Effects of intraspecific genetic diversity in willow short-rotation coppice on the associated arthropod community

Master Thesis

by

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List of Abbreviations

AIC	Akaikes Information Criterion
AS	Associational susceptibility
AR	Associational resistance
CO_2	Carbon dioxide
FGEC	First generation energy crops
GD	Genetic diversity / genetische Diversität
GHG	Greenhouse gas
GLMM	Generalized linear mixed-model
IPCC	Intergovernmental Panel on Climate Change
KUP	Kurzumtriebsplantagen
MIH	More individuals hypothesis
NMDS	Non-metric multidimensional scaling
OLRE	Observation level random effect
R^2	Coefficient of determination
RSH	Resource specialisation hypothesis
SD	Species diversity
SGEC	Second generation energy crops
SRC	Short rotation coppice
UNFCCC	United Nation Framework Convention on Climate Change

Content

Summary

Bioenergy has the potential to become an important global energy source, helping to replace fossil fuels and mitigate greenhouse gas emissions. Large scale land use change towards biomass plantations may impact habitat availability for various species. One of the most promising biomass production systems are willow short rotation coppice (SRC). There is evidence that increasing plant diversity in these plantations can affect the associated arthropod community and thereby relate to herbivory and ecosystem services delivered by arthropods. To investigate if the potential benefits of diversity can be induced by intraspecific genetic diversity (GD) in SRC, I examined effects of GD in experimental willow stands on the entire arthropod community in the ECOLINK-Salix experiment in Freiburg (southwest Germany). GD ranged from genetic monocultures to mixtures of four *Salix* genotypes. I sampled arthropods in a standardized design and tested for effects of genotype diversity on the richness and abundance of all arthropods, herbivores and predators using generalized linear mixed-effect models. My findings show that plant GD significantly increased the total richness of all arthropods and of herbivores, although arthropod community composition was similar among three of the four genotypes. Results varied between genotypes but all diversity effects were positive. Genotype specific effects on arthropod abundance did not affect the total data and significant effects on herbivores or predators occurred on different genotypes. This indicates for varying mechanisms of diversity effects (i.e. direct or indirect effects through trophic levels) between genotypes. The results of my study provide strong evidence that increased GD in willow SRC can have the potential to increase diversity in the associated arthropod community throughout trophic levels. Corresponding management strategies may enhance ecosystem services delivered by arthropods and thereby increase ecological benefits of bioenergy as a renewable energy source with the potential of mitigating anthropogenic climate change.

Zusammenfassung

Bioenergie verfügt über ein hohes Potential, eine weltweit bedeutende Energiequelle zu werden und somit zur Ablösung fossiler Brennstoffe und zur Eindämmung der Treibhausgasemissionen beizutragen. Großflächige Landnutzungsänderungen hin zu Biomasseplantagen können sich auf die Verfügbarkeit von Habitaten für verschiedene Spezies auswirken. Eines der vielversprechendsten Produktionssysteme für Biomasse stellen Weiden-Kurzumtriebsplantagen (KUP) dar. Es gibt Hinweise darauf, dass sich eine Erhöhung der pflanzlichen Diversität in solchen Plantagen auf die assoziierte Arthropodengemeinschaften auswirken und somit Herbivorie und von Arthropoden bereitgestellte Ökosystemdienstleistungen bedingen kann. Um zu erforschen, ob die potentiellen Vorteile von Diversität über intraspezifische genetische Diversität (GD) in KUP erreicht werden können, habe ich die Effekte von GD in experimentellen Weidenpflanzungen auf die gesamte Arthropodengemeinschaft in dem Experiment ECOLINK-Salix in Freiburg (Südwestdeutschland) untersucht. Das Maß der GD reichte von genetischen Monokulturen bis zu Mischungen aus vier verschiedenen Genotypen. Ich erhob die Arthropoden nach einem standardisierten Vorgehen und testete auf Diversitätseffekte auf die Artenzahlen und Abundanz aller Arthropoden sowie der Herbivoren und der Räuber unter Verwendung verallgemeinerter gemischter Modelle. Ich fand heraus, dass sich die GD der Weiden positiv auf die Gesamtartenzahl aller Arthropoden sowie der Herbivoren auswirkte, obwohl sich die Zusammensetzung der Arthropodengemeinschaften bei drei der vier Genotypen nicht unterschied. Die Ergebnisse variierten zwischen den Genotypen, aber alle Diversitätseffekte waren positiv. Genotyp-spezifische Effekte auf die Abundanz der Arthropoden hatten keinen Einfluss auf die gesamten Daten und signifikante Effekte auf Herbivoren oder Räuber traten bei unterschiedlichen Genotypen auf. Dies weist auf unterschiedliche Mechanismen der Diversitätseffekte (direkte oder indirekte Effekte über mehrere trophische Ebenen hinweg) zwischen den Genotypen hin. Die Ergebnisse meiner Arbeit legen den Schluss nahe, dass eine Erhöhung der GD in Weiden-KUP potentiell zu einer Erhöhung der Diversität der assoziierten Arthropodengemeinschaft über mehrere trophische Ebenen beitragen kann. Entsprechende Managementstrategien könnten von Arthropoden bereitgestellte Ökosystemdiensteistungen fördern und dabei den ökologischen Nutzen von Bioenergie als einer erneuerbaren Energiequelle mit Potential zur Eindämmung des anthropogenen Treibhauseffekts erhöhen.

Introduction

Bioenergy and biomass production

Human influence on climate change is generally accepted within the scientific community by now. Despite a growing focus on climate change mitigation policies, anthropogenic greenhouse gas (GHG) emissions are still increasing (IPCC 2014). Responding to this problem, the United Nation Framework Convention on Climate Change (UNFCCC) most recently adopted a global agreement governing GHG emissions as a result of the 21st United Nations Climate Change Conference in Paris (i.e. the Paris Agreement; UNFCCC 2015). The most important source for GHG is the emission of carbon dioxide (CO_2) from fossil fuels and industrial processes (IPCC 2014). The Intergovernmental Panel on Climate Change (IPCC) therefore argues that large scale changes in the energy system are an essential tool for reducing GHG emissions. Bioenergy systems with low lifecycle emissions are assumed to have a high potential mitigating anthropogenic climate change (Immerzeel et al. 2014; IPCC 2014; Weih et al. 2014). Besides energy crop identity (Parmer et al. 2015) marginal consequential emissions i.e. from land use change (e.g. altering carbon sequestration) are important elements of the bioenergy systems total lifecycle emissions (IPCC 2014; Kemper 2015). Hence, short rotation coppice (SRC) can sequester additional carbon in soil biomass if established on former cropland but not on former grassland (Don et al. 2012; Harris et al. 2015). Carbon sequestration may also increase over time, outperforming carbon release into the atmosphere during the establishment of the plantation (Verlinden et al. 2013). However, the production of biomass, especially on former cropland, leads to increased competition with food production for arable land (Immerzeel et al. 2014). In this context, second generation energy crops (SGEC) tend to have less negative effects than first generation energy crops (FGEC). Second generation bioenergy technologies are based on the conversion of lignocellulosic plant materials instead of carbohydrates and plant oils from food-products (i.e. FGEC). Therefore, fast growing trees or perennial grass species can be used, which are less dependent on highly productive agricultural soils (López-Bellido et al. 2014). Perennial SGEC such as SRC have also shown to reduce nitrogen resource depletion (Weih et al. 2014) and increase soil organic carbon concentration, soil fertility and soil biodiversity in the upper soil layer (Schrama et al. 2014) compared to annual FGEC. In general, benefits of perennial compared to annual energy crops are mainly achieved by increased canopy cover and longer rest periods for the soil because of less soil cultivation and lower pesticide inputs (Nerlich et al. 2012). One of the most promising biomass production systems regarding productivity, ecological sustainability and the mitigation of GHG emissions are willow SRC (Don et al. 2012; Schrama et al. 2014). Willows are characterized by fast growth and have among the highest CO_2-exchange rates, light use efficiencies and photosynthetic capacities of woody plant species. Therefore, they are among the most efficient perennial SGEC (Karp and Shield 2008).

Diversity effects on ecosystem services and stability

The efficiency and environmental sustainability of biomass production varies not only among different crops, but also among plant varieties, nutrient regimes, and environmental stressors (Karp and Shield 2008; Weih et al. 2014). Mixtures of different species or varieties of a single species are thereby assumed to improve productivity, yield stability, and resilience in the production system (Cook-Patton et al. 2011; Hulvey et al. 2013; Weih et al. 2014). Positive effects of plant diversity on productivity are usually explained by trait complementarity. Functional diversity of a production system is thereby increased through trait heterogeneity, leading to a wider niche space that can be utilized by species or varieties with complementary traits (Diaz and Cabido 2001; Hillebrand and Matthiessen 2009). In general, plant diversity can have positive effects on the provision of ecosystem services (Balvanera et al. 2006; Hillebrand and Matthiessen 2009; Lefcheck et al. 2015), functioning, and stability (Reusch et al. 2005; Isbell et al. 2015). Theory suggests that diverse systems support ecosystem stability due to food-web complexity (diversity-stability-hypothesis; MacArthur 1955; Goodman 1975) and an increased probability for communities to contain species that respond differently to environmental changes (McCann 2000).

Associated diversity in SRC

As bioenergy has a high potential to become one of the major global energy sources (Immerzeel et al. 2014; IPCC 2014; Weih et al. 2014), biomass plantations such as SRC are expanding. As a result, large-scale land use change towards biomass production systems may have profound impact on the landscape. Additional perennial habitats are provided with relatively low disturbances caused by cultivation activities compared to annual agriculture. The establishment of SRC may therefore have effects on ecosystem services similar to semi-natural areas (Veres et al. 2013). However, the expansion of SRC causes the loss of former land uses and habitats, too. Despite negative responses of open land specialists landscape ecology models suggest that the establishment of SRC in agricultural landscapes has predominantly positive effects on landscape diversity (Langeveld et al. 2012). Furthermore, over all bird richness and abundance has shown to be higher in and around SRC compared to equivalent arable or grassland, as many farmland specialists also used cut plantations (Sage et al 2006). In general, landscape and farm-scale biodiversity can be increased incorporating willow SRC along other crops, as community compositions of ground flora and arthropods in willow SRC differ from other agricultural land uses (Rowe et al. 2011; Baum et al. 2012).

Being key organisms in terrestrial ecosystems, arthropods provide various ecosystem services such as litter decomposition (Ebeling et al. 2014), pollination or pest suppression (Isaacs et al. 2009; Landis and Werling 2010; Veres et al. 2013). As arthropods hold an important role in food webs, arthropod rich SRC can serve as valuable foraging sites for birds and mammals

(Landis and Werling 2010). A strategy to promote a diverse arthropod community associated to SRC is to increase the habitats heterogeneity by planting mixtures of tree species or varieties. In addition to the positive effects on productivity and stability (e.g. Hillebrand and Matthiessen 2009; Isbell et al. 2015), increased plant diversity can affect abundance and diversity of arthropods on various trophic levels as well (e.g. Agrawal et al. 2006; Bangert et al. 2006; Johnson et al. 2006; Barbosa et al. 2009; Cook-Patton et al. 2011; Staudacher et al. 2013; Campos-Navarrete et al. 2015). Several studies also found diversity induced changes of the arthropod community to feed back on the plants performance (Cook-Patton et al. 2011).

Diversity effects across trophic levels

Many studies on the mechanisms of diversity effects distinguish between direct and indirect effects of plants on arthropod richness or diversity (e.g. Crutsinger et al. 2006; Haddad et al. 2009). Indirect effects can be described with the ‘more individuals hypothesis’ (MIH). The MIH states that diverse patches are more productive and can thereby support larger populations of each species due to increased resource availability. The increased abundance of arthropods decreases the probability of local absence of single species and leads to a higher probability of including new species, causing an increased arthropod diversity (Huston 1979; Srivastava and Lawton 1998; Crutsinger et al. 2006). The ‘resource specialisation hypothesis’ (RSH), however, describes direct diversity effects through different trophic levels, which are independent of changes in the systems’ productivity. This hypothesis states that increased plant diversity incorporates heterogeneity due to more diverse microhabitats and a higher amount of ecological niches. Therefore, a higher number of species should be able to coexist in a community (Hutchinson 1959; Price 1983; Schluter and Ricklefs 1993; Haddad et al. 2009). Studies regarding the relevance of direct and indirect effects are, however, inconsistent (Cook-Patton et al. 2011; Crawford and Rudgers 2013; Campos-Navarrete et al. 2015).

The characteristics of diversity effects have strong impact on the arthropods response on different trophic levels, too. On the one hand, there is evidence of indirect bottom-up effects where effects cascade across trophic levels (Crutsinger et al. 2006). The response of the arthropods to increased plant diversity may therefore be stronger on lower trophic levels where the interaction between plant and arthropod are more pronounced (Bailey et al. 2006; Johnson 2011). On the other hand, several studies found direct effects of plant diversity on predators due to increased habitat heterogeneity and niche availability (e.g. Johnson et al. 2006; Johnson 2008; Jones et al. 2011).

The occurrence of direct or indirect diversity effects may depend on the specific characteristics of the study system (Vehviläinen et al. 2007, Tack and Roslin 2011). Especially the response of herbivore abundance to increased plant diversity depends on the specific traits of the plant and herbivore species involved (Barbosa et al. 2009). The detection of general responses and the prediction of overall diversity effects on whole plantations or natural communities are therefore very difficult (Barton et al. 2015). Further research on detailed diversity effects in distinct production systems is required to investigate appropriate management designs for those systems.

Species and genetic diversity

Most biodiversity studies so far dealt with plant species diversity (SD) (e.g. Andow 1991; Jactel and Brockerhoff 2007; Haddad et al. 2009; Cardinale et al. 2011; Lefcheck et al. 2015) and only few studies focused on effects of intraspecific genetic diversity (GD) (e.g. Johnson and Agrawal 2005; Crutsinger et al. 2006; Castagneyrol et al. 2012; McArt et al. 2012), GD derived from interspecific hybridization (Hochwender and Fritz 2004; Wimp et al. 2004; Bangert et al. 2006) or on the combination of SD and GD (e.g. Crawford and Rudgers 2013; Abdala-Roberts et al. 2015; Campos-Navarrete et al. 2015). In general, diversity effects on arthropods are assumed to increase with phylogenetic distance of the plants involved in the polyculture (Dinnage et al. 2012). This implies that diversity effects should be stronger in species mixtures compared to genotype mixtures (Cook-Patton et al. 2012; Abdala-Roberts et al. 2015). However, recently studies also found that intraspecific GD or interactions between SD and GD could have comparable (Crutsinger et al. 2006; Moreira et al. 2014) or even stronger effects on the associated arthropod community than SD itself (Crawford and Rudgers 2013). SD and GD may differ in the characteristics of their effects on arthropods, as studies found the different kinds of diversity to affect arthropods on different trophic levels (Campos-Navarrete et al. 2015) or via different mechanisms (MIH or RSH; Cook-Patton et al. 2011, Crawford and Rudgers 2013). As interspecific hybrids comprise a wide range of plant relatedness, studies on GD derived by different types on hybridization could deliver new information on how plant genetics and different kinds of plant diversity shape arthropod community structures (Cook-Patton et al. 2011). Furthermore, *Salix* and *Populus* hybrids are usually used in SRC for biomass production (Karp and Shield 2008). The detailed evaluation of arthropod responses to hybrid mixtures can therefore reveal great progress in the development of SRC management strategies supporting a diverse arthropod community with various ecosystem services.

Current study and hypotheses

In the current study I have examined the effects of GD in experimental willow stands on the arthropod community at different trophic levels. I hypothesise that (1) the abundance and richness of the arthropods will be positively influenced by GD. Arthropod abundance might be increased by enhanced productivity in more diverse patches (MIH; Huston 1979; Srivastava and Lawton 1998). Direct diversity effects of diet-mixture (Castagneyrol et al. 2012), refuge heterogeneity (Russell 1989), or a spill-over among neighbouring trees (White and Whitham 2000; Barbosa et al. 2009; Utsumi et al. 2011) might also enhance herbivore performance and abundance in polycultures. Higher arthropod richness can either be indirectly triggered by increased abundances (MIH; Huston 1979; Srivastava and Lawton 1998) or be a direct result of increased habitat heterogeneity and niche availability (RSH; Hutchinson 1959; Price 1983). Although there is evidence that abundance driven increases in arthropod richness dominate for GD (Cook-Patton et al. 2012), several GD studies found that increases in arthropod richness cannot be entirely explained by increased abundances (Crutsinger et al. 2006; Campos-Navarrete et al. 2015). Hence, direct effects of plant diversity on arthropod richness may cause additional increases in arthropod richness without increasing abundance. I therefore expect (2) the diversity effects on arthropod richness to be stronger than the diversity effects on abundance. Furthermore, studies found that the responses of the arthropods to increased plant diversity differ between trophic levels (e.g. Bailey et al. 2006; Johnson et al. 2006). I therefore assume (3) the predator-herbivore ratio to change because of differences in the interactions between the arthropods and the plant (food for herbivores, refuge for predators). The recent literature is, however, inconsistent regarding the mechanisms of plant diversity effects on different trophic levels of the arthropod community (direct or indirect effects on predators; Johnson et al. 2006; 2008; Johnson 2011). Therefore, predictions about the direction of the change in the predator-herbivore ratio are not possible. As arthropods are generally assumed to specialize on plant species and not on genotypes (Cook-Patton et al. 2011), I hypothesise that (4) the arthropod community compositions of the different willow genotypes does not differ significantly.

Methods

Experimental setup

To assess the effects of GD in willow SRC on ecosystem functions the project ECOLINC-Salix has been established in spring 2014. The ecosystem functions investigated in this project mainly refer to ecological sustainability (e.g. water and nutrient use, carbon sequestration, biodiversity), tree growth, and yield stability (e.g. resistance to drought and pests). Three experimental sites have been established, one each in Uppsala (Sweden), Rostock (Germany), and Freiburg (Germany). ECOLINC-Salix is part of the TreeDivNet global network of forest diversity experiments to assess the potential advantages and disadvantages of diverse forest plantations (Verheyen et al. 2015). The experimental field sites in Freiburg (southwest Germany) (7°49'E, 48°01'N, altitude: ca. 240m) were established in spring 2014. The soil of the field site is shallow and compacted and consists mainly of sand and gravel. The soil type is cambisol. The field sites were used as a military area associated with a small airport until 1992. The subsequently developed grassland currently adjoining the experiment is grazed by sheep (Scherer-Lozrenzen et al. unpublished data). Woody vegetation is dominated by *Rubus* sp. and the exotic tree species *Robinia pseudacacia* L. and at least 80 m apart. The nearest buildings are located within a distance of 150 meters. The climate is oceanic (following Köppen climate classification) with 11.8 °C mean annual temperature and 858 mm mean annual precipitation (long term average 1990-2015; www.weatheronline.de).

The experimental field sites consist of a randomized block design with three replicates. Four different *Salix* genotypes are planted in plots consisting of 12 × 12 plants, with monocultures of single genotypes and mixtures of two, three, and four genotypes. The genotypes (i.e. 'Tora' (Svalöf-Weibull (SW) cultivar no. 910007, *S. schwerinii* × *S. viminalis*), 'Björn' (SW 910006, *Salix schwerinii* E. Wolf. × *S. viminalis* L.), 'Jorr' (SW 880013, *S. viminalis*) and 'Loden' (SW 890129, *S. dasyclados*)) are characterised by different taxonomic relationships that vary from closely related (siblings Björn and Tora) to different species (Loden) (Scherer-Lozrenzen et al. unpublished data). Each block consists of 15 plots that represent all possible genotype mixtures. In the two genotype plots, the genotypes were planted alternating and in the three and four genotype plots the arrangement of the genotypes is randomised (figure 1).

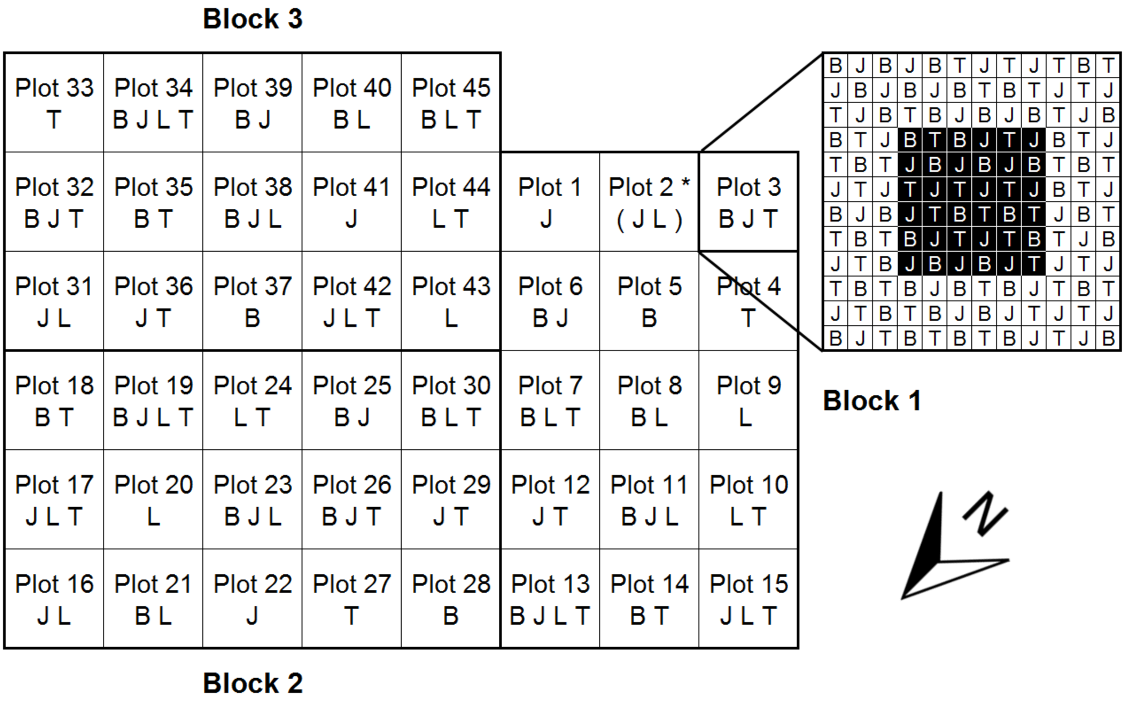

Figure 1: Experimental setup of the ECOLINC-Salix field sites in Freiburg (southwest Germany). The arrangement of the 45 plots in 3 blocks and the mixture of genotypes in each plot are given. The arrangement of individual trees within the plots is exemplarily represented for plot 3. B: Björn. J: Jorr. L: Loden. T: Tora. Black background: sampled core area. A planting error occurred in plot 2. The expected mixture is given in brackets. The actual mixture is B J, which is the same as in Plot 6. Plot 2 was therefore excluded from the sampling.*

The morphology of *S. viminalis* (Jorr) and its hybrids (Björn and Tora) is rather similar, as their leaves are long and narrow. They only differ in the colour of the stem and have slightly different habits. This morphological similarity is reflected in a close phylogenetic relationship, as *S. viminalis* and *S. schwerinii* are sister species (Leskinen and Alstrom-Rapaport 1999). Comprising a larger taxonomic distinction to the other genotypes, Loden (*S. dasyclados*) differs in its morphology, as its leaves are broader than the leaves of the other genotypes. However, the phylogenetic distance of the four genotypes is rather low compared to other *Salix* species (Leskinen and Alstrom-Rapaport 1999). Furthermore, interspecific genetic variation in the genus *Salix* is low compared to other taxa because the genus is evolutionary young (Leskinen and Alstrom-Rapaport 1999; Fahrenz and Weber 2012; Volf et al. 2015). Although different *Salix* species are involved in the ECOLINK-Salix experiment, their close relatedness make it appropriate to compare the results of this study to studies about intraspecific GD rather than to SD studies. The latter mostly deal with more taxonomically distant plant species from different genera or even families (Kostenko et al. 2012; Moreira and Mooney 2013, Moreira et al. 2014 ; Campos-Navarrete et al. 2015). The ECOLINC-Salix design is therefore characterized as a GD design (Verheyen et al. 2015). The genotypes used in the ECOLINK-Salix experiment and also other clones and hybrids of *S. viminalis*, *S. schwerinii* and *S. dasyclados* are commonly used in commercial willow SRC (Karp and Shield 2008).

Sampling

As arthropods are known to respond rapidly to environmental change (Kremen et al. 1993), it is appropriate to assume that the arthropods present in the experimental field site are representative for one year old willow plantations. Biotic effects of the willows on the arthropods can therefore be expected to be present despite their young age. The arthropods were sampled from 27 May to 16 June 2015, mostly between 8 am and 12 noon and between 3 and 7 pm. Thus, particularly hot hours in the early afternoon have been avoided. Sampling was only performed on days with a temperature > 20 °C, when the vegetation was dry and wind speeds were low enough that the trees were not in motion. To sample the arthropods a shaking technique was chosen instead of beating, as I found shaking to do less damage to the trees. The arthropods were shook on a beating tray (72 cm diameter) and collected using an aspirator and soft insect forceps. Due to this sampling method very mobile species are probably underrepresented in the sample as they had a chance to escape. However, such sampling effects are consistent within all sampled trees and should therefore not affect the results. The chosen sampling technique allows a direct assessment of a random share of the arthropods that are present on individual trees, as for every tree the same area (area of the beating tray, ca. 0.4 cm^2) is sampled without bias regarding the tree height. To prevent a neighbouring effect because of interactions between different plots (see Genung et al. 2012), only the inner core area in each plot was sampled, as it is common practise in plant diversity experiment (see also Staab et al. 2015). For the monocultures and the plots with two varieties the inner 4 × 4 and for the plots with three and four varieties the inner 6 × 6 and 8 × 8 plants were sampled. The number of plants per plot increases with the number of varieties to make sure that the sample include a sufficient number of all varieties within a plot. All together 1088 trees were sampled. The number of sampled trees per diversity level varies between 192 (one and four genotype plot) and 432 (tree genotype plots). A total number of 199 (18%) trees were dead or very small (height < 0.5 m) and had to be replaced by individuals of the same genotype outside the core area. The amount of replaced trees was highest in the 2 genotype plots (table 1).

Table 1: Details of sampling for all data (total) and the four genotype diversity levels respectively. The number of sampled plots, the number of sampled trees per plot, the total number of trees sampled, the number of trees that had to be replaced with individuals from outside the core area, the number of trees that did not host arthropods and the number of sampled species are given. Values in brackets refer to the proportion of all sampled trees per diversity level.

Genotype diversity	Number of plots	Trees per plot sampled	Total trees sampled	Trees outside core	Trees without arthropods	Total number of species
1	12	16	192	23 (12%)	19 (10%)	109
2	17*	16	272	59 (22%)	31 (11%)	135
3	12	36	432	82 (19%)	36 (14%)	158
4	3	64	192	35 (18%)	15 (8%)	117
Total	44	-	1088	199 (18%)	101 (9%)	257

* One 2 genotype plot (plot 2, figure 1) was excluded from the sampling because of a planting error

The arthropods were preserved in 70% ethanol and later identified as far as possible (e.g. Goulet and Huber 1993; Böhme 2001; Schaefer 2010; Klausnitzer 2011, Blackman and Eastop 2015), but at least to morphospecies level (hereafter referred to as species). Whenever the level of identification was precise enough, species were assigned to the categories herbivores, predators, or others based on natural history. For example spider were taken as predators while caterpillars, weevils, cicada, and aphids were taken as herbivores. For species that were identified to morphospecies level this classification was based on anatomic features such as mouthparts. Species from other feeding classes (e.g. detritivores) and species that could not be assigned certainly to a particular trophic level (i.e. herbivore or predator) were assigned to the category others.

Statistical analysis

Data were analysed using the statistic software R 3.2.2 (R Development Core Team 2015).

Sampling efficiency was evaluated for all data and for the data of each genotype respectively. The number of expected species was extrapolated using the jacknife 1 (‘jack1’) species richness estimator from the r-package ‘vegan’ (Oksanen et al. 2015). Species accumulation curves were calculated with the same package to visualize the increase in the accumulated number of species with increasing sampling effort. The calculations were performed on the level of individual trees using 1000 permutations.

Generalized linear mixed-effect models (GLMMs) (r-package ‘lme4’, Bates et al. 2015) were used to test for the effect of willow genotype diversity on arthropod richness and abundance on the level of individual trees. Separate models were calculated for all arthropods, only the herbivores and only the predators. To calculate the conditional (variance explained by fixed factors) and marginal (variance explained by fixed and random factors) coefficient of determination (R^2) the ‘r.squaredGLMM’ function from the package ‘MuMIn’ (Barton 2015) was used (Nakagawa and Schielzeth 2013). As arthropod richness and abundance per tree are count data, a poisson error distribution was used in all models analysing those data. Several studies in plant diversity experiments found diversity dependent changes in herbivore abundance being caused by benefits of only one or two dominant pest species (McArt et al. 2012; Campos-Navarrete et al. 2015). Therefore, the significant herbivore abundance models were also run with a reduced dataset, in which the four most abundant herbivore species with overall abundances over 300 individuals were excluded. Additionally, GLMMs were run on the predator-herbivore ratio to test for top-down effects of predators. As the data on the predator-herbivore ratio are proportional data, binomial GLMMs were used. Trees without arthropods and trees that hosted only arthropods assigned to the category others were excluded from this data. All models testing the effects of willow genotype diversity were run for the whole data set and for four subsets containing only the trees from one of the four willow genotypes to investigate if single genotypes respond differently to plot genetic diversity. Multiple comparisons (r-package 'multcomp', Hothorn et al. 2008) of additional GLMMs (fixed factor: genotype identity) were performed to compare tree-level arthropod richness and abundance of the different genotypes.

To account for unobserved environmental variation that differ spatially (e.g. soil quality) block and plot identity were included as a nested random factor (plot nested in block). The mixture of genotypes in each plot was chosen as a second random factor to account for potential mixture-specific variances. For overdispersed data (i.e. the variance exceeded the mean) the models were also run with an observation level random effect (OLRE), as this approach has shown to yield more accurate model-estimations for different kinds of overdispersion (Harrison, 2014). The model with the OLRE was chosen whenever the value of Akaikes Information Criterion (AIC) was distinctly ($\delta>2$) lower than the than the AIC of the model without the OLRE, providing that this model was not found to be unreliable (very unrealistic z-values and underestimation of the standard error). To check if the different sample sizes for each diversity level affected the models because of sampling effects, models were also calculated with a reduced data set in which all diversity levels are standardized to the same number of trees. For each diversity level 192 trees (i.e. the smallest number of trees per diversity level; see table 1) were drawn randomly without replacement. This was done 250 times for each model. Unreliable calculations of the model were excluded and the mean was calculated for each variable of the model output. Those models are hereafter referred to as subsample models to distinguish them from the original models. Models with p-values over the significance level of 0.05 but still under 0.1 are referred to as marginally significant trends.

Non-metric multidimensional scaling (NMDS) from the r-package 'vegan' was used to produce an ordination for visualizing the similarity of the arthropod communities on the different genotypes. The Morisita-Horn similarity index was chosen for the calculations, as it is relatively robust against potentially undersampled communities. This multidimensional scaling approach projects the objects with regard to a preferably small contortion of their real distance and therefore gives a more accurate illustration of the real similarity between the samples compared to other ordination approaches. Data were pooled for each genotype per plot. Rare species with less than five individuals were excluded from the data, as they are statistically irrelevant (Leyer and Wesche 2007). To test for differences between the arthropod communities of the different genotypes an analysis of similarity (function 'anosim') was performed.

Results

Altogether 4580 arthropods belonging to 257 different species from 19 orders were sampled on 1088 trees (table 1 and 2). There were 101 (9%) trees that did not host any arthropods. The highest amount of trees without arthropods was in the 3 genotype plots (table 1). The most dominant taxa, i.e. aphids (1850 Individuals) and cicadas (866 Individuals, mainly larva), were herbivores belonging to the order Hemiptera. The most dominant predacious arthropods ware spiders and parasitic wasps. Many species had low abundances. A total number of 176 (68%) species had total abundances below 5 and of those 113 species were singletons (table 2, for a detailed list of all species see table A3). Total herbivore and predator species richness were similar (herbivores: 106 species, predators: 105 species), however, total herbivore abundance was 6 times higher than total predator abundance (table 3).

Table 2: Taxonomic overview of the sampled arthropods. Richness and abundance is given on the level of orders for all arthropods (Total), only the herbivores and only the predators.

	All arthropods		**Herbivores**		**Predators**	
Order	**Richness**	**Abundance**	**Richness**	**Abundance**	**Richness**	**Abundance**
Acari 1	1	206	1	206	-	-
Acari 2	1	1	-	-	-	-
Araneae	25	254	-	-	25	254
Coleoptera	43	202	23	64	14	73
Collembola	3	151	1	113	-	-
Dermaptera	1	2	-	-	1	2
Diptera	29	173	-	-	4	12
Ensifera	1	1	1	1	-	-
Hemiptera	61	2957	55	2950	6	7
Hymenoptera	56	402	3	152	49	241
Ixodida	1	5	-	-	1	5
Lepidoptera	18	141	18	141	-	-
Mesostigmata	2	4	-	-	2	4
Neuroptera	2	7	-	-	2	7
Opiliones	1	3	-	-	1	3
Psocoptera	4	21	-	-	-	-
Thysanoptera	4	46	4	46	-	-
Trichoptera	1	1	-	-	-	-
Other	3	3	-	-	-	-
Total	257	4580	106	3673	105	608

Sampling efficiency

The jacknife1 species richness estimation suggests that the sampling contained 68.9% of the totally expected species pool present on the willows (table 3). As the species accumulation curve (figure 2) did not yet reach an asymptote, the probability of including new species in the sample is still high, if the sample size would be increased.

Table 3: Results of the species richness estimation for all data (Total) and the four genotypes respectively. The total arthropod abundance, the total number of sampled species, the estimated total species richness and the standard error from the jacknife1 estimation (Jack1 ±SE), the share of sampled species in the estimated total number of species in percent (% sampled) and the number of sampled trees (N) are given. The data for herbivores (H) and predators (P) are given in brackets.

Genotype	**Abundance**	**Species**	**Jack1 ±SE**	**% sampled**	**N**
Björn	1112 (H: 937, P: 128)	114 (H: 54, P:43)	176 ±9 (H: 78±5, P: 72±6)	64.9% (H: 69.3%, P: 60.0%)	273
Jorr	1114 (H: 900, P: 131)	126 (H: 51, P:51)	194 ±9 (H: 72±5, P: 83±6)	65.0% (H: 70.9%, P: 61.7%)	276
Loden	1156 (H: 915, P: 149)	152 (H: 69, P: 61)	229 ±11 (H: 97±6, P: 99±7)	66.5% (H: 71.2%, P: 61.9%)	268
Tora	1198 (H: 921, P: 200)	128 (H: 60, P: 46)	184 ±9 (H: 84±5, P: 64±5)	69.6% (H: 71.5%, P: 72.1%)	271
Total	4580 (H: 3673, P: 608)	257 (H: 106, P: 105)	373 ±11 (H: 152±7, P: 151±7)	68.9% (H; 69.8%, P: 69.6%)	1088

The share of sampled species in the total estimated species pool of the four genotypes was similar and between 64.9 and 69.6%. The total data suggest equal sampling efficiencies for herbivores and predators. However, Tora is characterized by a higher sampling efficiency for predators, while for the other genotypes the sampling efficiency for herbivores is higher than for predators (table 3).

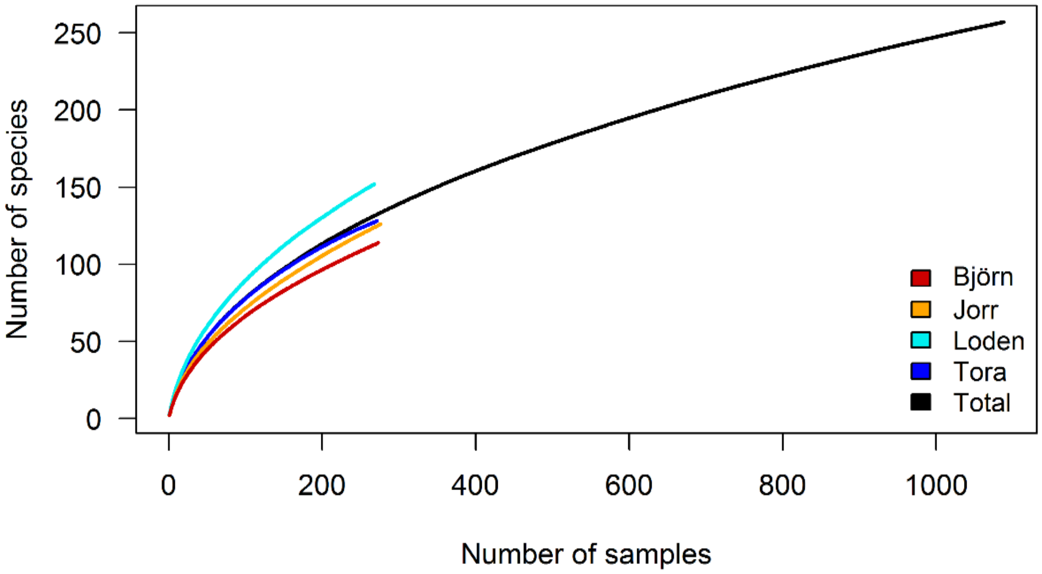

Figure 2: Species accumulation curve for all genotypes (Total) and for each genotype respectively. The curve represents the trend of the expected number of sampled species for an increasing number of samples (i.e. trees).

Effects of genetic diversity

Total arthropod richness increased significantly with the increase of genetic diversity (p=0.011, detailed modelling results are given in table 4). This effect is mainly derived from a significant increase of total herbivore richness (p=0.042). Total abundance data were unrelated to GD. The response of arthropod richness and abundance to the increase of GD varies between genotypes. However, all significant diversity effects and marginally significant trends in the arthropods richness and abundance throughout trophic levels are positive.

Table 4: Results of the original GLMMs for all data (Total) and subsets of the four genotypes respectively: Björn: B, Jorr: J, Loden: L, Tora: T. For each set of data results of the models on richness (Rich) and abundance (Ab) of all species (Rich all; Ab all), only the herbivores (Rich H; Ab H), only the predators (Rich P; Ab P) and the predator-herbivore ratio (Rich P/H; Ab P/H) per tree. For each model the estimate and standard error (SE), the value of the z-statistic (Z) and the p-value (P) are given. Significant (P≤0.05) models are printed in bold.

Data	**Model**	**Estimate ± SE**	**Z**	**P**	**Model**	**Estimate ± SE**	**Z**	**P**
Total	**Rich all**	**0.09 ±0.04**	**2.54**	**0.011**	Ab all*	0.06 ±0.05	1.24	0.217
	Rich H	**0.09 ±0.04**	**2.03**	**0.042**	Ab H*	0.04 ±0.09	0.47	0.640
	Rich P*	0.07 ±0.06	1.23	0.220	Ab P*	0.08 ±0.06	1.36	0.173
	Rich P/H	-0.02 ±0.08	-0.23	0.821	Ab P/H	0.04 ±0.14	0.27	0.789
B	Rich all	0.07 ±0.06	1.24	0.216	Ab all*	0.09 ±0.10	0.99	0.323
	Rich H	0.06 ±0.07	0.85	0.394	Ab H*	0.11 ±0.12	0.94	0.348
	Rich P	0.11 ±0.10	1.16	0.247	Ab P*	0.12 ±0.11	1.11	0.267
	Rich P/H	0.04 ±0.12	0.34	0.738	Ab P/H	-0.03 ±0.20	-0.14	0.894
J	Rich all	0.09 ±0.06	1.56	0.119	Ab all*	0.08 ±0.07	1.07	0.283
	Rich H	0.09 ±0.11	0.80	0.424	Ab H*	0.08 ±0.14	0.57	0.572
	Rich P	0.12 ±0.13	0.93	0.350	Ab P	0.13 ±0.13	1.00	0.317
	Rich P/H	0.01 ±0.25	0.04	0.965	Ab P/H	0.10 ±0.28	0.36	0.717
L	**Rich all**	**0.12 ±0.04**	**2.76**	**0.006**	Ab all*	0.04 ±0.06	0.71	0.478
	Rich H	0.09 ±0.05	1.67	0.096**	Ab H	-0.02 ±0.07	-0.24	0.808
	Rich P	**0.26 ±0.10**	**2.51**	**0.012**	**Ab P***	**0.26 ±0.11**	**2.49**	**0.013**
	Rich P/H	0.15 ±0.13	1.22	0.222	Ab P/H	0.25 ±0.14	1.85	0.064**
T	Rich all	0.11 ±0.06	1.94	0.053**	Ab all*	0.13 ±0.07	1.84	0.066**
	Rich H	**0.16 ±0.06**	**2.85**	**0.004**	**Ab H***	**0.18 ±0.08**	**2.38**	**0.017**
	Rich P	-0.05 ±0.11	-0.49	0.628	Ab P*	-0.08 ±0.11	-0.66	0.512
	Rich P/H	-0.20 ±0.11	-1.79	0.074**	Ab P/H	-0.21 ±0.18	-1,16	0.246

*Model with observation level random effect (OLRE) to account for overdispersion
**p-values between 0.05 and 0.1 indicate marginally significant trends

Arthropod richness and abundance on Björn and Jorr did not respond at all, as GLMMs are throughout insignificant. Loden showed a significant positive effect on predator richness (p=0.012) and a marginally significant positive trend (p=0.096) in herbivore richness, leading to a significant increase in the richness of all arthropods (p=0.006). There was also a significant increase (p=0.013) in Loden's predator abundance, but not in herbivore abundance. This resulted in a marginally significant positive trend in the predator-herbivore abundance ratio (p=0.064). Tora showed significant positive diversity effects on herbivore richness (p=0.004) and abundance (p=0.017), leading to marginally significant positive trends in the richness (p=0.053) and abundance of all arthropods (p=0.066). Predators were, however, not affected on Tora. Therefore, there was a marginally significant negative trend in Tora's predator-herbivore richness ratio (p=0.074). The predator-herbivore abundance ratio was, however, not affected by GD. The positive diversity effect on herbivore abundance on Tora did not change when the model was run with the reduced data without the most abundant arthropod species (data not shown). The subsample models reveal qualitatively similar results regarding the significant diversity effects and marginally significant trends, albeit with predominantly higher p-values due to smaller sample size (table A1).

The magnitude of the positive diversity effects on arthropod richness and abundance was throughout rather low, as the significant GLMMs only explaine up to 11.9% of the variance in the data (see conditional R^2 of the GLMM on total herbivore richness; detailed model outputs with R^2 estimations are given in table A2). A high amount of this variance is also explained by the random factors, as the conditional R^2 is about 8 times higher than the marginal R^2. For the R^2 estimations of the significant genotype specific effects differences between marginal and conditional R^2 are, however, less pronounced. For example, the conditional R^2 is about 2 times higher than the marginal R^2 for the significant effects on herbivore richness and diversity (Tora). For the significant effects on predator richness and diversity (Loden) marginal and conditional R^2 are the same.

Because of the low magnitude of the diversity effects, some of the genotype specific effects were not strong enough to affect the total data. Only the total richness of all arthropods (figure 3) and the herbivores (figure 4a-c) increased significantly, due to the combination of significant effects or marginally significant trends for Loden and Tora. The genotype specific diversity effect on herbivore abundance (Tora) was, however, not strong enough to affect the total data (figure 4d-f). The significant positive effects on predator richness and abundance (Loden) did not cause an increase in total predator data, too (figure 5).

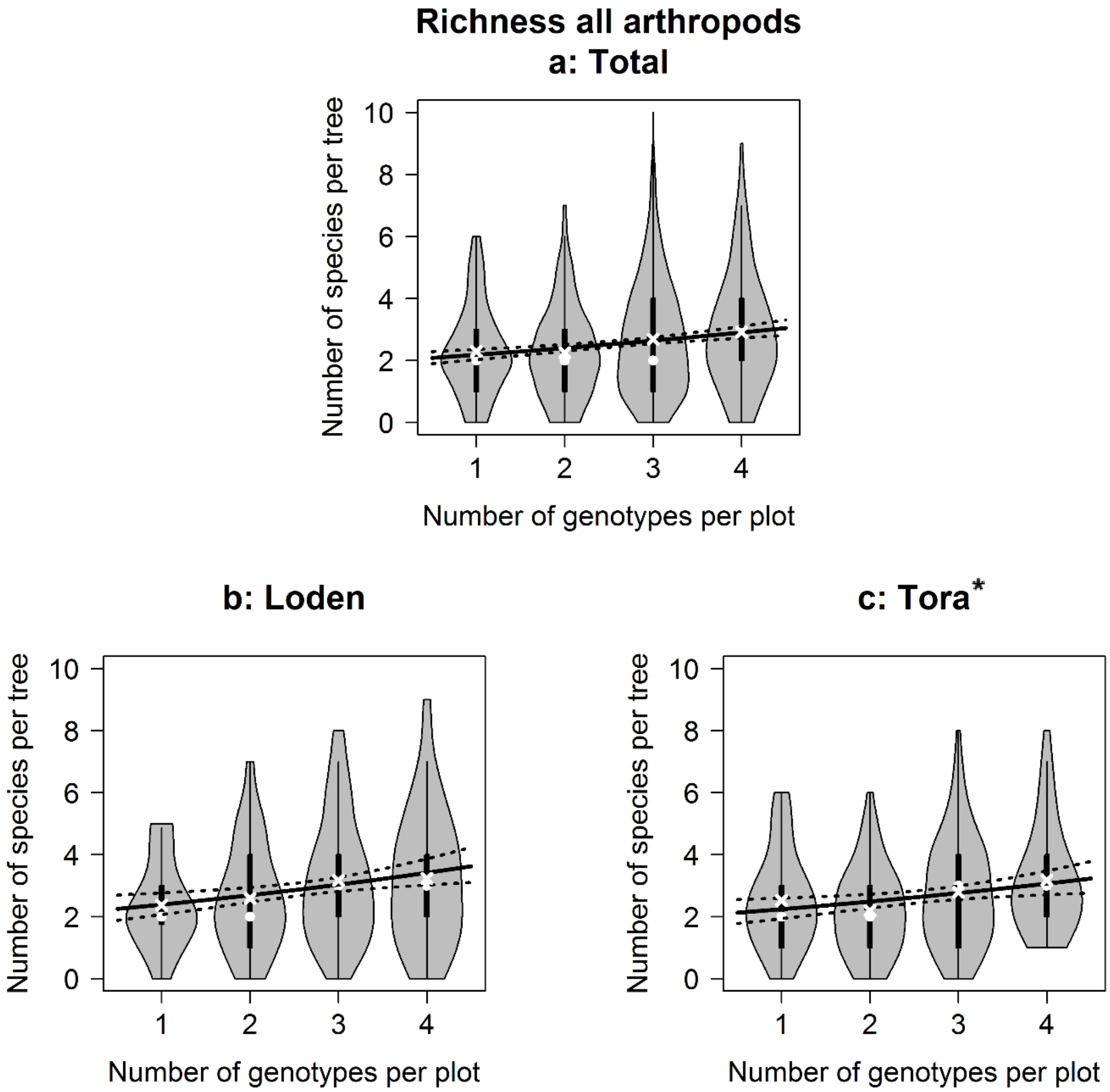

Figure 3: Violin plots (r-package 'vioplot', Adler 2005) for the diversity of all arthropods for the total dataset (a) and the data of Loden (b) and Tora (c) to visualize the data for each diversity level. Data of Björn and Jorr and the correspondent abundance data are not shown as they were unrelated to genetic diversity. Violin plots consist of a boxplot that also shows the probability density of the data. A rotated kernel density plot is added to each side of the boxplot. In addition to the median (white dot), the mean (white x) was included for each violin plot. The fit of the respective model (black line) and its confidence interval (dashed lines) are printed for the significant effects and marginally significant trends (*).

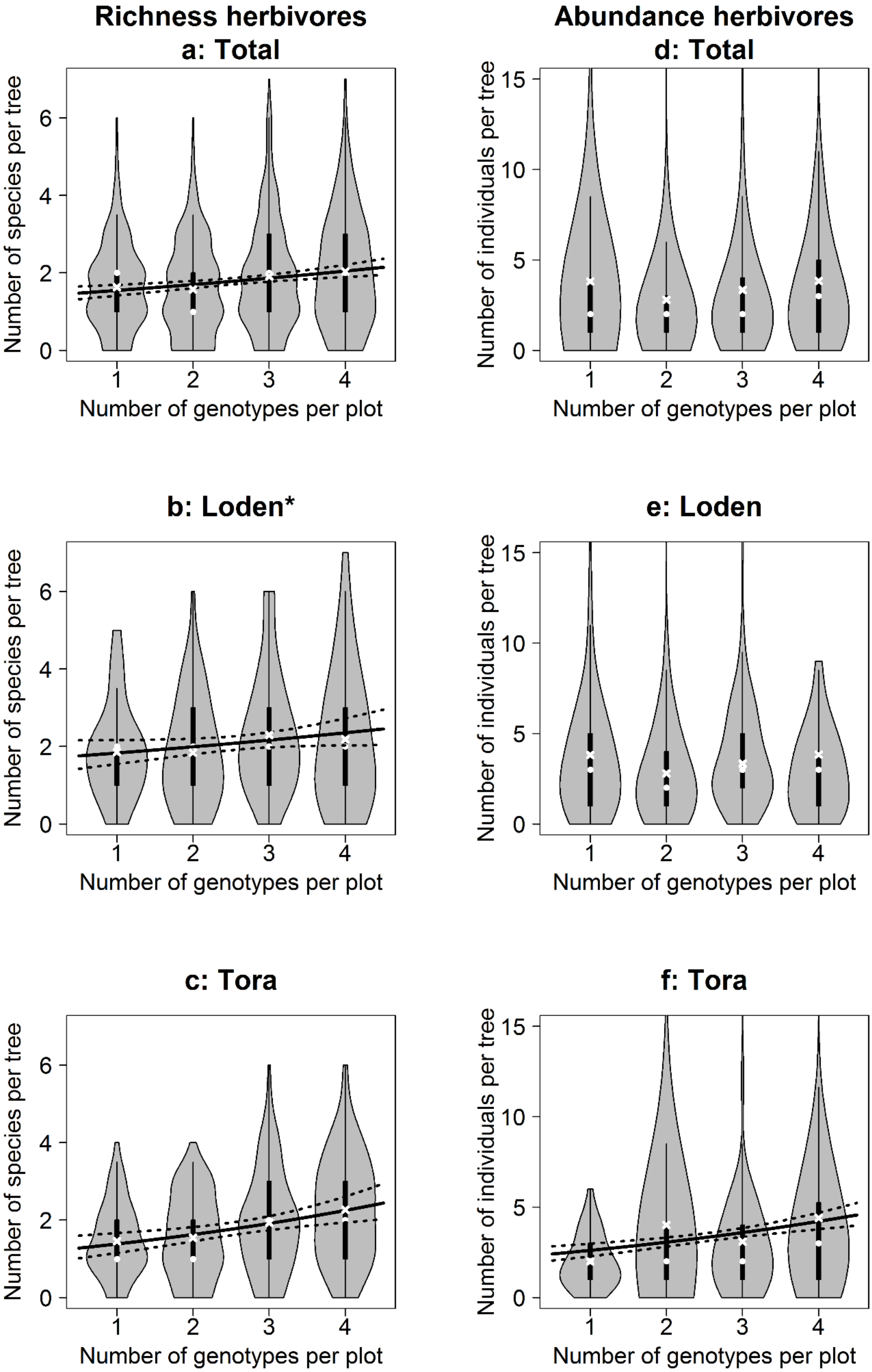

Figure 4: Violin plots for the herbivore richness (a,b,c) and abundance (d, e, f) for the total dataset (a,d) and the data of Loden (b,e) and Tora (c,f). For further details see figure 3. Only the range between 0 and 15 individuals per tree is shown for the abundance data to avoid data transformation.

The fact that there were no significant effects on the total predator data, while the diversity effect on total herbivore richness showed the highest conditional R^2 for al significant effects, suggests that diversity effects on herbivores were generally more pronounced than diversity effects on predators. Furthermore, the effects on arthropod richness were stronger than the effects on abundance, as there was no significant increase in the total abundances of all arthropods, only the herbivores, or only the predators (figures 4d and 5c). However, total predator richness did not show any significant effects or marginal significant trends, too (figure 5a). The variance in the data explained by GD is only slightly higher for predator diversity (3.9%, table A2) than for predator abundance (3.3%) in the significant genotype specific effects. The stronger influence of increased plant diversity on richness than on abundance was therefore restricted to herbivores. Although there were only significant effects on either herbivores or predators on one genotype, those effects were not strong enough to significantly affect the predator-herbivore ratios, but only caused marginally significant trends.

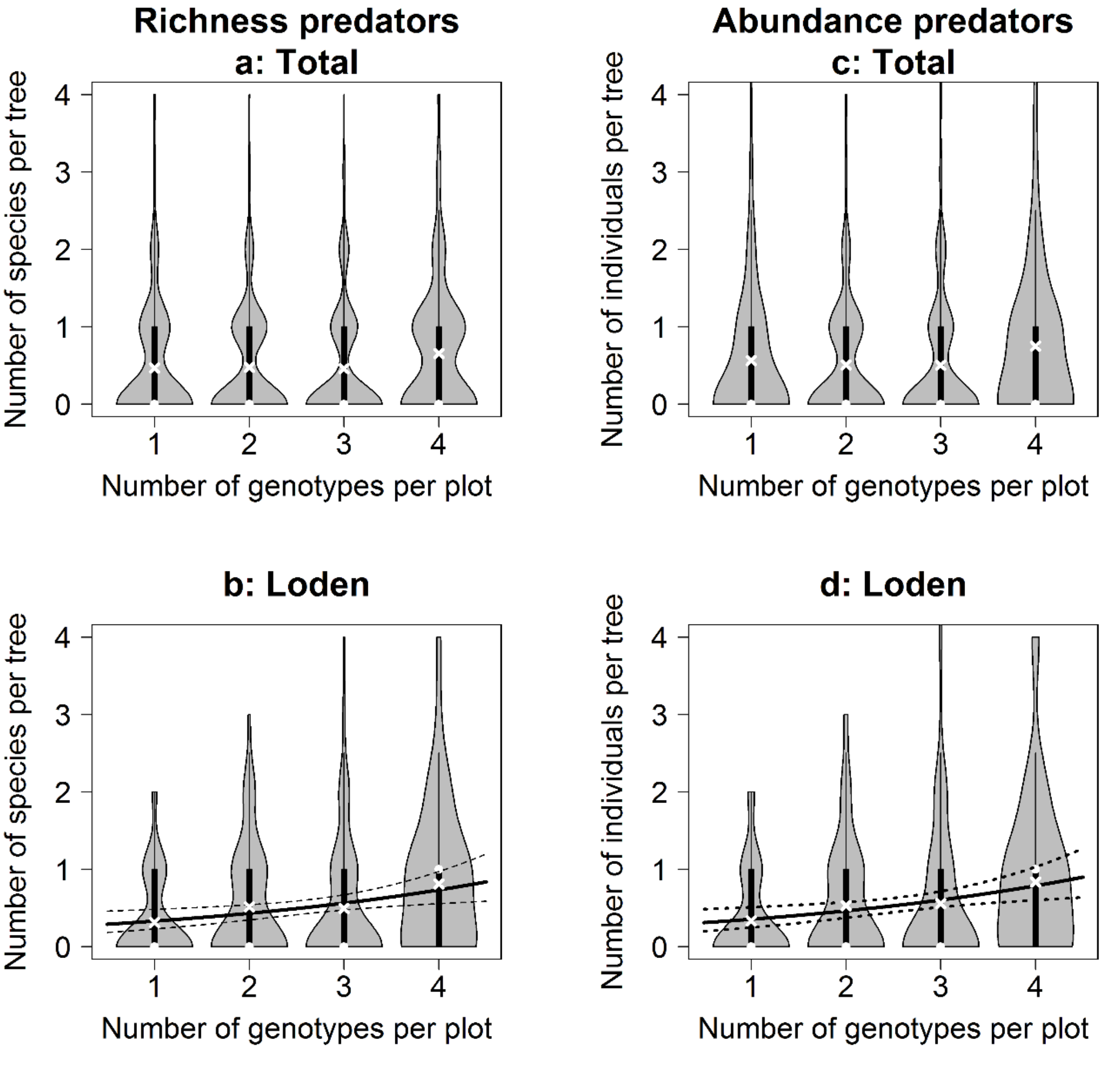

Figure 5: Violin plots for the predator richness (a,b) and abundance (c,d) for the total dataset (a,c) and the data of Loden (b,d). For further details see figure 3. Only the range between 0 and 4 individuals per tree is shown for the abundance data to avoid data transformation.

Effects of genotype identity

The highest total arthropod richness was on Loden. This genotype hosted 152 different species, while the other genotypes hosed between 114 and 128 species (table 3). Multiple comparisons of GLMMs testing the effect of genotype identity on the arthropods revealed additional information about significant differences in arthropod richness and abundance per tree between the genotypes. Loden's arthropod species richness per tree was significantly higher compared to Björn and Jorr but not compared to Tora (p=0.002, <0.001 and 0.435 for Björn, Jorr and Tora respectively, figure 6a). The higher arthropod richness on Loden is also visible in the species accumulation curves of the different genotypes (figure 2). Furthermore, Loden was characterized by a significantly higher herbivore richness and abundance per tree compared to Jorr (p=0.016 and <0.001 for abundance and richness respectively) but not compared to the other genotypes. Total arthropod abundance was highest on Tora, as 1198 individuals were found on Tora while 1112, 1114 and 1156 individuals were found on Björn, Jorr and Loden respectively (table 3). Tora was also characterized by a higher total predator abundance than the other genotypes (200 instead of 128-149, table 3). Predator abundance per tree was significantly higher for Tora compared to Björn and Jorr but not compared to Loden (p=0.026, 0.048 and 0.392 for Björn, Jorr and Loden respectively). This resulted in a higher abundance of all arthropods on Tora compared to Björn and Jorr (p=0.004 and 0.012 respectively, figure 6b). The relatively high predator abundance on Tora resulted in a lower total herbivore-predator abundance ratio compared to the other genotypes. While Björn, Jorr and Loden hosted 7.3, 6.9 and 6.1 times more herbivores than predators, Tora hosted only 4.6 times more herbivores (table 3). The predator-herbivore ratio on the level of individual trees, however, did not vary significantly between the genotypes (all p-values >0.4).

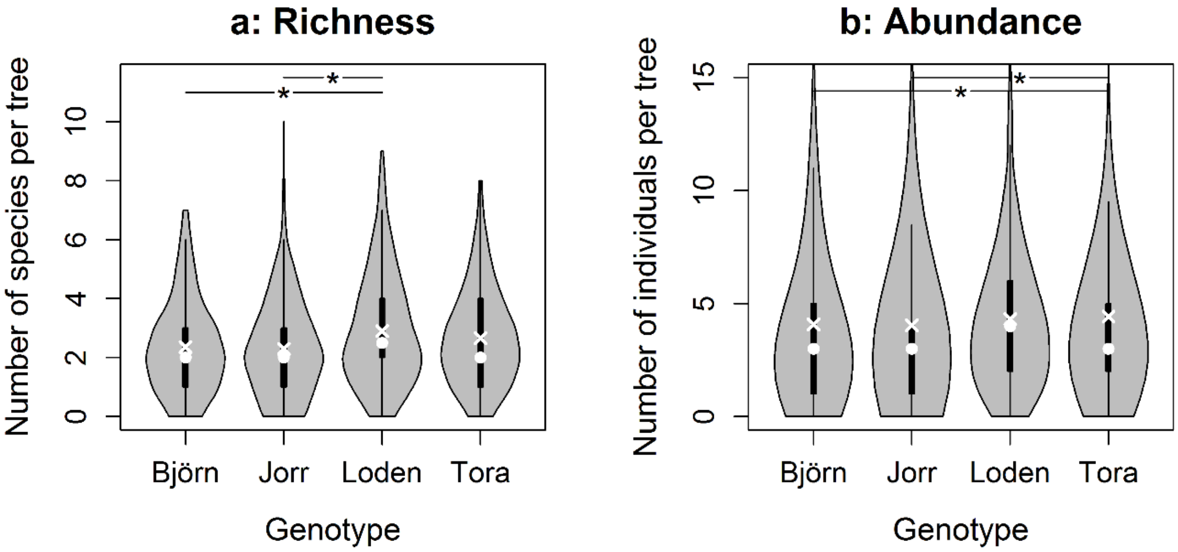

*Figure 6: Violin plots for the total arthropod richness (a) and abundance (b) per genotype. * indicates for significant differences based on multiple comparisons of the corresponding GLMMs. For further details see figure 3. Only the range between 0 and 15 individuals per tree is shown for the abundance data to avoid data transformation.*

Community Composition

The analysis of similarities show that the genotypes varied significantly (p=0.001) in the arthropod communities they hosted. However, genotype identity explained only 9.9% of the variance in the arthropod community composition. Although the distribution of the samples of the four genotypes and the dispersion ellipses in the NMDS-ordination overlap strongly, it is visible that the community composition of Loden differs from the others (figure 7). Additional analyses of similarities for only the samples of Björn, Jorr and Tora were not significantly different (p= 0.219, R^2= 0.013). This shows that there were no statistical dissimilarities between the arthropod communities of those genotypes and only Loden is characterized by a different community composition.

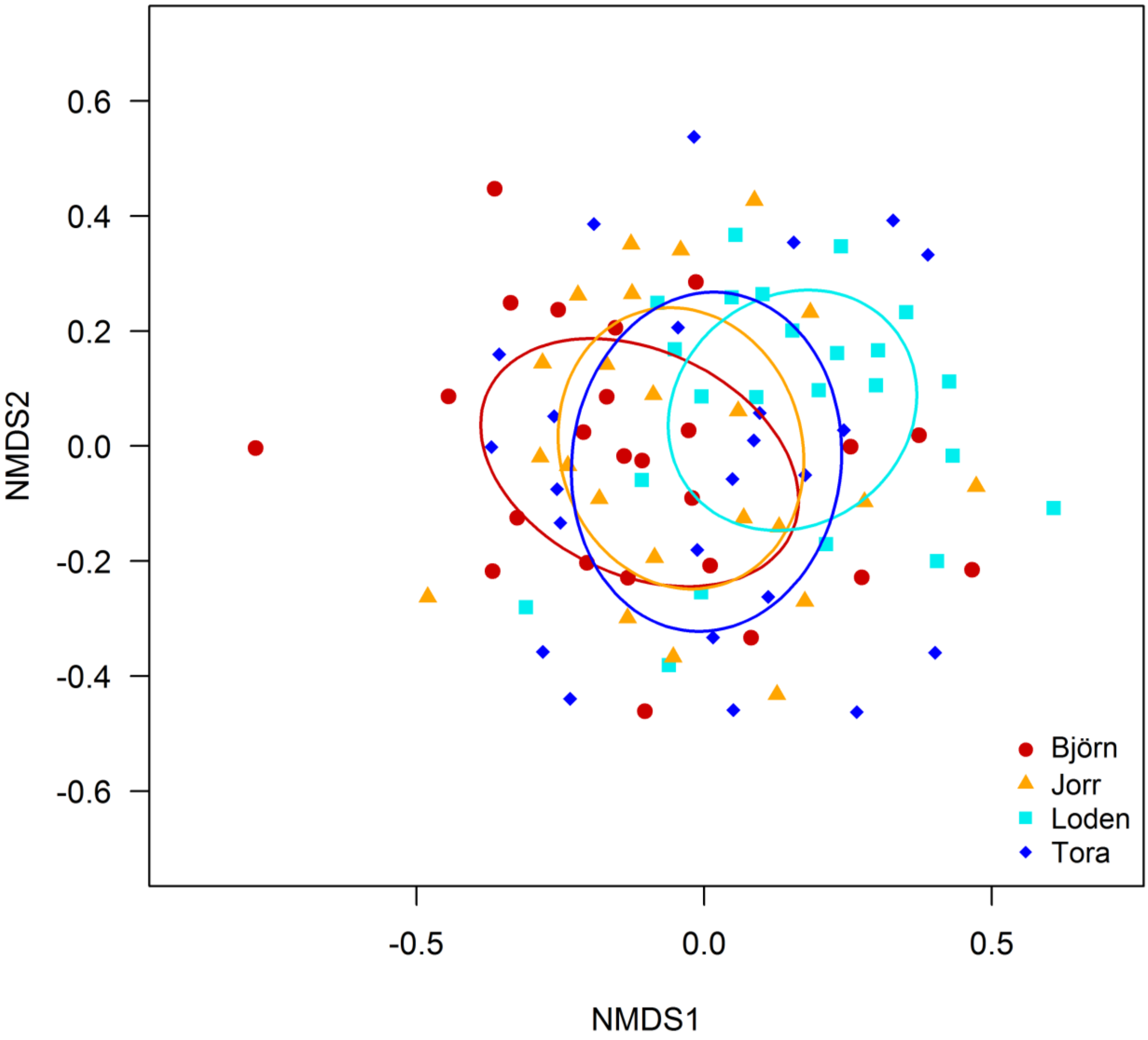

Figure 7: NMDS Ordination plot (stress = 0.325) based on the Morisita-horn index of the pooled abundance data per plot and genotype for each genotype respectively (N=94). Genotype identity is indicated by coloured symbols. Dispersion ellipses are calculated using standard deviations of point scores.

Discussion

Diversity effects

I found significant total positive diversity effects on the richness of all arthropods and only the herbivores. I also found significant positive effects on the total herbivore and predator abundance and the predator richness on single genotypes. Those effects were, however, not strong enough to affect the total community throughout the entire planting. All significant diversity effects were positive. The results therefore agree with my hypothesis that (1) arthropod richness and abundance increase with increasing GD. These results indicate that GD in willow plantations can promote a diverse arthropod community. The use of genetically diverse mixtures in commercial willow SRC for biomass production could therefore improve the value of these plantations as a habitat for arthropods.

As the strength of diversity effects generally increases with phylogenetic distance of the plants that are included in the mixture (Dinnage et al. 2012), GD effects are assumed to be less pronounced than SD effects (Cook-Patton et al. 2011; Castagneyrol et al. 2012, Abdala-Roberts et al. 2015). R^2 estimations of the significant diversity effects in the current study indicate that only a low amount of variance in the data was explained by GD. My results therefore agree with the assumption of GD effects being of low magnitude. However, the estimations of marginal and conditional R^2 exhibit various limitations and the total values should not be overvalued (Nakagawa and Schielzeth 2013).

Because I did not measure plant performance, it is not clear if the genotype specific increases in arthropod abundance were triggered by increased biomass production and resource availability, as the MIH suggests (Huston 1979; Srivastava and Lawton 1998). There is, however, evidence that tree height can have pronounced effects on herbivore abundance and diversity, due to increased availability of food resources (Campos et al. 2006). Furthermore, the significant increases in herbivore (Tora) and predator (Loden) richness and abundance indicate that at least part of the increase in richness was abundance-driven, as it is also stated by the MIH. High abundances hereby increase the probability of including additional species in the sample and decrease the probability that single species are absent on small spatial scales (Huston 1979; Srivastava and Lawton 1998). The importance of this hypothesis for GD is stated by Cook-Patton et al. (2011) who found the MIH to be predominantly responsible for increased arthropod diversity in GD. However, other studies found that plant GD induced increases in arthropod abundance (McArt et al. 2012; Crawford and Rudgers 2013; Moreira and Mooney 2013) or diversity (Kotowska et al. 2010; Campos-Navarrete et al. 2015) can only partly be explained by the MIH.

Positive diversity effects on herbivore abundance for example can be also explained by associational effects (Barbosa et al. 2009, Hambäck et al. 2014). Several previous studies found

GD to cause increased herbivore abundance and herbivory (i.e. associational susceptibility (AS)) (Koricheva et al. 2000; Crutsinger et al. 2006; Utsumi et al. 2011; Castagneyrol et al. 2012). The increase in herbivore abundance can thereby be explained by a benefitting effect on herbivores in mixtures through enhanced patch detection, diet-mixture (Castagneyrol et al. 2012), and spill-over among neighbouring trees (White and Whitham 2000). In the current study, an increase in herbivore abundance was only detectable on Tora. This genotype was characterized by a significantly higher predator abundance than the other genotypes causing a lower total herbivore-predator abundance ratio. This relatively low abundance of herbivores could have been a possible result of Tora being less palatable than the other genotypes to some herbivores. In general, more palatable plants are assumed to be the source of herbivores in spill-over dynamics (White and Whitham 2000; Barbosa et al. 2009; Utsumi et al. 2011). This strengthens the assumption of a spill-over of herbivores from preferred hosts to neighbouring less preferred individuals of Tora. The increase in herbivore abundance did not derive from benefits of a single dominant herbivore species, which was previously found in other studies (McArt et al. 2012; Campos-Navarrete et al. 2015). This suggests that genotype mixtures provided general benefits for several herbivores on Tora. Opposing effects of associational resistance (AR; i.e. diversity induces decrease in herbivore performance) were not present in this study, as the underlying mechanisms are predominantly restricted to specialist herbivores and the presence of non-host trees in the polycultures (Andow 1991; Root 1973; Russell 1989). Because herbivores can be expected not to specialize on different genotypes (Cook-Patton et al. 2011) these mechanisms did not apply here. However, effects of AR and discrimination between genotypes have previously been shown in genetic diverse willow plantings for the pest species *Phratora vulgatissima* (Peacock and Herrick 2000; Peacock et al. 2001). Other than the significant responses of herbivores to increased GD on Tora, the diversity effects on Loden are probably triggered by general differences in the arthropod community composition compared to the other genotypes. In general, it is very likely that the same variables that cause differences in the arthropod communities are also responsible for diversity effects (Johnson et al. 2006).

The existence of direct diversity effects on arthropod richness is supported by stronger effects on richness than on abundance. This was the case for herbivores in the current study (see diversity effects on herbivores on Tora and in the total data), as I expected (2). A greater strength of both SD and GD effects on herbivore richness than abundance was also described by Campos-Navarrete et al. (2015). Crawford and Rudgers (2013) found effects of GD without SD to affect only arthropod richness but not abundance. Indirect abundance-driven effects could therefore not have been responsible for the increases in herbivore richness alone. It is very likely that direct effects of increased intraspecific plant heterogeneity attracted more species that coexisted in a community due to a higher amount of microhabitats and ecological niches (RSH; Hutchinson 1959; Price 1983). Although plant traits were not measured in the current study, they can be assumed to vary between the genotypes, providing a more heterogeneous habitat in genotype mixtures (Barbour et al. 2015). A strong influence of direct SD and GD effects on herbivore richness due to increased resource heterogeneity has been stated by various authors (SD: Haddad et al. 2009; Ebeling et al. 2014; GD: Kotowska et al. 2010; Campos-Navarrete et al. 2015). Other than the effects on herbivores, Haddad et al. (2009) found positive SD effects on predators to be entirely derived from an increase in predator abundance (MIH; Huston 1979; Srivastava and Lawton 1998). Unlike my expectations (2), the effects on predator richness were not considerably stronger than the effects on abundance (see diversity effects on predators on Loden). This indicates for abundance driven increases in predator richness in the current study. The relatively strong diversity effect on total arthropod richness, without affecting total abundance was therefore only derived by the diversity effects on herbivores.

Variance of diversity effects across trophic levels

Diversity effects on the total herbivore community were stronger than diversity effects on the predators as there was only a significant effect on total herbivore but not on total predator richness. Smaller amounts of explained variance in Loden’s predator effects compared to Tora’s herbivore effects also reflect the more pronounced response of the herbivores. However, there was no significant diversity effect on the predator-herbivore ratio for the total data. The genotype specific effects on herbivores (Tora) and predators (Loden) only partly caused marginally significant trends in the predator-herbivore ratio on the level of single genotypes, too. My expectations for changes in the herbivore-predator ratio (3) have therefore only partly been supported.

The stronger total effects on herbivores than on predators agree with evidence for indirect bottom-up effects of GD, where effects weaken towards higher trophic levels (Bailey et al. 2006; Johnson 2011). The significant effects on herbivores without affecting predators on Tora also support this mechanism. Loden’s results, however, support the existence of direct effects of plant diversity (i.e. the first trophic level) on richness and abundance of predators (i.e. the third trophic level) with only a weak marginally significant trend in the richness of herbivores (i.e. the second trophic level). Many other studies also found GD to affect predators directly (Johnson et al. 2006; Johnson 2008; Jones et al. 2011) and more strongly than herbivores (Crutsinger et al. 2009, Campos-Navarrete et al. 2015). Direct positive diversity effects on predators can also increase top-down control of predacious arthropods as suggested by the enemies hypothesis (Root 1973; Russell 1989). This theory states that predators are more effective in more diverse habitats (Andow 1991; Root 1973; Russell 1989). The increase in predator richness and abundance on Loden could have increased top-down control and might thereby have suppressed a positive diversity effect on herbivores. However, this increase in the top-down control was not strong enough to negatively affect herbivores (i.e. AR), as there was a marginally significant positive trend in herbivore richness on Loden.

My prediction that mechanisms of diversity effects (i.e. direct or indirect effects) vary between trophic levels are supported, because effects on different trophic levels are restricted to different genotypes. Furthermore, this shows that the effects on different trophic levels are at least partly independent from each other. The mechanism of indirect bottom-up effects supported by the total data can therefore be rejected when focusing on single genotypes. Hence, it is very important to consider genotype specific effects and not just the total effects to be able to make appropriate assumptions about the mechanisms that underlie the observed effects. However, as the recent literature on the mechanisms causing diversity effects on higher trophic levels is inconsistent, the occurrence of direct or indirect effects may be dependent on the plant species or genotype and the specific arthropods that are involved in the study.

Community composition

My results demonstrate that the community composition from Loden significantly differed from the other genotypes and was characterized by higher sampled and expected total arthropod species richness. However, as the community compositions of the other three genotypes did not vary significantly, my corresponding hypothesis (4) can still partly be supported. Because no specific plant traits were measured, it is not clear what caused these differences. However, Loden’s morphology varies from the morphology of the other genotypes, which is probably due to the more distant phylogenetic relatedness of Loden to the other genotypes (Leskinen and Alstrom-Rapaport 1999). This variation could have attracted additional arthropod species because of increased structural heterogeneity and additional refuges. The diversity effects found on Loden mainly refer to predator richness and abundance. In general, many predators (e.g. several spider species) prefer structural complex habitats (Halaj et al. 2000; Borges and Brown 2001) and benefit from the increased availability of refuges in structurally complex polycultures (Russell 1989). This increased refuge availability could imply more opportunities for sheltering ambush predators or allow a greater amount of coexisting hunting techniques.

Furthermore, the larger phylogenetic distance of Loden is probably reflected in additional semiochemicals or different defensive secondary metabolites compared to the other three genotypes. This variation could have attracted additional arthropod species, too. As I did not measure plant chemical traits, this cannot be confirmed. Previously, leaf phenolic chemistry has, however, shown to be a better predictor of herbivore community responses than plant morphology (Wimp et al. 2007; Poelman et al. 2009; Barbour et al. 2015). As those studies dealt with effects on herbivores, it is not sure whether the diversity effects on predators found on Loden were related to plant chemistry as well. Plant chemical traits were, however, most likely responsible for the positive diversity effects on herbivores and the probably lower palatability of Tora to some herbivores.

Previous studies on hybridisation induced GD effects in *Salix* spec. found that interspecific hybridization can affect the herbivore community associated to the willows (Fritz et al. 1994; Fritz et al. 1998; Hochwender and Fritz 2004). However, in my study the herbivore community did not vary between Jorr (i.e. *S. viminalis*) and its hybrids Björn and Tora, as the only significant differences in genotype specific herbivore richness and abundance were between Jorr and Loden. Furthermore, the total arthropod community composition did not differ significantly between Brörn, Jorr and Tora. In general the genotype specific variance in the arthropod community in my study is rather low compared to the influence of genotype identity in other GD studies (e.g. Wimp et al. 2004; Johnson and Agrawal 2005; Poelman et al. 2009; Barbour et al. 2015). The low amount of variance between the genotypes, however, agrees with the assumption that the arthropods do not specialize on genotypes (Cook-Patton et al. 2011).

Further research needs

A high level of variance in my herbivore data is explained by the random factors of the GLMMs, as the conditional R^2 is distinctly higher than the marginal R^2 in the accordant models. There is evidence that a high amount of variance can be assigned to the block and plot identity of the trees. Plots were therefore not consistent in environmental conditions, which had an additional effect on the data. Especially the plants on the north east edge of the planting were performing poorly. This could be a result of potentially poor soil conditions and a nearby path. As tree height can have strong effects on herbivore abundance and diversity (Campos et al. 2006), effects of tree performance caused by unequal environmental conditions may have covered some of the GD effects. However, as I did not measure tree performance, these effects are not quantifiable. Additional studies on the ECOLINK-Salix field sites should therefore measure tree heights. This will improve the ability to better take into account the spatial variances in the performance of the trees. This approach would also provide evidence whether or not the increased herbivore abundance on Tora can be explained by positive GD effects on biomass production.

Furthermore, temporal changes or consistencies in the arthropods responses to GD need to be explored, as recent studies do not consent in the consistency of diversity effects and long-time studies are rare (Johnson et al. 2006; Wimp et al. 2007; Barton et al. 2015). Although early- and late-season arthropod communities are known to differ distinctly in temperate climates, there is evidence that diversity effects may still be consistent throughout the season (Johnson et al. 2006; Crutsinger et al. 2008; Barton et al. 2015). Further investigation of temporal dynamics in the quantity and quality of plant diversity effects on the associated arthropod community is assumed to help uncover the mechanisms that link plant diversity to the structure of arthropod community (Crutsinger et al. 2008). My study should therefore be repeated on a yearly basis including a comparison of effects on early- and late-season arthropod communities in the ECOLINK-Salix plantings.

Previous studies found the combination of SD and GD in one planting could have comparable or more pronounced effects on the arthropod community than SD or GD alone (Crawford and Rudgers 2013; Campos-Navarrete et al. 2015). Further research on GD should therefore not only study the effects of GD alone but also of GD in plants that are planted in species mixtures. Furthermore, my data show strong differences in the genotype specific diversity effects. It is therefore important to evaluate GD effects on additional *Salix* clones and hybrids and their combination with other tree species used in SRC (e.g. *Populus* spec.) to provide appropriate plant combinations for SRC.

Conclusions

My results show that GD in a willow planting, consisting of four different genotypes, led to a positive effect on the total arthropod richness. However, GD effects were generally of low magnitude and inconsistent among genotypes. The use of genetically diverse mixtures in willow SRC for biomass production can therefore improve the value of these plantations as habitats for arthropods, thereby enhancing biodiversity within the plantation itself and the surrounding landscape. A diverse arthropod community can deliver various ecosystem functions such as pollination and biological pest control and serve as a valuable foraging site for higher trophic levels (Landis and Werling 2010). Increases in the herbivore abundance on a single genotype were not strong enough to affect total abundances. Considerable increases in herbivore damage due to effects of AS in the overall planting can therefore not be expected, especially since herbivore abundances are not necessarily linked to increased herbivore consumption and plant damage (McArt and Thaler 2013). As diversity effects on herbivores were throughout positive, beneficial ecological effects of GD such as decreased herbivory and ecological pest control were not detectable in the current study. In this context Begley et al. (2009) concluded that at least seven different *Salix viminalis* genotypes are needed to achieve significant and constant disease control. Other biodiversity induced ecological benefits may, however, positively affect biomass yield (Johnson et al. 2006; Kotowska et al. 2010; Weih et al. 2014) and increase resilience to climatic extremes (Reusch et al. 2005; Isbell et al. 2015) in genotype mixtures. The detailed responses of plant performance and possible feedbacks (Agrawal et al. 2006; Cook-Patton et al. 2011; Abdala-Roberts and Mooney 2014) of changes in the arthropod community need to be evaluated in additional studies on the ECOLINK-Salix plantings. The results of my study, however, provide strong evidence that GD in willow SRC positively affects the associated arthropod community throughout trophic levels. The use of genetically diverse mixtures in SRC can therefore increase ecological benefits of bioenergy as a renewable energy source with the potential of mitigating anthropogenic climate change.

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Appendix

Table A1: Results of the subsample generalised linear mixed-effect models (GLMMs) for all data (Total) and subsets of the four genotypes respectively: Björn: B, Jorr: J, Loden: L, Tora: T. For each set of data results of the models on richness (Rich) and abundance (Ab) of all species (Rich all; Ab all), only the herbivores (Rich H; Ab H), only the predators (Rich P; Ab P) and the predator-herbivore ratio (Rich P/H; Ab P/H) per tree. For each model the estimate and standard error (SE), the value of the z-statistic (Z), the p-value (P) and marginal and conditional coefficients of determination (R^2m and R^2c respectively) are given. Significant ($P \leq 0.05$) models are printed in bold.

Data	**Model**	**Estimate ± std.err**	**Z**	**P**	**R^2m**	**R^2c**	**Model**	**Estimate ± srd.err**	**Z**	**P**	**R^2m**	**R^2c**
Total	**Div all**	**0.09 ±0.04**	**2.36**	**0.023**	**0.025**	**0.108**	Ab all*	0.06 ±0.05	1.16	0.259	0.006	0.086
	Div H	0.09 ±0.04	1.90	0.065**	0.018	0.118	Ab H*	0.06 ±0.06	0.88	0.389	0.004	0.101
	Div P*	0.08 ±0.07	1.10	0.291	0.006	0.065	Ab P*	0.08 ±0.07	1.05	0.313	0.004	0.045
	Div P sh	-0.12 ±0.09	-0.12	0.837	<0.001	0.047	Ab P sh	0.04 ±0.15	0.25	0.778	<0.001	0.067
B	Div all	0.06 ±0.06	1.07	0.295	0.013	0.105	Ab all*	0.09 ±0.11	0.87	0.392	0.011	0.149
	Div H	0.05 ±0.07	0.72	0.478	0.007	0.120	Ab H*	0.12 ±0.13	0.81	0.426	0.012	0.182
	Div P	0.13 ±0.10	1.34	0.196	0.013	0.014	Ab P*	0.15 ±0.11	1.35	0.183	0.014	0.014
	Div P sh	0.07 ±0.12	0.65	0.526	0.003	0.019	Ab P sh	<0.01 ±0.21	0.02	0.811	0.001	0.013
J	Div all	0.09 ±0.05	1.70	0.109	0.022	0.044	Ab all*	0.07 ±0.07	1.35	0.281	0.007	0.022
	Div H	0.08 ±0.09	0.88	0.396	0.014	0.120	Ab H*	0.06 ±0.11	0.58	0.568	0.004	0.062
	Div P	0.15 ±0.12	1.38	0.220	0.023	0.055	Ab P	0.16 ±0.12	1.47	0.193	0.024	0.044
	Div P sh	0.04 ±0.23	0.29	0.748	0.002	0.081	Ab P sh	0.12 ±0.27	0.53	0.637	0.004	0.125
L	**Div all**	**0.11 ±0.05**	**2.37**	**0.024**	**0.044**	**0.083**	Ab all*	0.02 ±0.06	0.34	0.730	0.001	0.023
	Div H	0.08 ±0.05	1.42	0.164	0.016	0.114	Ab H	-0.03 ±0.08	-0.46	0.648	0.003	0.044
	Div P	**0.27 ±0.11**	**2.94**	**0.023**	**0.064**	**0.086**	**Ab P***	**0.27 ±0.11**	**2.47**	**0.019**	**0.052**	**0.064**
	Div P sh	0.18 ±0.13	1.45	0.183	0.013	0.038	Ab P sh	0.28 ±0.15	1.96	0.080**	0.028	0.046
T	Div all	0.11 ±0.06	1.79	0.079**	0.038	0.124	Ab all*	0.13 ±0.07	1.89	0.081**	0.030	0.076
	Div H	**0.16 ±0.05**	**2.95**	**0.005**	**0.065**	**0.090**	**Ab H***	**0.20 ±0.07**	**2.75**	**0.018**	**0.065**	**0.090**
	Div P	-0.07 ±0.12	-0.59	0.568	0.005	0.093	Ab P*	-0.08 ±0.13	-0.61	0.551	0.004	0.053
	Div P sh	-0.21 ±0.11	-2.04	0.062**	0.017	0.060	Ab P sh	-0.23 ±0.21	-1.17	0.290	0.020	0.082

*Model with observation level random effect (OLRE) to deal with overdispersion
**p-values between 0.05 and 0.1 indicate for insignificant trends

Table A2: Detailed results of the original GLMMs for all data (Total) and subsets of the four genotypes respectively: Björn: B, Jorr: J, Loden: L, Tora: T. For each set of data results of the models on richness (Rich) and abundance (Ab) of all species (Rich all; Ab all), only the herbivores (Rich H; Ab H), only the predators (Rich P; Ab P) and the predator-herbivore ratio (Rich P/H; Ab P/H) per tree. For each model the estimate and standard error (SE), the value of the z-statistic (Z), the p-value (P) and marginal and conditional coefficients of determination (R^2m and R^2c respectively) are given. Significant (P≤0.05) models are printed in bold.

Data	**Model**	**Estimate ± SE**	**Z**	**P**	**R^2m**	**R^2c**	**Model**	**Estimate ± SE**	**Z**	**P**	**R^2m**	**R^2c**
Total	**Rich all**	**0.09 ±0.04**	**2.54**	**0.011**	**0.019**	**0.097**	Ab all*	0.06 ±0.05	1.24	0.217	0.005	0.088
	Rich H	**0.09 ±0.04**	**2.03**	**0.042**	**0.015**	**0.119**	Ab H*	0.04 ±0.09	0.47	0.640	0.003	0.105
	Rich P*	0.07 ±0.06	1.23	0.220	0.004	0.033	Ab P*	0.08 ±0.06	1.36	0.173	0.003	0.010
	Rich P/H	-0.02 ±0.08	-0.23	0.821	<0.001	0.041	Ab P/H	0.04 ±0.14	0.27	0.789	<0.001	0.055
B	Rich all	0.07 ±0.06	1.24	0.216	0.011	0.102	Ab all*	0.09 ±0.10	0.99	0.323	0.009	0.143
	Rich H	0.06 ±0.07	0.85	0.394	0.007	0.133	Ab H*	0.11 ±0.12	0.94	0.348	0.011	0.181
	Rich P	0.11 ±0.10	1.16	0.247	0.006	0.006	Ab P*	0.12 ±0.11	1.11	0.267	0.007	0.007
	Rich P/H	0.04 ±0.12	0.34	0.738	<0.001	0.018	Ab P/H	-0.03 ±0.20	-0.14	0.894	<0.001	<0.001
J	Rich all	0.09 ±0.06	1.56	0.119	0.016	0.062	Ab all*	0.08 ±0.07	1.07	0.283	0.006	0.050
	Rich H	0.09 ±0.11	0.80	0.424	0.012	0.147	Ab H*	0.08 ±0.14	0.57	0.572	0.004	0.109
	Rich P	0.12 ±0.13	0.93	0.350	0.011	0.048	Ab P	0.13 ±0.13	1.00	0.317	0.012	0.035
	Rich P/H	0.01 ±0.25	0.04	0.965	<0.001	0.089	Ab P/H	0.10 ±0.28	0.36	0.717	0.001	0.123
L	**Rich all**	**0.12 ±0.04**	**2.76**	**0.006**	**0.035**	**0.060**	Ab all*	0.04 ±0.06	0.71	0.478	0.003	0.037
	Rich H	0.09 ±0.05	1.67	0.096**	0.015	0.108	Ab H	-0.02 ±0.07	-0.24	0.808	<0.001	0.054
	Rich P	**0.26 ±0.10**	**2.51**	**0.012**	**0.039**	**0.039**	**Ab P***	**0.26 ±0.11**	**2.49**	**0.013**	**0.033**	**0.033**
	Rich P/H	0.15 ±0.13	1.22	0.222	0.006	0.032	Ab P/H	0.25 ±0.14	1.85	0.064**	0.016	0.031
T	**Rich all**	0.11 ±0.06	1.94	0.053**	0.032	0.118	Ab all*	0.13 ±0.07	1.84	0.066**	0.020	0.061
	Rich H	**0.16 ±0.06**	**2.85**	**0.004**	**0.052**	**0.095**	**Ab H***	**0.18 ±0.08**	**2.38**	**0.017**	**0.033**	**0.072**
	Rich P	-0.05 ±0.11	-0.49	0.628	0.002	0.058	Ab P*	-0.08 ±0.11	-0.66	0.512	0.003	0.031
	Rich P/H	-0.20 ±0.11	-1.79	0.074**	0.012	0.051	Ab P/H	-0.21 ±0.18	-1,16	0.246	0.013	0.068

*Model with observation level random effect (OLRE) to deal with overdispersion

**p-values between 0.05 and 0.1 indicate for insignificant trends

Table A3: List of all sampled morphospecies sorted by order. Familiy, category (i.e. trophic level: Herbivore/Predator/Other) and total abundances are given for each morphospecies.

Morphospecies	**Family**	**Category**	**Abundance**
Order: Acari 1			
Acari 1	NA	Herbivore	206
Order: Acari 2			
Acari 2	NA	Other	1
Order: Araneae			
Spinne 1	NA	Predator	55
Spinne 2	NA	Predator	1
Spinne 3	NA	Predator	3
Spinne 4	NA	Predator	1
Spinne 5	NA	Predator	52
Spinne 6	NA	Predator	1
Spinne 7	NA	Predator	12
Spinne 8	NA	Predator	1
Spinne 9	NA	Predator	42
Spinne 10	NA	Predator	2
Spinne 11	NA	Predator	2
Spinne 12	NA	Predator	48
Spinne 13	NA	Predator	3
Spinne 14	NA	Predator	8
Spinne 15	NA	Predator	7
Spinne 16	NA	Predator	1
Spinne 17	NA	Predator	1
Spinne 18	NA	Predator	1
Spinne 19	NA	Predator	2
Spinne 20	NA	Predator	5
Spinne 21	NA	Predator	1
Spinne 23	NA	Predator	1
Spinne 24	NA	Predator	1
Spinne 26	NA	Predator	2
Spinne 27	NA	Predator	1
Order: Coleoptera			
Acalyptus carpini	Curculionidae	Herbivore	5
Amphimallon solstitiale	Scarabaeidae	Herbivore	1
Apion cruentatum	Apionidae	Herbivore	5
Blattkäferlarve 1	NA	Herbivore	1
Blattkäferlarve 2	NA	Herbivore	1
Coccinella magnifica	Coccinellidae	Predator	2
Cortinicara gibbosa	Latridiidae	Other	55
Crepidodera spec	Chrysomelidae	Herbivore	6
Dorytomus hirtipennis	Curculionidae	Herbivore	1

Morphospecies	Family	Category	Abundance
Order: Coleoptera (continuation)			
Dorytomus spec	Curculionidae	Herbivore	1
Harmonia axyridis	Coccinellidae	Predator	2
Käfer 1	NA	Herbivore	2
Käfer 2	NA	Herbivore	1
Käfer 3	NA	Herbivore	4
Käfer 4	NA	Other	2
Käfer 5	NA	Herbivore	2
Käfer 6	NA	Other	4
Käfer 7	NA	Herbivore	1
Käfer 8	NA	Other	2
Käfer 9	Cantharidae	Predator	1
Käfer 11	NA	Other	1
Käfer 13	Latridiidae	Other	1
Kurzflügelkäfer 1	Staphylinidae	Predator	1
Kurzflügelkäfer 2	Staphylinidae	Predator	1
Kurzflügelkäfer 3	Staphylinidae	Predator	5
Kurzflügelkäferlarve 1	NA	Predator	1
Marienkäfer 1	Coccinellidae	Predator	1
Marienkäfer 2	Coccinellidae	Predator	1
Marienkäferlarve 1	Coccinellidae	Predator	3
Marienkäferlarve 2	Coccinellidae	Predator	3
Marienkäferlarve 3	Coccinellidae	Predator	36
Marienkäferlarve 4	Coccinellidae	Predator	10
Melanapion minimum	Apionidae	Herbivore	17
Propylea quatuordecimpunctata	Coccinellidae	Predator	6
Rhampus pulicarius	Rhynchaeninae	Herbivore	1
Rüsselkäfer 3	NA	Herbivore	1
Rüsselkäfer 5	Rhynchitidae	Herbivore	1
Rüsselkäfer 9	NA	Herbivore	1
Rüsselkäfer 10	NA	Herbivore	1
Rüsselkäfer 11	NA	Herbivore	2
Rüsselkäfer 12	NA	Herbivore	1
Rüsselkäfer 13	NA	Herbivore	1
Tachyerges salicis	Curculionidae	Herbivore	7
Order: Collembola			
Collembole 1	Entomobryidae	Other	2
Collembole 2	Entomobryidae	Other	36
Sminthurus spec	Sminthuridae	Herbivore	113
Order: Dermaptera			
Chelidurella acanthopygia	Forficulidae	Predator	2

Morphospecies	Family	Category	Abundance
Order: Diptera			
Diptera 1	NA	Other	1
Diptera 2	NA	Other	1
Diptera 3	NA	Other	1
Diptera 4	NA	Other	1
Diptera 5	NA	Other	5
Diptera 6	NA	Other	1
Diptera 7	NA	Other	12
Diptera 8	NA	Other	3
Diptera 9	NA	Other	1
Diptera 11	NA	Other	1
Diptera 12	NA	Other	11
Diptera 13	NA	Other	2
Diptera 15	Sciaridae	Other	1
Diptera 16	NA	Other	62
Diptera 17	NA	Other	3
Diptera 18	NA	Other	7
Diptera 19	NA	Other	3
Diptera 20	Sciaridae	Other	33
Diptera 21	NA	Other	2
Diptera 22	NA	Other	5
Diptera 23	NA	Other	1
Diptera 25	NA	Other	1
Diptera 26	NA	Other	1
Diptera 27	NA	Other	1
Diptera 28	NA	Other	1
Schwebfliegenlarve 1	NA	Predator	8
Schwebfliegenlarve 2	NA	Predator	1
Schwebfliegenlarve 3	NA	Predator	2
Schwebfliegenlarve 4	NA	Predator	1
Order: Ensifera	NA		
Langfühlerheuschrecke	NA	Herbivore	1
Order: Hemiptera	NA		
Aphis farinose	Aphididae	Herbivore	357
Aphis gossypii	Aphididae	Herbivore	515
Blattlaus 3	NA	Herbivore	17
Blattlaus 4	NA	Herbivore	29
Blattlaus 6	NA	Herbivore	12
Blattlaus 7	NA	Herbivore	3
Blattlaus 10	NA	Herbivore	9
Blattlaus 11	NA	Herbivore	1
Blattlaus 13	NA	Herbivore	3

Morphospecies	Family	Category	Abundance
Order: Hemiptera (continuation)			
Blattlaus 14	NA	Herbivore	3
Blattlaus 15	NA	Herbivore	25
Blattlaus 16	NA	Herbivore	1
Blattlaus 17	NA	Herbivore	2
Cavariella theobaldi	Aphididae	Herbivore	549
Cavariellea aegopodii	Aphididae	Herbivore	291
Cercopis vulnerata	Cercopidae	Herbivore	1
Delphacodes venosus	Delphacidae	Herbivore	2
Errastunus ocellaris	Cicadellidae	Herbivore	1
Hemiptera 1	NA	Herbivore	11
Megophthalmus scanicus	Cicadellidae	Herbivore	1
Philaenus spumarius	Aphrophoridae	Herbivore	3
Tuberolachnus salignus	Aphididae	Herbivore	33
Wanze 1	NA	Herbivore	65
Wanze 2	NA	Herbivore	1
Wanze 3	NA	Herbivore	1
Wanze 4	NA	Herbivore	2
Wanze 5	NA	Herbivore	1
Wanze 6	NA	Herbivore	1
Wanze 7	NA	Predator	1
Wanze 8	NA	Predator	2
Wanze 9	NA	Predator	1
Wanze 10	NA	Herbivore	1
Wanze 11	NA	Herbivore	3
Wanze 12	NA	Herbivore	89
Wanze 13	NA	Herbivore	1
Wanze 14	NA	Predator	1
Wanze Larve 1	NA	Predator	1
Wanze Larve 2	NA	Herbivore	5
Wanze Larve 3	NA	Herbivore	28
Wanze Larve 4	NA	Herbivore	5
Wanze Larve 5	NA	Predator	1
Wanze Larve 6	NA	Herbivore	1
Zikade 1	NA	Herbivore	1
Zikade 2	NA	Herbivore	1
Zikade 3	NA	Herbivore	2
Zikade 4	NA	Herbivore	1
Zikade 5	NA	Herbivore	1
Zikade 6	NA	Herbivore	16
Zikade 7	NA	Herbivore	2
Zikade Larve 2	NA	Herbivore	1
Zikade Larve 3	NA	Herbivore	1
Zikade Larve 4	NA	Herbivore	1
Zikade Larve 5	NA	Herbivore	12

Morphospecies	Family	Category	Abundance
Order: Hemiptera (continuation)			
Zikade Larve 6	NA	Herbivore	30
Zikade Larve 7	NA	Herbivore	49
Zikade Larve 8	NA	Herbivore	731
Zikade Larve 11	NA	Herbivore	1
Zikade Larve 12	NA	Herbivore	3
Zikade Larve 13	NA	Herbivore	14
Zikade Larve 14	NA	Herbivore	9
Zikade Larve 15	NA	Herbivore	1
Order: Hymenoptera			
Apocrita 1	NA	Predator	1
Apocrita 2	NA	Predator	2
Apocrita 3	NA	Predator	6
Apocrita 4	NA	Predator	2
Apocrita 5	NA	Predator	2
Apocrita 6	NA	Predator	1
Apocrita 7	Mymaridae	Predator	1
Apocrita 8	Braconidae	Predator	2
Apocrita 10	NA	Predator	1
Apocrita 11	Perilampidae	Predator	6
Apocrita 12	NA	Predator	1
Apocrita 13	NA	Predator	34
Apocrita 15	NA	Predator	1
Apocrita 16	NA	Predator	43
Apocrita 17	Dryinidae	Predator	1
Apocrita 18	NA	Predator	2
Apocrita 19	NA	Predator	2
Apocrita 20	NA	Predator	3
Apocrita 21	Platygastridae	Predator	11
Apocrita 22	NA	Predator	6
Apocrita 23	NA	Predator	23
Apocrita 24	NA	Predator	1
Apocrita 26	NA	Predator	5
Apocrita 27	NA	Predator	1
Apocrita 28	NA	Predator	4
Apocrita 29	NA	Predator	2
Apocrita 30	Braconidae	Predator	5
Apocrita 31	NA	Predator	1
Apocrita 32	NA	Predator	3
Apocrita 33	Mymaridae	Predator	9
Apocrita 34	NA	Predator	2
Apocrita 35	NA	Predator	1
Apocrita 36	NA	Predator	3
Apocrita 37	NA	Predator	24

Morphospecies	Family	Category	Abundance
Order: Hymenoptera (continuation)			
Apocrita 39	NA	Predator	2
Apocrita 40	NA	Predator	1
Apocrita 41	NA	Predator	1
Apocrita 42	NA	Other	1
Apocrita 43	NA	Predator	1
Apocrita 44	NA	Predator	1
Apocrita 45	NA	Predator	1
Apocrita 46	NA	Predator	1
Apocrita 49	NA	Predator	1
Blattwespenlarve 1	Tenthredinidae	Herbivore	149
Blattwespenlarve 2	Tenthredinidae	Herbivore	2
Dryinidae 1	Dryinidae	Predator	8
Dryinidae 2	Dryinidae	Predator	1
Formicidae 1	Formicidae	Predator	5
Formicidae 2	Formicidae	Predator	2
Formicidae 3	Formicidae	Predator	1
Formicidae 5	Formicidae	Predator	1
Furchenbiene 1	Apidae	Other	1
Furchenbiene 2	Apidae	Other	1
Hymenoptera 1	NA	Herbivore	1
Lasius 1	Formicidae	Predator	2
Lasius 2	Formicidae	Predator	6
Order: Ixoida			
Milbe 1	NA	Predator	5
Order: Lepidoptera			
Orgyia antiqua	Lymantriidae	Herbivore	1
Raupe 1	NA	Herbivore	7
Raupe 2	NA	Herbivore	17
Raupe 3	NA	Herbivore	9
Raupe 4	NA	Herbivore	54
Raupe 5	NA	Herbivore	2
Raupe 6	NA	Herbivore	1
Raupe 7	NA	Herbivore	1
Raupe 8	NA	Herbivore	1
Raupe 9	NA	Herbivore	1
Raupe 10	NA	Herbivore	1
Spanner 1	Geometridae	Herbivore	19
Spanner 2	Geometridae	Herbivore	16
Spanner 3	Geometridae	Herbivore	4
Spanner 4	Geometridae	Herbivore	2
Spanner 5	Geometridae	Herbivore	1
Spanner 6	Geometridae	Herbivore	1
Spanner 7	Geometridae	Herbivore	3

Morphospecies	Family	Category	Abundance
Order: Mesostigmata			
Raubmilbe 1	NA	Predator	2
Raubmilbe 2	NA	Predator	2
Order: Neuroptera	NA		
Blattlauslöwe 1	NA	Predator	5
Blattlauslöwe 2	NA	Predator	2
Order: Opiliones			
Weberknecht	NA	Predator	3
Order: Psocoptera			
Psocoptera 1	NA	Other	3
Psocoptera 2	NA	Other	1
Psocoptera 4	NA	Other	11
Psocoptera 5	NA	Other	6
Order: Thysanoptera			
Thysanoptera 1	NA	Herbivore	18
Thysanoptera 2	NA	Herbivore	5
Thysanoptera 3	NA	Herbivore	12
Thysanoptera 4	NA	Herbivore	11
Order: Trichoptera			
Köcherfliege 1	NA	Other	1
Others			
Larve 1	NA	Other	1
Larve 3	NA	Other	1
Puppe 1	NA	Other	1

Declaration according to § 20 (8) of the examination regulations

I hereby declare, that I am the sole author and composer of my thesis and that no other sources or learning aids, other than those listed, have been used. Furthermore, I declare that I have acknowledged the work of others by providing detailed references of said work. I hereby also declare, that my thesis has not been prepared for another examination or assignment, either wholly or excerpts thereof.

Erklärung nach § 20 (8) der Prüfungsordnung

Hiermit versichere ich, die vorliegende Arbeit selbständig verfasst zu haben. Alle Stellen, die wörtlich oder sinngemäß aus Veröffentlichungen entnommen sind, habe ich als solche kenntlich gemacht. Die Arbeit wurde noch nicht anderweitig als Masterarbeit eingereicht.

[redacted]

Place, Date

Signature