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Invertebrate Abundance, Biomass, and Richness Associated with an Exotic Invasive Shrub (*Lonicera morrowii* A. Gray)

Jason P. Love[1,2], James T. Anderson[1]

[1]Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV, USA
[2]Highlands Biological Station, Western Carolina University, Highlands, NC, USA
Email: jim.anderson@mail.wvu.edu

Abstract

Exotic bush honeysuckles (*Lonicera* spp.) are becoming increasingly common in the eastern and mid-western United States, but little is known about their impacts on invertebrates. We used a modified leaf vacuum to sample invertebrates in the shrub strata and understory of three shrub types (and open plots in the understory): single Morrow's honeysuckle (*L. morrowii* A. Gray) shrubs, single native southern arrowwood (*Viburnum recognitum* Fernald) shrubs, and dense thickets of Morrow's honeysuckle, in southwestern PA, USA during 2004 and 2005. We also assessed the degree of herbivory on the two species of shrubs. Within the shrub strata, invertebrate biomass was lower in southern arrowwood shrubs, but there was no difference in invertebrate abundance or family richness. Invertebrate abundance and richness were lowest in August, but there was no difference in biomass among the months. Invertebrate abundance, biomass, and family richness were lowest in the understory below dense thickets of Morrow's honeysuckle. Overall, the percent cover of herbs was the proximate factor responsible for driving patterns of invertebrate abundance, though ultimately these patterns were being driven by shrub type. Abundance and biomass of larval leaf chewers were highest in the native shrub; Morrow's honeysuckle had a mean of 29.7 cm^2 of leaf area consumed per 1 m^2 of leaf area, while the native shrub had a mean of 284.3 cm^2 of leaf area consumed. Our results suggest that areas dominated by the exotic shrub negatively impact invertebrate biomass, which may in turn affect organisms at higher trophic levels.

Keywords

Invertebrate Biomass, *Lonicera morrowii*, Morrow's Honeysuckle, Southern Arrowwood, Terrestrial Invertebrates, *Viburnum recognitum*

1. Introduction

Invasions of exotic plants have increased in both frequency and scale [1] so that today approximately 5000 non-native plant species have become established in the United States alone [2]. These invasions threaten biodiversity [3] [4], alter ecosystem functions [5], and impair local and global economies [2]. Several studies describe the factors that produce successful plant invasions [6] [7] [8]. The enemy release hypothesis predicts that some exotic plants are successful invaders because they lack the specialist herbivores and diseases from their native habitat, thereby conferring a competitive advantage over native plants [9] [10] [11]. Measurements of herbivore loads on native and exotic plants typically find higher numbers of invertebrates on native plants [12] [13] [14]. However, no published studies have examined patterns of invertebrate biomass on native versus exotic plants [15]. Since invasive exotic plants are becoming increasingly widespread, their impacts on invertebrates could affect members of higher trophic levels, such as insectivorous mammals, herpetofauna, and terrestrial birds. For example, 96% of terrestrial birds in North America rear their young on invertebrate protein [16]; subsequently, bird fitness is linked closely to the quality and quantity of their invertebrate food supplies [17]-[22].

Morrow's honeysuckle (*Lonicera morrowii* A. Gray) is an invasive exotic shrub that has spread throughout the northeastern and mid-Atlantic states [23]. The shrub is one of a suite of closely-related bush honeysuckles originally introduced into North America for horticultural purposes, including *Amur honeysuckle* (*L. maackii* [Rupr.] Maxim), *Tatarian honeysuckle* (*L. tatarica* L.), and Bell's honeysuckle (*L. × bella* Zabel) [24] [25]. Several studies reveal that Morrow's honeysuckle and its close relatives negatively impact native herbaceous communities [4] [26] [27] [28], seedling survival [26] [27] [29], spiders [30], and vertebrates [31] [32] [33]. Additional studies describe mechanisms that may account for the shrub's success in invading foreign soils, including seed characteristics [34], seed dispersal [35] [36] [37], plant phenology [38] [39] [40] [41] [42], and allelopathy [43] [44].

Despite the relatively large body of literature on the impacts and mechanisms of bush honeysuckle invasions, no studies have addressed the impacts of the shrubs on invertebrate abundance, biomass, and diversity. The only studies that have examined invertebrate hosts of bush honeysuckles have focused their attention on the honeysuckle aphid (*Hyadaphis tataricae* Aizenberg, Homoptera: Aphididae), one of the few pests of bush honeysuckle [45] [46]. Examining invertebrate abundance and diversity on Morrow's honeysuckle versus native shrubs might help in our understanding of how Morrow's honeysuckle is able to successfully invade foreign regions (*i.e.* the enemy release hypothesis). Concurrently, invertebrate abundance and diversity may provide a measuring stick on which future restoration efforts can be assessed [47] [48] [49] [50] [51].

Little information is available about how exotic plants impact ground-dwelling invertebrates [30]. Since exotic shrub honeysuckles reduce herb richness and ab-

undance [4] [26], the shrubs are likely to affect invertebrates found in the understory, since the type and quantity of vegetation cover strongly influences the spatial distribution of invertebrates [12] [52]. However, the shrub also may affect abiotic parameters, such as soil moisture, soil temperature, amount of leaf litter, and leaf litter nutrient content. Soil moisture [53] [54] [55] and soil temperature [56] often drive patterns of invertebrate activity, abundance, and diversity. Leaf litter quantity [53] [57] [58] and quality [57] [58] also may regulate ground-dwelling invertebrate composition and abundance.

Our objectives were to 1) compare invertebrate abundance, biomass, and diversity among single Morrow's honeysuckle shrubs, single southern arrowwood shrubs (*Viburnum recognitum* Fern.), and dense thickets of Morrow's honeysuckle; 2) compare ground-dwelling invertebrate abundance, biomass, and diversity among the understory of single shrubs of Morrow's honeysuckle, single shrubs of southern arrowwood, dense thickets of Morrow's honeysuckle, and open plots with no overstory; 3) determine environmental variables that drive patterns of ground-dwelling invertebrate abundance, biomass, and diversity in the understory of the four understory types; and 4) assess differences in leaf herbivory between Morrow's honeysuckle and southern arrowwood.

2. Materials and Methods

2.1. Study Site

Our study took place at Fort Necessity National Battlefield, Fayette County, southwestern Pennsylvania, USA (39°48'43"N, 84°41'50"W) during 2004 and 2005. The park is situated in the Allegheny Mountain subregion of the Appalachian Plateau, an area also known as the southern Laurel Highlands. Our study site was a 14.6 ha meadow located in the park. The study site was formerly a mixed hardwood/conifer forest [59], but prior to 1933 the site was cleared for livestock grazing. After acquiring the land, the Park Service maintained the meadow by periodic mowing until the mid-1980s, at which time mowing ceased. It was thought that natural forest succession would eventually approximate historical vegetative conditions that existed during the 1754 battle at Fort Necessity, when George Washington and his troops unsuccessfully defended the fort against French and Indians in a battle that sparked the French-Indian War (C. Ranson, 2004, Fort Necessity National Battlefield, Farmington, PA, personal communication). However, Morrow's honeysuckle invaded the site, dominating the meadow (67,920 ± 4480 shrubs/ha), and preventing regeneration of native hardwoods [42]. The site is typical of many abandoned fields in the region that have been heavily invaded by Morrow's honeysuckle and other exotic bush honeysuckle species (personal observation). Other woody shrubs and saplings found in the meadow include red maple (*Acer rubrum* L.), southern arrowwood, waxyfruit hawthorne (*Crataegus pruinosa* [Wendl. f.] K. Koch), black cherry (*Prunus serotina* Ehrh.), and sweet crabapple (*Malus coronaria* [L.] P. Mill.). Common herbaceous species include sweet vernal grass (*Anthoxanthum odoratum* L.), wrin-

kleleaf goldenrod (*Solidago rugosa* P. Mill.), early goldenrod (*S. juncea* Ait.), northern dewberry (*Rubus flagellaris* Willd.), and orchard grass (*Dactylis glomerata* L.) [42].

Low lying areas are characterized by Philo silt loams. These soils are deep, poor to moderately drained, medium textured, and were formed from acidic sediments derived from sandstone and shale. Upland sites within the meadow consist of Brinkerton and Armagh silt loams, Cavode silt loams, and Gilpin channery silt loams. These soils are moderately deep, moderate to well drained, medium-textured, and underlain by acidic shale and sandstone bedrock [60].

The climate is moderate continental. The average annual temperature is 9°C, with a mean winter temperature of −3°C and a mean summer temperature of 22°C. Average annual precipitation is 119 cm (Fort Necessity National Battlefield, 1991, General Management Plan/Development Concept Plan/Interpretive Prospectus, Unpublished report of Fort Necessity National Battlefield, Farmington, PA).

2.2. Invertebrate Sampling and Identification

Prior to sampling, we selected 45 Morrow's honeysuckle and 45 southern arrowwood shrubs (both species are in the family Caprifoliaceae) that were ≥1.3 m in height and >2 m from another woody shrub. Additionally, we selected 45 sites where dense thickets of Morrow's honeysuckle were growing. One-third of the shrubs from each of the three shrub types were randomly selected without replacement to determine shrubs to be sampled for each of three sampling periods: 7-11 July 2004, 26-31 May 2005, and 1-4 August 2005. Fifteen open plots containing no shrub cover were randomly selected and evenly paired with the three shrub types and sampling period (*i.e.* five open plots per shrub type and sampling period). To determine the location of the open plot, a cardinal direction was randomly selected; we followed this direction from the paired shrub until an open area was found that was >3 m from another shrub.

We used a modified vacuum-blower (STIHL model SH 85 D Shredder Vacuum/Blower) to sample invertebrates [61]. This method was found to be superior to sweep netting in scrub/shrub habitat [62]. We collected invertebrates from two different strata: 1) on and within the shrubs, and 2) in the understory below the shrubs. We vacuumed shrubs for one minute in a steady up and down motion while slowly circling the shrub [63]. The 1.3 m minimum shrub height requirement ensured that shrubs were large enough so that portions of the shrubs would not be resampled before time expired. We vacuumed > 0.5 m above the base of the shrub to avoid sampling invertebrates found on understory plants. When sampling invertebrates in the understory, we used a 23 cm diameter steel cylinder with sides 30.5 cm in height to delineate plots. For plots with a shrub overstory, the cylinder was placed midway between the base of the shrub and the outer perimeter of the shrub canopy. The area inside the cylinder was vacuumed for 30 sec. We sampled on relatively calm days with no rain and sampled after the dew had evaporated from the shrubs and herbs to make it easier to extract

samples from the collection bag.

We placed the contents of each sample in a plastic bag and kept the samples on ice until the specimens could be placed in a freezer for storage. We hand-sorted invertebrates from debris under a dissecting microscope; invertebrates ≥ 2 mm were identified to the lowest taxonomic group (typically Family level) [64] [65] and measured to the nearest 0.1 mm using an ocular micrometer. We classified holometabolous insects as adults, larvae, or pupae. Ametabolous or hemimetabolous nymphs were classified as adults, since nymphs we encountered changed little as they matured, except in size and proportions. We used previously developed length-weight regression formulas to estimate dry mass of each specimen [66]-[72]. Because length-weight regression equations were not available for insect pupae, we excluded insect pupae from our biomass estimations (shrub pupae, n = 4; understory pupae, n = 11). After identification, we stored specimens in 70% ethanol and placed voucher specimens in the West Virginia University Division of Forestry and Natural Resources.

2.3. Factors Influencing Ground-Dwelling Invertebrates

We measured several biotic and abiotic variables at each understory plot after reviewing the literature for factors that influence ground-dwelling invertebrate loads. We identified and measured percent cover of herbaceous cover contained within each understory plot; nomenclature follows [73]. Additionally, we noted whether plants were native or exotic. Because the number of invertebrates might be related to the amount of debris (leaf litter and live plant material) vacuumed into the collection bag while sampling, we weighed debris vacuumed from each plot (wet weight). After vacuuming each plot for invertebrates, the remaining leaf litter was hand-collected in the area delineated by the cylinder. This litter was later added to the leaf litter (minus the live plant material) collected while vacuuming. We dried the litter at 60°C for 72 hrs. and then weighed it to obtain dry mass. We then ground the litter in a Wiley mill fitted with a 1 mm sieve; percent nitrogen was determined using the automated Kjeldahl method [74]. Afterwards we used a spade to extract the soil within the plots to a depth of about 20 cm; soil was thoroughly hand-mixed and a sub-sample was placed in a plastic bag. We sieved the soil and a 20 g sub-sample was weighed, dried at 60°C for >48 hrs., then weighed again to derive percent moisture content. We used a soil temperature probe to determine soil temperature at a depth of 4 cm.

2.4. Leaf Herbivory

We collected one live 35 - 40 cm long branch located 1.3 m above the base of each of the single Morrow's honeysuckle and southern arrowwood shrubs sampled for invertebrates. Branches were placed in a plant press and the leaves were later analyzed for herbivory. We measured herbivory using three metrics. For the first metric, we placed leaves in two categories: 1) evidence of herbivory, and 2) no evidence of herbivory. Comparisons of herbivory between shrubs were based on the number of leaves with evidence of herbivory divided by the total

number of leaves. For the second metric, we estimated the amount of leaf area consumed (cm^2) by invertebrate herbivores using software that determines leaf area based on the number of pixels within a polygon (ImageJ version 1.33u: [75]). From each branch, we randomly selected ≤15 leaves that showed evidence of herbivory and ≤15 leaves with no evidence of herbivory. We used a digital camera (Kodak Easyshare LS443, 4.0 megapixels) to photograph the leaves. We determined the total area and amount of herbivory of each leaf to the nearest 0.1 mm^2 with ImageJ software. Leaf area loss was determined by dividing the total leaf area by the area of leaf loss. For the third metric, we examined all leaves and ranked the herbivory from 0 - 5 based on visual estimation: 0 = no herbivory; 1 = 1% - 5% herbivory; 2 = 6% - 25% herbivory; 3 = 26% - 50% herbivory; 4 = 51% - 75% herbivory, and 5 = 76% - 100% herbivory.

2.5. Statistical Analyses

When analyzing invertebrates, shrub species, and sample period (months) were the independent variables, while invertebrate abundance, biomass, and richness were the dependent variables. We used analysis of variance (ANOVA) (PROC GLM, SAS version 9.1; SAS Institute, Inc., Cary, NC, USA) to assess differences among shrub types, sample month, and to determine whether shrub type effects differed among sample months; Duncan's multiple range tests were used to compare differences between pairs. Invertebrate data were tested for normality and homogeneity of variance; assumptions were met using the following transformations: shrub invertebrates—eighth-root (abundance), quarter-root (biomass), and square-root (richness); understory invertebrates—square-root (abundance), quarter-root (biomass), and square-root ($x + 1$) (richness).

We used information-theory to determine biotic and abiotic factors driving patterns of ground-dwelling invertebrate abundance and biomass [76]. We tested all dependent (invertebrate abundance and biomass) and independent variables (biotic and abiotic parameters) for normality and homogeneity of variance. We used the following transformations to meet assumptions prior to data analysis: square-root—invertebrate abundance (all months), invertebrate biomass (May), soil moisture (May), litter nitrogen (August), wet debris weight (August); quarter-root—invertebrate biomass (July and August), dry litter mass (all months), wet debris weight (May and July); and arcsine—percent native herbaceous cover (July and August). We ranked (PROC RANK, SAS version 9.1) soil temperature (May and July) and soil moisture (July) data; these data did not meet assumptions even after transformations. Data transformed into ranks are thought more likely to satisfy assumptions of the parametric model than would the original non-normal data [77]. We reviewed relevant literature to specify sets of a priori candidate models for explaining ground-dwelling invertebrate abundance and biomass. We specified seven models; a global model containing all eight parameters and a subset of models representing potential influences of biotic and abiotic factors on ground-dwelling invertebrates (Tables 1-3). Following model specification, we searched for redundant variables (Spearman's r ≥ 0.70)

Table 1. Biotic and abiotic habitat parameters, measured in the understory of a degraded meadow, included in linear regression models explaining microhabitat relationships of invertebrate abundance and biomass at Fort Necessity National Battlefield, Pennsylvania, USA.

Variable	Units	Abbreviation	Additional description
Shrub type	Categorical	SH	Morrow's honeysuckle, southern arrowwood, dense thickets of Morrow's honeysuckle, or open plots
Herb cover	%	HC	% Total herb cover within the plot
Native herb cover	%	NC	Ratio of native herb cover to total herb cover
Litter mass	g	LM	Leaf litter dry weight within plot
Litter nitrogen	%	LN	% Litter nitrogen within plot
Soil moisture	%	SM	% Moisture content of 20 g sample of soil from plot
Soil temperature	˚C	ST	Soil temperature to a depth of 4 cm
Debris mass	g	DM	Wet weight of debris collected in vacuum within plot

Table 2. Linear regression models explaining influence of biotic and abiotic environmental variables on patterns of invertebrate abundance under different shrub types during different months in a degraded meadow at Fort Necessity National Battlefield, Pennsylvania, USA. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Model[a]	R^2	$K^{[b]}$	$(Q)AIC_c^{[c]}$	$\Delta(Q)AIC_c^{[d]}$	$w_i^{[e]}$
May (n = 59)					
Shrub (SH)	0.36	7	154.82	0.00	0.99
Debris (DM)	0.09	4	164.96	10.14	0.01
Native herbs (NC)	0.03	4	168.91	14.10	0.00
Total herbs (HC)	0.03	4	169.07	14.25	0.00
Litter (LM, LN)	0.05	5	170.17	15.35	0.00
Soil (SM, ST)	0.01	5	172.06	17.24	0.00
Global (SH, HC, NC, LM, LN, SM, ST, DM)	0.38	14	172.56	17.74	0.00
July (n = 50)					
Total herbs (HC)	0.26	3	136.55	0.00	0.97
Debris (DM)	0.13	3	144.80	8.25	0.02
Shrub (SH)	0.25	6	144.85	8.30	0.02
Soil (SM, ST)	0.08	4	149.84	13.29	0.00
Native herbs (NC)	0.03	3	150.12	13.57	0.00
Litter (LM, LN)	0.06	4	150.92	14.38	0.00
Global (SH, HC, NC, LM, LN, SM, ST, DM)	0.43	13	153.20	16.65	0.00
August (n = 58)					
Total herbs (HC)	0.03	3	181.67	0.00	0.40
Debris (DM)	0.01	3	182.72	1.04	0.24
Native herbs (NC)	0.01	3	183.00	1.33	0.21
Soil (SM, ST)	0.01	4	185.00	3.33	0.08

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Continued

Litter (LM, LN)	<0.01	4	185.51	3.84	0.06
Shrub (SH)	0.03	6	188.89	7.21	0.01
Global (SH, HC, NC, LM, LN, SM, ST, DM)	0.12	13	203.72	22.04	0.00

[a]Abbreviations in parentheses correspond to model parameters in **Table 1**. [b]Number of estimable parameters in approximating model. For May, there is one extra parameter added to take into account the estimation of c, the variance inflation factor. [c]In May, we used $QAIC_c$; for July and August we used AIC_c. [d]Difference in value between AIC_c (or $QAIC_c$) of the current model versus the best-approximating model (AIC_{cmin}). [e]Akaike weight. Probability that the current model (i) is the best-approximating model among those considered.

Table 3. Linear regression models explaining influence of biotic and abiotic environmental variables on patterns of invertebrate biomass under different shrub types during different months in a degraded meadow at Fort Necessity National Battlefield, Pennsylvania, USA. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Model[a]	R^2	K^b	AIC_c	ΔAIC_c^c	w_i^d
May (n = 59)					
Total herbs (HC)	0.04	3	194.44	0.00	0.47
Debris (DM)	0.01	3	196.29	1.85	0.19
Native herbs (NC)	<0.01	3	196.95	2.51	0.13
Litter (LM, LN)	0.03	4	197.53	3.09	0.10
Shrub (SH)	0.09	6	198.81	4.37	0.05
Soil (SM, ST)	0.01	4	198.91	4.47	0.05
Global (SH, HC, NC, LM, LN, SM, ST, DM)	0.16	13	214.69	20.25	0.00
July (n = 50)					
Total herbs (HC)	0.16	3	55.47	0.00	0.81
Debris (DM)	0.10	3	59.03	3.56	0.14
Native herbs (NC)	0.03	3	62.57	7.10	0.02
Shrub (SH)	0.13	6	64.42	8.95	0.01
Litter (LM, LN)	0.04	4	64.59	9.12	0.01
Soil (SM, ST)	0.04	4	64.64	9.17	0.01
Global (SH, HC, NC, LM, LN, SM, ST, DM)	0.26	13	78.90	13.84	0.00
August (n = 58)					
Shrub (SH)	0.15	6	105.04	0.00	0.47
Native herbs (NC)	0.01	3	107.05	2.00	0.17
Debris (DM)	<0.01	3	107.56	2.52	0.13
Total herbs (HC)	<0.01	3	107.59	2.54	0.13
Litter (LM, LN)	0.01	4	109.41	4.37	0.05
Soil (SM, ST)	<0.01	4	109.87	4.83	0.04
Global (SH, HC, NC, LM, LN, SM, ST, DM)	0.17	13	124.09	19.05	0.00

[a]Abbreviations in parentheses correspond to model parameters in **Table 1**. [b]Number of estimable parameters in approximating model. [c]Difference in value between AIC_c of the current model versus the best-approximating model (AIC_{cmin}). [d]Akaike weight. Probability that the current model (i) is the best-approximating model among those considered.

to assess whether our models could be simplified; we found no significant correlations among the variables that we measured, so we retained eight variables for inclusion in the models. We used linear regression (PROC GENMOD, SAS version 9.1) to analyze the model set for invertebrate abundance and biomass for each of the three months separately. We checked for overdispersion within our data sets by assessing the goodness-of-fit chi-square statistic of the global models divided by their degrees of freedom (*i.e.* estimated single variance inflation factor, ĉ), following the protocols of [76]. Invertebrate abundance in May was overdispersed (ĉ = 1.16, P < 0.15), so we corrected for the overdispersed data using quasi-likelihood modifications (*i.e.* QAICc) [76]. No distinct lack of fit was found in the other data sets.

Because the number of plots sampled (n ≤ 59) was small relative to the number of parameters (K) (*i.e.* n/K < 40), we used Akaike's Information Criterion corrected for small sample size (AICc and QAICc) for model selection [76]. We used formulas presented in [76] to calculate AICc from our maximum likelihood methods. We ranked all models according to their AICc values; the best model (*i.e.* the most parsimonious) was the model with the smallest AICc value [76]. We drew primary inference from models within two units of AICcmin, although models within four to seven units may have some empirical support [76]. We calculated Akaike weights (wi) to determine the strength of evidence in favor of each model and to estimate the relative importance of individual parameters [76].

When analyzing leaf herbivory data, shrub species and sample period (months) were the independent variables; percent of leaves with evidence of herbivory, leaf area consumed, and herbivory ranks were the dependent variables. We used analysis of variance (ANOVA) (PROC GLM, SAS version 9.1) to assess differences of leaf herbivory between Morrow's honeysuckle and southern arrowwood, among months, and to determine shrub × month interaction effects; we used Duncan's multiple range tests to compare differences in herbivory between shrubs and among months. We tested all leaf herbivory data for normality and homogeneity of variance; data were not normal even after transformations, so we ranked the data (PROC RANK, SAS version 9.1) prior to analysis. Untransformed means and SEs are reported throughout the results.

3. Results

3.1. Invertebrates

We collected 3133 invertebrates from the shrub strata of lone Morrow's honeysuckle shrubs, lone southern arrowwood shrubs, and dense thickets of Morrow's honeysuckle. We identified 3 Classes, 16 Orders, and 129 Families of invertebrates [42]. Composition of invertebrates based on the most abundant families and the highest biomasses differed among the three shrub types (Table 4). Total invertebrate biomass was lower in lone southern arrowwood shrubs (F = 3.24; df = 2, 126; P = 0.043), but there was no difference in invertebrate abundance or

Table 4. The 5 most common invertebrates (≥2 mm in length) collected from the shrub strata of 3 shrub types (n = 45) based on abundance (total number of invertebrates per Family) and biomass (total dry weight (mg)) at Fort Necessity National Battlefield, Pennsylvania, USA.

Shrub type	Top 5 based on total abundance					Top 5 based on total biomass (mg)				
	Order	Family	n	wt.	F[a]	Order	Family[b]	wt.	n	F
Lone Morrow's honeysuckle shrubs	Homoptera	Cicadellidae	267	130.4	40	Opiliones	Phalangiidae	180.3	23	15
	Coleoptera	Staphylinidae	72	53.2	6	Hymentoptera	Apidae	136.1	3	2
	Hymenoptera	Formicidae	58	20.3	19	Homoptera	Cicadellidae	130.4	267	40
	Homoptera	Psyllidae	58	22.3	16	Hemiptera	Pentatomidae	122.2	27	16
	Diptera	Chironomidae	40	10.0	8	Orthoptera	Gryllidae	110.6	14	10
Lone southern arrowwood shrubs	Hymenoptera	Formicidae	292	121.8	32	Coleoptera	Coccinellidae	266.0	17	13
	Homoptera	Cicadellidae	106	87.3	32	Hemiptera	Pentatomidae	124.9	33	10
	Hymenoptera	Scelionidae	67	9.9	26	Hymenoptera	Formicidae	121.8	292	32
	Diptera	Chironomidae	67	17.8	7	Hymenoptera	Symphyta	98.9	28	14
	Homoptera	Aphididae	62	13.0	5	Homoptera	Cicadellidae	87.3	106	32
Dense thickets of Morrow's honeysuckle	Homoptera	Cicadellidae	139	78.0	40	Opiliones	Phalangiidae	171.3	27	22
	Diptera	Drosophilidae	59	16.4	21	Coleoptera	Chrysomelidae	131.2	19	10
	Hemiptera	Miridae	47	33.1	22	Hemiptera	Pentatomidae	130.4	23	14
	Hemiptera	Reduviidae	41	75.6	20	Orthoptera	Acrididae	129.0	14	8
	Coleoptera	Staphylinidae	34	29.3	9	Hemiptera	Coreidae	96.9	7	6

[a]Frequency (number of occurrences out of 45). [b]Symphyta is a suborder; these specimens were also larvae.

richness among the three shrub types (F ≤ 0.94; df = 2, 126; P ≥ 0.394). Invertebrate abundance and richness was lowest in August (F ≥ 11.37; df = 2, 126; P < 0.001), but there was no difference in biomass among months (F = 2.85; df = 2, 126; P = 0.062). There were no shrub type × month interaction effects for invertebrate abundance, biomass, or richness (F ≤ 0.92; df = 4, 126; P ≥ 0.456) (Table 5). Larval leaf chewers (*i.e.* Lepidoptera and Symphyta larvae) were lowest in dense thickets of Morrow's honeysuckle (n = 11, biomass = 30.9 mg), followed by lone Morrow's honeysuckle shrubs (n = 16, biomass = 107.9 mg) and lone southern arrowwood shrubs (n = 54, biomass = 153.8 mg).

We collected 2589 invertebrates from the understory below lone Morrow's honeysuckle shrubs, lone southern arrowwood shrubs, dense thickets of Morrow's honeysuckle, and in open plots with no overstory. We identified 6 Classes, 17 Orders, and 115 Families of invertebrates [42]. Composition of invertebrates below the four shrub types differed based on abundance and biomass (Table 6). Invertebrate abundance, biomass, and richness were lowest in the understory below dense thickets of Morrow's honeysuckle (F ≥ 5.75; df = 3, 168; P < 0.001). Invertebrate abundance and richness were lowest in August (F ≥ 13.84; df = 2, 168; P < 0.001), but there was no difference in invertebrate biomass among the three months (F = 0.75; df = 2, 168; P = 0.476). We found a significant shrub type

Table 5. Mean (±SE) abundance, biomass (dry weight (mg)), and richness (Family or lowest taxonomic group) of invertebrates (≥2 mm in length) sampled within the shrub strata based on shrub type and month at Fort Necessity National Battlefield, Pennsylvania, USA.

Variable	n	Abundance	Biomass (mg)	Richness
		$\bar{X} \pm SE^*$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Shrub type				
Lone Morrow's honeysuckle shrubs	45	24.0 ± 2.2 A	41.8 ± 6.3 A	10.7 ± 0.7 A
Lone southern arrowwood shrubs	45	25.8 ± 3.0 A	28.3 ± 3.8 B	10.3 ± 0.7 A
Dense thickets of Morrow's honeysuckle	45	19.9 ± 1.6 A	38.8 ± 4.2 A	11.0 ± 0.6 A
Month				
May	45	26.4 ± 3.0 A	30.6 ± 4.1 A	10.5 ± 0.6 B
July	45	26.8 ± 1.8 A	39.2 ± 3.3 A	13.2 ± 0.6 A
August	45	16.4 ± 1.5 B	39.2 ± 6.7 A	8.3 ± 0.6 C

*Means in columns with different letters and under different variables are significantly different (P < 0.05), based on Duncan's multiple range tests.

Table 6. The 5 most common invertebrates (≥2 mm in length) collected from the understory of 4 shrub types (n = 45) based on abundance (total number of invertebrates per Family) and biomass (total dry weight (mg)) at Fort Necessity National Battlefield, Pennsylvania, USA.

Shrub type	Top 5 based on total abundance				Top 5 based on total biomass (mg)				
	Order	Family[a]	n	wt.	F[b]	Order	Family[a]	wt.	n	F
Lone Morrow's honeysuckle shrubs	Collembola	Isotomidae	185	14.0	37	Stylommatophora	-	80.6	13	8
	Homoptera	Cicadellidae	130	49.7	35	Opiliones	Phalangiidae	73.4	11	12
	Hymenoptera	Formicidae	59	14.5	26	Hemiptera	Pentatomidae	59.3	4	3
	Coleoptera	Chrysomelidae	30	2.4	14	Coleoptera	Chrysomelidae	54.2	18	17
	Coleoptera	Curculionidae	27	29.3	13	Homoptera	Cicadellidae	49.7	130	35
Lone southern arrowwood shrubs	Homoptera	Cicadellidae	160	83.4	36	Homoptera	Cicadellidae	83.4	160	36
	Collembola	Isotomidae	145	12.7	29	Opiliones	Phalangiidae	71.9	7	6
	Hymenoptera	Formicidae	67	17.7	27	Stylommatophora	-	50.6	9	8
	Araneae	Lycosidae	28	39.9	14	Coleoptera	Chrysomelidae	48.1	10	9
	Coleoptera	Curculionidae	28	23.3	18	Araneae	Lycosidae	39.9	28	14
Dense thickets of Morrow's honeysuckle	Collembola	Isotomidae	106	8.1	28	Hemiptera	Pentatomidae	85.0	9	7
	Homoptera	Cicadellidae	44	20.0	18	Stylommatophora	-	72.1	13	12
	Hymenoptera	Formicidae	38	11.6	17	Coleoptera	Curculionidae	30.8	23	14
	Coleoptera	Curculionidae	23	30.8	14	Homoptera	Cicadellidae	20.0	44	18
	Diptera	Sciaridae	17	3.8	6	Araneae	Thomasidae	20.0	1	1
Open plots with no overstory	Homoptera	Cicadellidae	195	97.7	37	Homoptera	Cicadellidae	97.7	195	37
	Collembola	Isotomidae	152	8.4	31	Araneae	Lycosidae	65.6	31	16
	Hymenoptera	Formicidae	70	37.2	21	Stylommatophora	-	45.4	7	7
	Coleoptera	Chrysomelidae	54	4.0	10	Lepidoptera	Noctuidae	38.8	10	5
	Homoptera	Psyllidae	44	15.2	16	Hymenoptera	Formicidae	37.2	70	21

[a]Specimens in the Families Chrysomeldidae and Noctuidae are larvae (caterpillars). [b]Frequency (number of occurrences out of 45).

× month interaction for invertebrate abundance and richness (F ≥ 3.02; df = 6, 168; P ≤ 0.008), but not for invertebrate biomass (F = 1.72; df = 6, 168; P = 0.118) (Figure 1; Table 7).
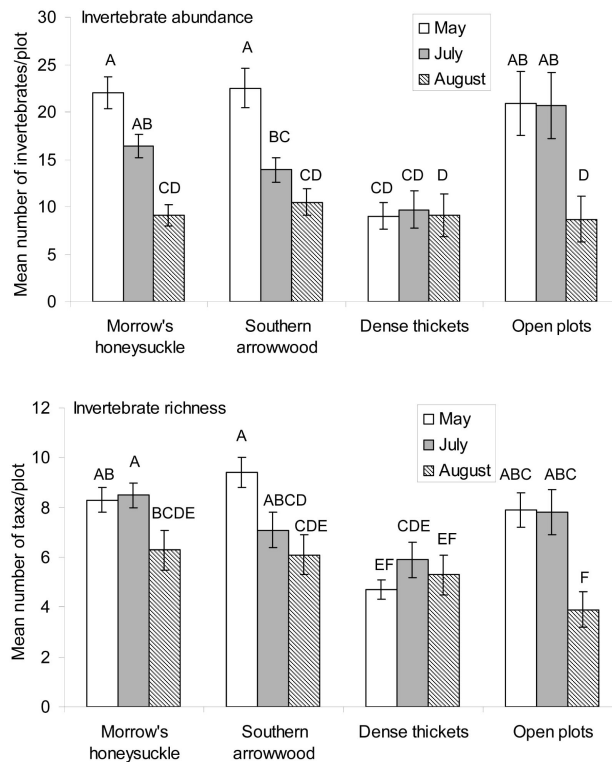

Figure 1. Mean (±SE) ground-dwelling invertebrate abundance (top) and richness (bottom) differed depending on shrub understory type and month at Fort Necessity National Battlefield, Pennsylvania. Means with different letters are significantly different, based on Duncan's multiple range tests (P < 0.05).

Table 7. Mean (±SE) abundance, biomass (dry weight (mg)), and richness (Family or lowest taxonomic group) of invertebrates (≥2 mm in length) sampled in the understory based on shrub type and month at Fort Necessity National Battlefield, Pennsylvania, USA.

Variable	n	Abundance $\bar{X}$ ± SE*	Biomass (mg) $\bar{X}$ ± SE	Richness $\bar{X}$ ± SE
Shrub type				
Lone Morrow's honeysuckle shrubs	45	15.8 ± 1.1 A	14.5 ± 2.0 A	7.7 ± 0.4 A
Lone southern arrowwood shrubs	45	15.6 ± 1.2 A	14.5 ± 1.7 A	7.5 ± 0.5 A
Dense thickets of Morrow's honeysuckle	45	9.2 ± 1.1 B	8.6 ± 1.8 B	5.3 ± 0.4 B
Open plots with no overstory	45	16.8 ± 2.0 A	12.3 ± 2.0 AB	6.5 ± 0.5 B
Month				
May	60	18.6 ± 1.3 A	11.6 ± 1.1 A	7.6 ± 0.4 A
July	60	15.2 ± 1.2 B	12.7 ± 1.7 A	7.3 ± 0.4 A
August	60	9.4 ± 0.9 C	13.2 ± 2.0 A	5.4 ± 0.4 B

*Means in columns with different letters are significantly different (P < 0.05), based on Duncan's multiple range tests.

3.2. Factors Influencing Ground-Dwelling Invertebrates

For invertebrate abundance in May, the model "shrub" was the best-approximating model (wi = 0.99). The remaining models received no empirical support (ΔAIC_c ≥ 10.14; wi ≤ 0.01) (Table 2). For invertebrate abundance in July, the model "total herbs" (wi = 0.97) was the best-approximating model, while the remaining six models had no empirical support (ΔAIC_c ≥ 8.25; wi ≤ 0.02) (Table 2). In August, the model "total herbs" was the best-approximating model; the models "debris" (ΔAIC_c = 1.04; wi = 0.24) and "native herbs" (ΔAIC_c = 1.33; wi = 0.21) also received strong empirical support, while the models "soil" (ΔAIC_c = 3.33; wi = 0.08) and "litter" (ΔAIC_c = 3.84; wi = 0.06) received limited support (Table 2).

For invertebrate biomass in May, the model "total herbs" (wi = 0.47) was the best approximating model, though the models "debris" (ΔAIC_c = 1.85; wi = 0.19), "native herbs" (ΔAIC_c = 2.51; wi = 0.13), and "litter" (ΔAIC_c = 3.09; wi = 0.10) also had strong empirical support. The remaining models had little to no support (ΔAIC_c ≥ 4.37; wi ≤ 0.05) (Table 3). In July, the model "total herbs" (wi = 0.81) was the best-approximating model to determine patterns of invertebrate biomass, although the model "debris" (ΔAIC_c = 3.56; wi = 0.14) also had some empirical support; the remaining models received no empirical support (ΔAIC_c ≥ 7.10; wi ≤ 0.02) (Table 3). For invertebrate biomass in August, the model "shrub" (wi = 0.47) was the best-approximating model, though the models "native herbs" (ΔAIC_c = 2.00, wi = 0.17), "debris" (ΔAIC_c = 2.52, wi = 0.13), and "total herbs" (ΔAIC_c = 2.54, wi = 0.13) also had strong empirical support. The remaining models had little or no empirical support (ΔAIC_c ≥ 4.37, wi ≤ 0.05). Overall, there was a strong relation among both invertebrate abundance and biomass to total herbaceous cover and shrub type relative to other biotic and abiotic factors (Figure 2; Table 8). Moreover, the proportion of native herbs was
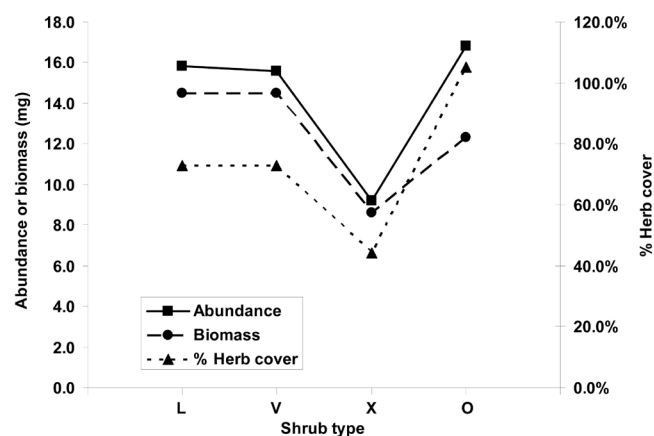

Figure 2. Ground-dwelling mean invertebrate abundance and biomass over all months was positively related to percent herbaceous cover, which in turn was regulated by shrub type (L = lone Morrow's honeysuckle; V = lone southern arrowwood; X = dense thickets of Morrow's honeysuckle; and O = open plots with no overstory) within a degraded meadow at Fort Necessity National Battlefield, Pennsylvania, USA.

Table 8. Mean (±SE) values of microhabitat variables recorded under Morrow's honey-suckle shrubs (L), southern arrowwood shrubs (V), dense thickets of Morrow's honey-suckle (X), and open plots with no shrub cover (O) based on month at Fort Necessity National Battlefield, Pennsylvania, USA.

Microhabitat variables[a]	Shrub type[b]			
	L	V	X	O
	$\bar{X}$ ± SE	$\bar{X}$ ± SE	$\bar{X}$ ± SE	$\bar{X}$ ± SE
May, n = 58				
Herb cover (%)	50.2 ± 5.6	49.6 ± 5.4	34.1 ± 5.3	75.0 ± 4.1
Native cover: total cover (%)	48.5 ± 6.9	64.8 ± 5.4	39.4 ± 5.9	61.7 ± 6.1
Dry litter wt. (g)	21.57 ± 4.27	30.99 ± 5.35	20.66 ± 4.84	17.16 ± 3.01
Litter N (%)	1.30 ± 0.12	1.49 ± 0.08	1.48 ± 0.12	1.22 ± 0.07
Soil moisture (%)	24.7 ± 0.8	24.7 ± 0.7	24.9 ± 1.1	23.3 ± 0.7
Soil temp. (˚C)	15.0 ± 0.3	16.1 ± 0.4	14.8 ± 0.3	16.7 ± 0.3
Wet debris wt. (g)	2.09 ± 0.45	1.99 ± 0.22	5.60 ± 1.08	0.62 ± 0.09
July, n = 50				
Herb cover (%)	99.1 ± 11.0	106.8 ± 10.5	50.6 ± 8.0	155.5 ± 11.7
Native cover: total cover (%)	64.6 ± 8.0	68.3 ± 8.1	56.7 ± 6.8	72.8 ± 7.8
Dry litter wt. (g)	13.06 ± 3.99	23.66 ± 4.46	17.10 ± 3.37	22.10 ± 4.73
Litter N (%)	1.07 ± 0.12	1.28 ± 0.12	1.23 ± 0.12	1.11 ± 0.07
Soil moisture (%)	19.9 ± 1.14	22.8 ± 0.8	21.6 ± 0.7	21.2 ± 2.3
Soil temp. (˚C)	21.8 ± 0.9	20.4 ± 0.4	20.6 ± 0.3	22.9 ± 0.6
Wet debris wt. (g)	1.03 ± 0.16	0.92 ± 0.19	2.86 ± 0.52	0.92 ± 0.16
August, n = 59				
Herb cover (%)	61.3 ± 6.2	64.1 ± 7.4	46.0 ± 7.4	88.9 ± 6.3
Native cover: total cover (%)	75.4 ± 3.4	77.7 ± 4.5	58.0 ± 7.4	81.5 ± 4.0
Dry litter wt. (g)	19.69 ± 2.76	40.68 ± 4.92	16.00 ± 2.94	27.84 ± 4.71
Litter N (%)	1.27 ± 0.12	1.53 ± 0.11	1.45 ± 0.11	1.13 ± 0.09
Soil moisture (%)	14.2 ± 0.5	14.5 ± 0.3	13.6 ± 0.4	13.5 ± 0.6
Soil temp. (˚C)	25.2 ± 0.6	25.3 ± 0.7	24.2 ± 0.5	26.2 ± 0.5
Wet debris wt. (g)	2.35 ± 0.27	3.33 ± 0.55	3.31 ± 0.51	3.56 ± 0.50

[a]Microhabitat variables correspond to model parameters in **Table 1**. [b]L = single Morrow's honeysuckle shrubs; V = single southern arrowwood shrubs; X = dense thickets of Morrow's honeysuckle shrubs; and O = open plots with no shrub canopy.

consistently depressed under dense thickets of Morrow's honeysuckle relative to the other shrub types (Table 8).

3.3. Leaf Herbivory

Over the course of the three sample periods, we analyzed and assigned ranks to 4465 leaves of Morrow's honeysuckle and 1121 leaves of southern arrowwood. Additionally, we photographed 181 leaves of Morrow's honeysuckle and 308 leaves of southern arrowwood that showed signs of herbivory; 615 leaves of Morrow's honeysuckle and 91 leaves of southern arrowwood were photographed that did not shows signs of leaf herbivory. Mean (±SE) total leaf area of Mor-

row's honeysuckle with leaf herbivory was 3.38 ± 0.17 cm², while mean leaf area of leaves that were entire was 3.13 ± 0.07 cm². Mean (±SE) total leaf area of southern arrowwood leaves with signs of herbivory was 9.77 ± 0.31 cm², while mean area of leaves without signs of herbivory was 7.13 ± 0.48 cm².

Southern arrowwood was significantly greater than Morrow's honeysuckle in percent of leaves with evidence of herbivory and leaf rank (F ≥ 139.30; df = 1, 84; P < 0.001), as well as leaf area consumed (F = 18.31, df = 1, 77; P < 0.001). Overall, southern arrowwood had 284.3 cm² of leaf area consumed per 1 m² of leaf area, while Morrow's honeysuckle had 29.7 cm² of leaf area consumed per 1 m² of leaf area. Herbivory metrics in May were consistently lower relative to metrics in July and August. There were significant differences among months for percent of leaves with evidence of herbivory and leaf rank (F ≥ 49.61; df = 2, 84; P < 0.001), as well as leaf area consumed and percent of leaf consumed (F = 5.40; df = 2, 77; P = 0.006). Moreover, there were significant shrub × month interaction effects for percent of leaves with evidence of herbivory and leaf rank (F ≥ 8.89; df = 2, 84; P < 0.001) (Figure 3), though there were no significant differences in mean leaf area consumed (F = 2.90; df = 2, 77; P = 0.061) (Table 9).
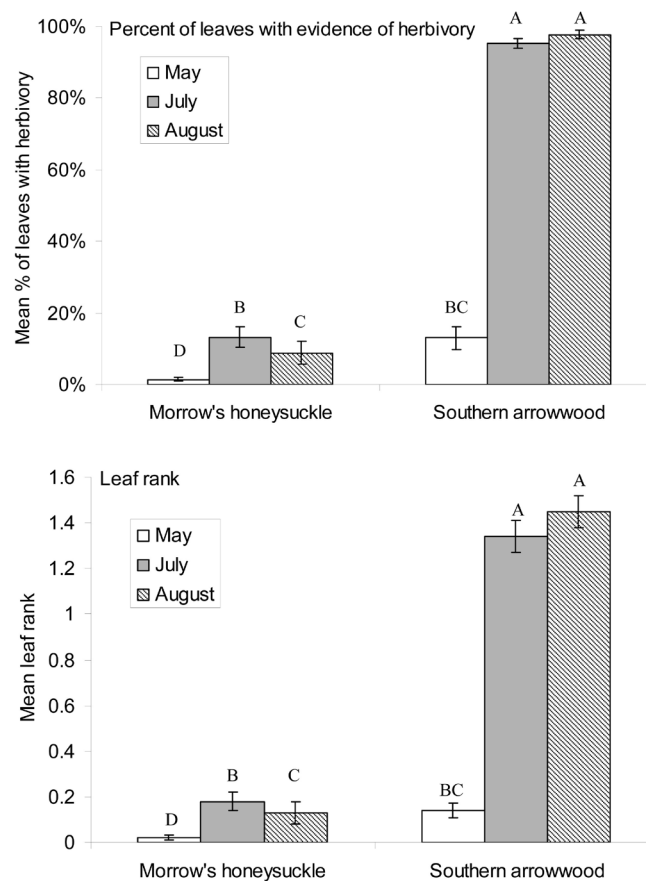
Figure 3. Mean (±SE) percent of leaves with evidence of herbivory (top) and leaf rank (bottom; see last sentence in Section 2.4 for rank definitions) differed between shrub type and seasons at Fort Necessity National Battlefield, Pennsylvania. Means with different letters are significantly different, based on Duncan's multiple range tests (P < 0.05).

Table 9. Morrow's honeysuckle and southern arrowwood mean (±SE) percent of leaves with evidence of herbivory, leaf area consumed (cm^2), and herbivory rank at Fort Necessity National Battlefield, Pennsylvania, USA.

Variable	n^a	Percent of leaves w/evidence of herbivory	Leaf area consumed (cm^2)	Leaf rank
		$\bar{X}$ ± SE^b	$\bar{X}$ ± SE	$\bar{X}$ ± SE
Shrub				
Morrow's honeysuckle	45	7.9 ± 1.5 B	0.12 ± 0.03 B	0.11 ± 0.02 B
Southern arrowwood	45	68.6 ± 6.1 A	0.38 ± 0.07 A	0.98 ± 0.10 A
Month				
May	30	7.2 ± 2.0 B	0.17 ± 0.05 B	0.08 ± 0.02 B
July	30	54.2 ± 7.8 A	0.26 ± 0.06 A	0.76 ± 0.11 A
August	30	53.3 ± 8.4 A	0.31 ± 0.08 A	0.79 ± 0.13 A

[a]For leaf area consumed, n is as follows: Morrow's honeysuckle (n = 42), southern arrowwood (n = 41), May (n = 25), July (n = 30), August (n = 28). [b]Means in columns with different letters are significantly different (P < 0.05), based on Duncan's multiple range tests.

4. Discussion

4.1. Invertebrates

While several studies have examined invertebrate abundance on exotic versus native plants [12] [13] [14], this is the first study we are aware of that examined the effects of exotic plants on invertebrate biomass [15]. Since invertebrate biomass is closely linked to the energetic value of an invertebrate food item [78] [79] [80], our findings could have implications for organisms at higher trophic levels, such as songbirds. For instance, we found that within the shrub strata, the native shrub contained lower overall invertebrate biomass than either dense thickets or single shrubs of exotic Morrow's honeysuckle (though there was no such trend when mean biomass was divided by shrub type and month). However, the native shrub contained five times more larval leaf chewer biomass than found in thickets of the exotic shrub and one and one-half times more than found on single Morrow's honeysuckle shrubs. Lower levels of larval leaf chewers could possibly increase foraging distance and time for some species of songbirds [81], particularly during the nesting season when invertebrate protein, especially from larval leaf chewers, makes up a large portion of the diet of nestlings [82]. For example, Prairie Warblers (*Dendroica discolor* Vieillot) were common nesting songbirds within our study site and primarily feed their young larval leaf chewers such as caterpillars [82], which are higher in nutrients than most other groups of invertebrates [83]. Other studies reveal that birds nesting in Amur honeysuckle have lower rates of nest success than nests found in native shrubs and trees; lower nest height, greater shrub volume, lack of sharp thorns, and branch architecture that facilitate movement of predators are thought to contribute to higher rates of nest predation in these exotic shrubs relative to native shrubs and trees [31] [32]. If these nests are in a matrix of exotic shrubs which

produce few larval leaf chewers, then the extra time and effort spent foraging for preferred prey could also be a contributing factor leading to increased rates of nest predation. Clearly more research is needed to ascertain whether there is a link between reduced biomass of important invertebrate prey items on exotic bush honeysuckles and bird foraging behavior and subsequent nest success.

Invertebrate composition within the shrub strata differed among the three shrub types. Ants (Hymenoptera: Formicidae) were five times more abundant on southern arrowwood relative to lone shrubs of Morrow's honeysuckle and nearly 14 times more abundant relative to dense thickets of the exotic shrub. We attribute this pattern to large numbers of aphids (Homoptera: Aphididae) feeding on the native shrub. Ants feed on honeydew produced by aphids and protect aphid colonies from predators and sooty mold contamination [84] [85]; this strong correlation between aphid and ant abundance has been observed before (e.g. [83]). Moreover, we also observed ants feeding directly from sugar exudates arising from immature berries of southern arrowwood, even in the absence of aphids. Lady beetles (Coleoptera: Coccinellidae) had the greatest biomass on southern arrowwood, where they were the top invertebrate in terms of biomass. We also attribute this pattern to the presence of aphids feeding on southern arrowwood; the beetles were observed feeding on the aphids, a favorite prey item for ladybugs [64].

Invertebrate biomass was consistently reduced in the understory below dense thickets of Morrow's honeysuckle over all months. In a Kentucky forest, northern slimy salamanders (*Plethodon glutinosus* Green) and green frogs (*Rana clamitans* Latreille) found in areas with a dense cover of Amur honeysuckle had lower body mass compared to non-invaded areas, suggesting that the shrub might be reducing the availability of prey items, although no quantitative data on invertebrate availability was obtained [33]. Invertebrate richness also was significantly lower under dense thickets of Morrow's honeysuckle, a trend also found with spiders found in the understory of hedges dominated by Amur honeysuckle [30].

4.2. Factors Influencing Invertebrate Patterns

Overall, patterns of invertebrate abundance and biomass in the understory were driven by percent cover of herbs, which in turn was ultimately influenced by the type of shrub overstory. Reduced herbaceous cover in areas dominated by Amur honeysuckle was thought to be the proximate factor responsible for depressing spider richness [30] and amphibian condition and diversity [33]. Other studies also have documented the positive correlation of understory herbaceous cover and invertebrate abundance [86]-[91] but not all studies support this [92]. The reduced abundance, biomass, and richness under dense thickets of Morrow's honeysuckle is not surprising given the numerous studies showing the shrubs' impact on herbaceous diversity and cover [4] [26] [27]. It is interesting to note that the proportion of native herbaceous species was reduced under dense thickets of Morrow's honeysuckle relative to the other shrub types; future studies

should assess whether this trend occurs with other bush honeysuckle species.

Our study revealed that patterns of invertebrate abundance are not necessarily correlated with invertebrate biomass. For instance, invertebrates captured in the shrub strata of southern arrowwood were greater in abundance than the other two shrub types but had significantly less biomass compared to the other shrub types. Moreover, there were few invertebrate families that were among both the five most abundant invertebrate groups and five heaviest groups in terms of total biomass. We caution researchers that correlating invertebrate abundance with biomass may be misleading.

One limitation of our study is that we did not identify invertebrates to species. There is a possibility that exotic invertebrates may have contributed a significant portion of the overall invertebrate abundance, biomass, and richness and may have skewed our expected results (*i.e.* enemy release hypothesis—significantly greater abundance, biomass, and richness of invertebrates found in the shrub strata of the native shrub relative to the exotic shrub). For instance, honey bees (*Apis mellifera* L, Hymenoptera: Apidae) were sampled during May on Morrow's honeysuckle when the shrubs were flowering. We only captured three of these insects on single shrubs of Morrow's honeysuckle, but because of their large size relative to other invertebrates, they had the second most total mass of invertebrate groups found on this shrub type. We also captured one Japanese beetle (*Popillia japonica*, Coleoptera: Scarabaeidae) on southern arrowwood. It is possible that more species of exotic invertebrates were sampled. For example, in a simultaneous experiment at our study site researching patterns of earthworm abundance, biomass, and richness, only four species of earthworms were sampled and all four species were exotic [93]. However, based on the limited herbivory on Morrow's honeysuckle relative to southern arrowwood, we believe that if any exotic phytophagous invertebrates were present that fed on Morrow's honeysuckle, we would have observed more leaf damage.

It is also possible that native Lonicera-specific herbivores may have been feeding on Morrow's honeysuckle. Related species of plants often present similar chemical cues that attract herbivores [94]. Introduced plants that are closely related to native plants often draw the same suite of herbivores and have similar rates of herbivory [95] [96]. However, native bush honeysuckles are rare in Pennsylvania, making it doubtful that a host shift to Morrow's honeysuckle has occurred. Three of the four native species, hairy honeysuckle (*L. hirsuta* Eat.), swamp fly honeysuckle (*L. oblongifolia* (Goldie) Hook.), and mountain fly honeysuckle (*L. villosa* (Michx.) J. A. Schultes) have a state heritage rank of S1 (<5 populations recorded in the state) [97] [98]. While not ranked in Pennsylvania, a fourth native honeysuckle, limber honeysuckle (*L. dioica* L.) has a rank of S3 (21 - 100 occurrences in the state) in neighboring West Virginia and is infrequently encountered [98]. Moreover, no native bush honeysuckles have been recorded at Fort Necessity National Battlefield and the relatively low rates of herbivory that we documented support our belief that few, if any, native Lonicera-specific hosts feed on Morrow's honeysuckle.

Because the native shrubs that we sampled occurred in a landscape matrix dominated by the exotic Morrow's honeysuckle, there is a possibility that the exotic shrubs impeded herbivores from moving to these patches of native shrubs (*i.e.* fragmentation), thereby reducing the overall abundance, biomass, and richness of invertebrates found on the native shrubs. For example, a planthopper (Homoptera: Cicadellidae) and its specialist parasitoid (Hymenoptera: Mymaridae) were 50% lower in native patches of the host plant that were embedded in a matrix of exotic grass compared to a matrix dominated by the native host plant [99]. Other studies reveal that the composition of the habitat between host-patch patches can significantly affect interpatch movement rates of herbivores [100] [101] [102]. Our results may have differed if the native shrubs we sampled were located in native vegetative communities, though we can only speculate since we did not measure landscape effects.

4.3. Leaf Herbivory

Leaf herbivory was nearly 10 times more on the native southern arrowwood than on Morrow's honeysuckle. Herbarium specimens of Amur honeysuckle had less leaf damage compared to native shrubs, suggesting that the shrub may be relatively free from herbivores and/or pathogens; the lack of herbivores and pathogens may be partly responsible for its success in invading foreign soils [41]. Branches that were newly formed on Morrow's honeysuckle typically had larger leaves than older branches (personal observation). Since insects often prefer newer, more palatable leaves [12], we believe the larger size of leaves on younger branches explains the reason why larger leaves were more likely to have herbivory. On southern arrowwood, we believe the larger leaves were older and thereby had a greater chance of being exploited by herbivores. In our samples, we observed shrubs affected by the fungus *Insolibasidium deformans* C. J. Gould (Auriculariaceae) (fungus id confirmed by W. MacDonald 2004, West Virginia University, Morgantown), a blight specific to *Lonicera* that causes a crinkling and browning of the leaves [103]. However, we did not quantitatively measure this disease and it did not seem to have a deleterious impact on the shrub. Overall our results suggest that the enemy release hypothesis is at least partly responsible for the success of Morrow's honeysuckle invading and persisting at our study site.

4.4. Conclusion

Many land managers believe that bush honeysuckles, including Morrow's honeysuckle, create sufficient habitat for songbirds and game species [104]. Moreover, the abundant, conspicuous red berries are often cited as being beneficial for wildlife, particularly songbirds [35] [105] [106]. However, in light of recent studies showing increased rates of nest predation in bush honeysuckles [31] [32] and evidence of deleterious effects of the shrubs on amphibians [33], coupled with our findings of decreased larval leaf chewer biomass in the shrub strata of the exotic shrub and significantly lower invertebrate biomass under dense thick-

ets of the shrub, we believe that areas dominated by Morrow's honeysuckle may be at best, marginal bird habitat, and at worst, ecological traps.

Acknowledgements

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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