rates (AC: 20% of 175 caterpillar individuals and AN: 14% of 65 caterpillar individuals; H. Krebs, unpublished data). This does not suggest that herbivores colonizing box elder suffer from lower fitness due to their own natural enemies.

Overall, the assemblage of herbivore arthropods on the two maple species was dominated by polyphagous species. However, when I compared the assemblages within individual insect orders very large differences emerged. On field maple the order Hemiptera comprised 36% (of 441 individuals) monophagous individuals, and lepidopteran caterpillars were even to 70% (of 175 individuals) host-specific on the genus *Acer*. On the non-native maple it exists no abundant monophagous species. It could be that the herbivore communities on *A. negundo* comprise in generally of opportunists in contrast to the native maple who is stronger shaped by specialization. This would be supported from the study of Lind (2008), who could also detect a high proportion of polyphagous caterpillar species in the Lepidoptera assemblage on *A. negundo* in its native North-American range.

Interestingly, I found one *Acer* specialist (*Japananus hyalinus*, Cicadeliidae) on native field maple which is an alien species from Japan (first record in Austria: 1942 in Graz; Wagner & Franz, 1961), but is meanwhile distributed all over the world (e.g. Europe, North America, Australia). I could not detect any specimen of this leafhopper on invasive box elder.

Leaf area loss through herbivores

So far only few studies compared the herbivore damage on an invasive alien species with the damage on related native species. Dietz et al. (2004) compared the median percentage of leaf damage by herbivores on ten invasive alien species and ten native species along an altitudinal gradient on an island of the Seychelles. In this study the native species were significantly more damaged by herbivores (50%) than the invasive ones (27%). Same results detected Hartley et al. (2010) on the Chinese tallow tree which had a lower herbivore damage as the three compared native tree species. In contrast, Agrawal & Kotanen (2003) observed that exotic species on a Canadian old-field were damaged more by folivorous insects. These observations do not appear to be consistent with my study. The average relative leaf area loss at the end of the sampling period did not differ significantly between the invasive and the native *Acer* species. I observed that the seasonal development of leaf damage differed between both *Acer* species. The non-native *Acer* species had a higher leaf

area loss at the beginning of the vegetation period, but later in the season this difference vanished. These results do not match with the prediction of the enemy release hypothesis. The rather high herbivore damage on invasive box elder despite lower observed herbivore abundance may be related to the low specialist–generalist ratio. Most herbivores found on *Acer negundo* were generalists (e.g. polyphagous snails) and thus have no fixed preference in terms of plant species (ratio snails:herbivore arthropods, AN = 1:2; AC = 1:1). Quantitatively these few generalists of box elder induced a similar leaf area loss as the more numerous specialists on field maple.

A. negundo is more plastic in biomass allocation than related native species in Europe. Hence, *A. negundo* could rapidly benefit from environmental conditions such as increased nutrition and light availability (which are found in floodplain forests through the regular flooding and related disturbances), allowing this tree to overgrow native plants (Porté et al., 2011). This could explain its invasiveness especially in European riparian forests. This finding would also support the evolution of increased competitive ability hypothesis, which predicts that an alien plant must invest less resources into herbivore defense given the lack of predation (Pyšek, 1994; Pyšek & Pyšek, 1995; Blossey & Nötzold, 1995; Bossdorf et al., 2004a). I did, however, not find any evidence for a lack of natural enemies, because *A. negundo* suffered almost equal foliage loss from herbivory as its native congener.

Most other studies on herbivores on invasive plants differ from my study with regard to the habitat, environmental parameters, plant life form, or climatic zone. These factors could explain variation in results, because not every ecosystem is equally sensitive for invasions (Walter et al., 2005). The lower herbivore abundance (especially specialists) on the invasive plant box elder does not necessarily hint to a stronger phytochemical defense or lower nutritional value of *A. negundo*. Existing literature from North America recorded around one hundred lepidopteran species alone, including specialized plant gall builders and leaf miners, to occur on this tree species (Gilman & Watson, 1993; Lind, 2008; Robinson et al., 2010; <http://www.brc.ac.uk/DBIF/hosts.aspx>). This means that *Acer negundo* only recruits about 19% of the indigenous Lepidoptera species in the Danube floodplain forest in contrast to its native range. Maybe one could therefore expect in the next few

decades that more herbivore species (in particular polyphagous ones) will include this non-native tree into their host ranges.

Conclusions

My study from the Danube floodplain showed that the invasive alien tree species *Acer negundo* and its native congener *A. campestre* are affected by a similar herbivore pressure, which indicates that the invasive tree species is already integrated into the food web of the Danube floodplain forest (with regard to the herbivore feeding damage and to the species composition of the local fauna) . Herbivorous invertebrates are an important component of terrestrial food webs. Many other taxa (i.e. zoophagous predators) depend on them for food (Tallamy, 2004). Should *Acer negundo* be able to replace native pioneer trees (especially the silver willow floodplain) in the National Park "Donau-Auen", the consequences for the associated food web, however, cannot yet be predicted. Herbivore communities of *Salix* do hardly overlap with those of *Acer* species, because they do not share similar secondary plant metabolites phytochemical substances. Hence, specialist *Salix* herbivores are not expected to switch on the neophyte and would therefore lose their host if this would be completely outcompeted. The specialist herbivore community of *Salix alba* would likely be replaced by an insect assemblage dominated by generalists recruited from other deciduous broad-leaved trees occurring in the region. This could have unpredictable effects on interactions at higher trophic levels (Gratton & Denno, 2005). Two major question will be (1) whether herbivore damage can contribute to constrain the fitness of *A. negundo* to such an extent that this may affect the future distribution and abundance of this tree species in the Danube floodplain forest and (2) to what extent the different herbivores that occur in the area (whether specialist or generalist) will be able to include the invasive box elder more strongly into their host range.

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Appendix

Table A1. Species list of all identified herbivorous invertebrates (individual numbers) collected on *Acer campestre* (AC) and *Acer negundo* (AN) over the seven sampling rounds (m= monophagous; o= oligophagous; p= polyphagous).

Order	Family	Species	Indiv. on AC	Indiv. on AN	Nutrition
Hemiptera	Cicadellidae	<i>Acericerus ribauti</i>	35	0	m
Hemiptera	Cicadellidae	<i>Acericerus vittifrons</i>	11	0	m
Coleoptera	Elateridae	<i>Adrastus pallens</i>	6	3	p
Coleoptera	Elateridae	<i>Adrastus rachifer</i>	30	12	p
Lepidoptera	Geometridae	<i>Agriopsis aurantiaria</i>	2	0	p
Hemiptera	Cicadellidae	<i>Alebra wahlbergi</i>	35	1	p
Hemiptera	Cicadellidae	<i>Allygus modestus</i>	0	1	p
Lepidoptera	Geometridae	<i>Alsophila aescularia</i>	2	0	p
Lepidoptera	Noctuidae	<i>Amphipyra berbera</i>	1	0	p
Lepidoptera	Gelechiidae	<i>Anacampsis populella</i>	2	3	p
Coleoptera	Scarabaeidae	<i>Anomala dubia</i>	0	1	p
Hemiptera	Cicadellidae	<i>Aphanus rolandri</i>	0	1	p
Hemiptera	Aphrophoridae	<i>Aphrophora alni</i>	7	6	p
Lepidoptera	Tortricidae	<i>Archips crataeganus</i>	0	2	p
Lepidoptera	Tortricidae	<i>Archips rosanus</i>	3	3	p
Pulmonata	Helicidae	<i>Arianta arbustorum</i>	458	284	p
Pulmonata	Arionidae	<i>Arion vulgaris</i>	5	17	p
Coleoptera	Elateridae	<i>Athous haemorrhoidalis</i>	74	34	p
Lepidoptera	Erebidae	<i>Calliteara pudibunda</i>	2	0	p
Lepidoptera	Gracillariidae	<i>Caloptilia onustella</i>	6	0	m
Coleoptera	Cantharidae	<i>Cantharis rufa</i>	3	5	p
Coleoptera	Cantharidae	<i>Cantharis thoracica</i>	5	4	p
Coleoptera	Curculionidae	<i>Chlorophanus viridis</i>	1	0	p
Coleoptera	Elateridae	<i>Cidnopus aeruginosus</i>	0	1	p
Hemiptera	Miridae	<i>Closterotomus fulvomaculatus</i>	2	2	p
Lepidoptera	Noctuidae	<i>Colocasia coryli</i>	1	0	p
Lepidoptera	Geometridae	<i>Colotois pennaria</i>	1	0	p
Lepidoptera	Noctuidae	<i>Cosmia trapezina</i>	2	2	p
Lepidoptera	Geometridae	<i>Cyclophora annularia</i>	98	0	m
Lepidoptera	Chimabachidae	<i>Diurnea fagella</i>	1	0	p
Hemiptera	Drepanosiphidae	<i>Drepanosiphum acerinum</i>	41	2	m
Hemiptera	Drepanosiphidae	<i>Drepanosiphum aceris</i>	1	0	m
Hemiptera	Drepanosiphidae	<i>Drepanosiphum platanoidis</i>	12	1	m
Lepidoptera	Geometridae	<i>Ectropis crepuscularia</i>	2	24	p
Lepidoptera	Erebidae	<i>Eilema sororcula</i>	5	6	p
Hemiptera	Acanthosomatidae	<i>Elasmucha grisea</i>	0	1	p
Lepidoptera	Geometridae	<i>Ennomos autumnaria</i>	1	0	p
Lepidoptera	Geometridae	<i>Erannis defoliaria</i>	3	0	p
Pulmonata	Vitrinidae	<i>Eucobresia diaphana</i>	0	3	p
Lepidoptera	Erebidae	<i>Euproctis similis</i>	1	0	p
Lepidoptera	Noctuidae	<i>Eupsilia transversa</i>	0	2	p
Pulmonata	Bradybaenidae	<i>Fruticicola fruticum</i>	576	406	p
Coleoptera	Elateridae	<i>Hemicrepidius hirtus</i>	1	0	p
Coleoptera	Elateridae	<i>Hemicrepidius niger</i>	0	1	p
Lepidoptera	Geometridae	<i>Hemithea aestivaria</i>	1	0	p
Hemiptera	Miridae	<i>Heterotoma merioptera</i>	1	0	p
Lepidoptera	Geometridae	<i>Hypomecis punctinalis</i>	1	3	p
Lepidoptera	Geometridae	<i>Hypomecis roboraria</i>	0	1	p
Hemiptera	Issidae	<i>Issus coleoptratus</i>	8	7	p
Hemiptera	Cicadellidae	<i>Japananus hyalinus</i>	20	0	m
Hemiptera	Cicadellidae	<i>Ledra aurita</i>	0	3	p
Lepidoptera	Geometridae	<i>Lycia hirtaria</i>	1	0	p
Hemiptera	Miridae	<i>Lygocoris pabulinus</i>	1	3	p
Lepidoptera	Erebidae	<i>Lymantria dispar</i>	0	3	p
Coleoptera	Cantharidae	<i>Malthinus A</i>	5	1	p
Ensifera	Meconematidae	<i>Meconema thalassinum</i>	39	11	p
Hemiptera	Miridae	<i>Mermitelocerus schmidtii</i>	20	22	p
Lepidoptera	Geometridae	<i>Operophtera brumata</i>	11	2	p
Lepidoptera	Erebidae	<i>Orgyia antiqua</i>	2	2	p
Lepidoptera	Noctuidae	<i>Orthosia cerasi</i>	5	1	p

Table A1. (Cont.)

Order	Family	Species	Indiv. on AC	Indiv. on AN	Nutrition
Lepidoptera	Noctuidae	<i>Orthosia cruda</i>	0	2	p
Hemiptera	Miridae	<i>Orthotylus prasinus</i>	86	21	p
Coleoptera	Curculionidae	<i>Otiorhynchus fullo</i>	1	0	o
Hemiptera	Pentatomidae	<i>Palomena prasina</i>	0	2	p
Lepidoptera	Tortricidae	<i>Pandemis corylana</i>	1	1	p
Lepidoptera	Tortricidae	<i>Pandemis heperana</i>	1	2	p
Hemiptera	Pentatomidae	<i>Pentatoma rufipes</i>	14	28	p
Lepidoptera	Geometridae	<i>Peribatodes rhomboidaria</i>	2	3	p
Hemiptera	Drepanosiphidae	<i>Periphyllus acericola</i>	2	0	m
Hemiptera	Drepanosiphidae	<i>Periphyllus aceris</i>	9	2	m
Hemiptera	Drepanosiphidae	<i>Periphyllus lyropictus</i>	5	8	m
Hemiptera	Drepanosiphidae	<i>Periphyllus testudinaceus</i>	3	5	m
Coleoptera	Curculionidae	<i>Phyllobius calcaratus</i>	7	11	p
Coleoptera	Curculionidae	<i>Phyllobius oblongus</i>	126	12	p
Coleoptera	Curculionidae	<i>Phyllobius pomaceus</i>	1	1	p
Coleoptera	Curculionidae	<i>Phyllobius sinuatus</i>	2	1	p
Lepidoptera	Gracillariidae	<i>Phyllonorycter acerifoliella</i>	6	0	m
Hemiptera	Tingidae	<i>Physatocheila harwoodi</i>	2	0	m
Hemiptera	Miridae	<i>Phytochoris A</i>	16	2	p
Hemiptera	Miridae	<i>Phytochoris longipennis</i>	32	8	p
Hemiptera	Piesmidae	<i>Piesma maculatum</i>	1	0	p
Hemiptera	Miridae	<i>Pilophorus clavatus</i>	3	0	p
Hemiptera	Miridae	<i>Pinalitus cervinus</i>	0	1	p
Coleoptera	Curculionidae	<i>Pogonocherus hispidus</i>	3	2	p
Coleoptera	Curculionidae	<i>Polydrusus corruscus</i>	1	1	p
Coleoptera	Curculionidae	<i>Polydrusus pterygomalis</i>	11	9	p
Coleoptera	Curculionidae	<i>Polydrusus sericeus</i>	52	23	p
Hemiptera	Miridae	<i>Psallus A</i>	1	1	p
Hemiptera	Miridae	<i>Psallus ambiguus</i>	1	0	o
Hemiptera	Miridae	<i>Psallus assimilis</i>	2	0	m
Lepidoptera	Notodontidae	<i>Ptilodon cucullina</i>	3	0	m
Lepidoptera	Notodontidae	<i>Ptilophora plumigera</i>	7	2	m
Hemiptera	Coccidae	<i>Pulvinaria spec.</i>	45	40	o
Hemiptera	Pentatomidae	<i>Rhaphigaster nebulosa</i>	0	1	p
Hemiptera	Psyllidae	<i>Rhinocola aceris</i>	16	20	m
Lepidoptera	Geometridae	<i>Selenia dentaria</i>	1	0	p
Lepidoptera	Geometridae	<i>Selenia tetralunaria</i>	1	1	p
Coleoptera	Curculionidae	<i>Simo hirticornis</i>	1	0	p
Pulmonata	Succineidae	<i>Succinea putris</i>	0	8	p
Coleoptera	Elateridae	<i>Synaptus filiformes</i>	19	54	p

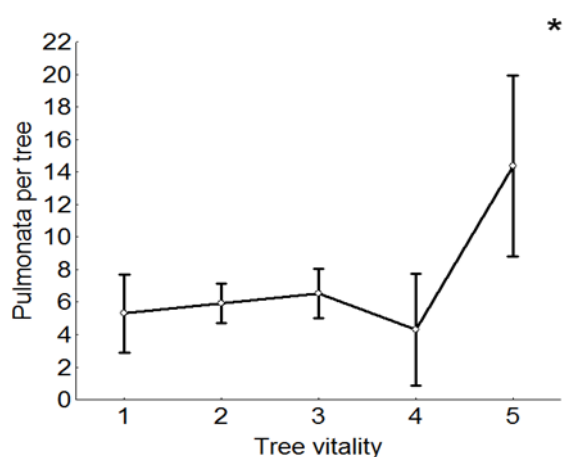


Figure A1. Least square means (\pm 95% CI) of Pulmonata individuals (\sqrt{x} transformed) per tree relative to tree vitality. Significant effect of tree vitality class according to GLMs testing indicated by asterisk (* $p < 0.05$). Tree vitality classified on a rank scale from 1 (very good condition) to 5 (single dead branches, some twigs without leaves).

Lebenslauf

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