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ORIGINAL PAPER

Multi-trophic interactions and niche partitioning in the native range informs biological control in forests invaded by the hemlock woolly adelgid

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Abstract Understanding natural enemy communities in the native range of pest insects is critical for implementing management decisions where such pests are invasive. The hemlock woolly adelgid (HWA) is a destructive invasive insect, causing decline of hemlock forests in eastern North America. We studied patterns of predator coexistence and prey suppression among native predators in western North America to inform biological control strategies in the invaded eastern range. In particular, we examined the structure and interactions of HWA's specialist predator complex (a beetle *Laricobius nigrinus*, and two flies *Leucotaraxis argenticollis* and *Le. piniperda*) across five western populations over two years. Field surveys quantified spatial and temporal overlap, while a laboratory experiment assessed competition between the two *Leucotaraxis* species. We employed species-specific RT-qPCR to quantify populations of cryptic *Leucotaraxis* immatures. Supporting the notion of complementary predation, predators exhibited clear temporal and spatial niche partitioning: (1) the two *Leucotaraxis* species were temporally separated, (2) while *La. nigrinus* overlapped with both *Leucotaraxis* species, they showed negative spatial co-occurrence on twigs, and (3) no evidence of competition between *Leucotaraxis* species was observed in the lab. These native predators appear to partition resources facilitating prey suppression, and they may be complementary in biological control. Nonetheless, during our study we observed only one HWA pest generation annually in the native western range, contrasting with bivoltine populations in the invaded east. This difference in pest voltinism, along with climatic differences between native and invaded communities, will likely influence predator–prey synchrony as the natural enemy complex establishes in invaded range.

Keywords Biological control · Competition · Community ecology · Resource partitioning · Phenology · Co-occurrence

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Introduction

Species interactions and coexistence are fundamental drivers of community structure and ecosystem function in natural systems. Predator–prey interactions in multi-predator systems are highly variable in their ability to facilitate top-down control of damaging herbivores (Finke and Denno 2003; Northfield et al. 2010). For example, complementary natural enemies that feed on pests in different ways are predicted to increase predation rates compared to systems with ecologically redundant enemies (Stiling and Cornelissen 2005; Finke and Snyder 2008). The effects of multiple predator species on prey populations can be additive (sum of predator consumption) or facilitative (increased impact beyond the sum of two predators), resulting in enhanced prey suppression (Polis et al. 1989; Losey and Denno 1998; Northfield et al. 2010). Alternatively, when predators compete for prey or engage in intraguild predation, prey control is typically less effective (Polis et al. 1989; Finke and Denno 2003). In classical biological control, predator interactions are often understudied in their native range (Hierro et al. 2005; Kenis et al. 2017), potentially limiting the success of introductions to manage invasive species and supporting the need for a better understanding of community ecology in these scenarios.

Classical biological control is a focal strategy for managing introduced pests, regardless of whether the pests are invasive plants or herbivorous insects (McFadyen 1998; Kenis et al. 2017). Effective biocontrol typically involves specialist natural enemies targeting key developmental stages of pests, with complementary species enhancing prey suppression when efficiently partitioned (Hood et al. 2021; Stiling and Cornelissen 2005). Understanding the ecology of plant-herbivore-predator interactions in the native and introduced regions, especially those with diverse ecologies, can improve biocontrol success in invaded areas by informing agent selection and release strategy (Schröder et al. 2020). Indeed, as a means to understand plant invasions, there has been a strong push for biogeographical comparisons of the native and introduced ranges (Hierro et al. 2005). As forest pest invasions increase globally, ecological insight from the native range is becoming ever more critical for management decisions in the invaded range, and can help explain the success, or lack thereof, from management decision (Fischbein and Corley 2022).

The hemlock wooly adelgid (HWA) (*Adelges tsugae* Annand, Hemiptera: Adelgidae), is an aphid-like, host specific herbivore of hemlock trees, native to Asia and western North America (NA). In eastern NA, an invasive HWA lineage originating from southern Japan (Havill et. al. 2016) is feeding on eastern and Carolina hemlock (*T. canadensis* (L.) Carrière and *T. caroliniana* Engelmann), and leading to widespread tree decline and mortality of these important foundation tree species (Orwig et al. 2002, Limbu et al. 2018). The western NA HWA lineage feeds on western and mountain hemlock (*Tsuga heterophylla* Rafinesque and *T. mertensiana* (Bong.) Carrière) (Havill et al. 2016), with predator exclusion studies suggesting top-down control by specialist predators (Crandall et al. 2022). This sympatric group of specialists comprises two predatory fly species, *Leucotaraxis argenticollis* (Zetterstedt) and *Le. piniperda* (Malloch) (previously in the genus *Leucopis*; Gaimari and Havill 2021), and the beetle *Laricobius nigrinus* (Mayfield et. al. 2023). There has been wide-scale release and establishment of *La. nigrinus* in eastern NA (Mayfield et al. 2023) and increasing evidence of *Leucotaraxis* spp. suitability in the east (Dietschler et. al. 2023; Preston et al. 2023b). Currently, little is known about resource partitioning between HWA specialist predators from western NA; nonetheless, they are hypothesized to provide complementary prey suppression (Crandall et al. 2022). Such multi-predator systems are likely most effective in top-down control when predators partition resources, minimizing overlap, or feed in specialized ways that complement each other (Polis et al. 1989; Northfield et al. 2010; Hood et al. 2021).

Predator communities partition shared prey either spatially or temporally to avoid direct interactions such as intraguild predation and interspecific competition. For example, a recent meta-analysis showed that temporal separation of parasitoid oviposition reduced interspecific competition, likely fostering coexistence in multi-predator communities (Hood et al. 2021). In specialist predators with overlapping phenologies, spatial separation of exploitation facilitates coexistence on a shared resource (Duan et al. 2021). Occupation of unique foraging space by predators can sometimes increase prey consumption by sandwiching prey (Losey and Denno 1998). Thus, an understanding of predator-predator interactions not only offers insight into community structure, but also into the potential to manipulate the interaction for management of invasive pests.

The occurrence of HWA in eastern and western North America provides a unique opportunity to study forest pest community dynamics in native and introduced populations. Here we investigate the native predator–prey HWA community in western NA to inform management in the introduced eastern range. We use data on prey density, predator species abundance, and predator developmental stage over time and spatial scales (sites, trees, branches, and twigs) to test hypotheses on predator division of prey resources and predator-predator interactions. This study utilized naturally occurring HWA populations in Washington state (USA), describing sympatric specialist predators in their native western NA range. Five sites with large populations of HWA were selected for a longitudinal study (2022–2023) during peak predator activity (Grubin et al. 2011; Kohler et al. 2016; Rose et al. 2020; Dietschler et al. 2021). Additionally, we conducted a laboratory experiment assessing the likelihood of two congeneric fly predators (*Leucotaraxis* spp.) to directly compete, when feeding on the introduced HWA lineage on eastern hemlock. We predicted (1) HWA specialist predator feeding stages would be temporally separated, (2) during times of overlap predator species would display spatial partitioning, and (3) that the two *Leucotaraxis* spp. would compete when overlapping.

Methods

Study species

Hemlock woolly adelgid offers a unique opportunity for biogeographical comparisons between native and invaded ranges; including nine genetically distinct lineages native to Asia and western NA, each specializing on different *Tsuga* species, with rare host switching (Tshering et al. 2025, Havill et al. 2016). All lineages exhibit a complex life cycle involving a facultative primary (*Picea* spp.) and an obligate secondary (*Tsuga* spp.) host, with sexual reproduction on the primary host and parthenogenesis on the secondary. Several lineages have lost or lack described sexual reproduction (Havill and Foottit 2007, Havill et al. 2016). In their native ranges, HWA is not a major contributor to tree decline, so most research focuses on the invasive eastern NA population, introduced from the southern Japanese lineage where it specializes on *T. sieboldii*, and *P. torano* (Havill et al. 2016). In the invasive range, HWA has two parthenogenic generations (exules) per year, each undergoing a distinct developmental strategy on their hemlock hosts (McClure 1989). The first generation enters summer dormancy (aestivation) before developing over the winter, laying their eggs in late winter through spring (called “sistentes”; hereafter referred to as the overwintering generation). The second annual generation, experiences no diapause and is referred to as the spring–summer generation (also called the “progredientes”) (McClure 1989, Havill and Foottit 2007) (Fig. 1). Genetic evidence suggests western HWA are most closely related to the lineage on *T. sieboldii* (diverged, 14–57 *kya*) but have lost sexual reproduction and are only known from hemlock hosts (Havill et al. 2016).

Specialist predators are believed to be important for population regulation in Adelgidae, with a complete lack of parasitoids across the entire family (Havill and Foottit, 2007). Surveys for HWA biocontrol agents in western NA identified three specialist predators (*La. nigrinus*, *Le. argenticollis*, and *Le. piniperda* on *T. heterophylla*), with additional predators located from the native Asian ranges (Mayfield et al. 2023). *Laricobius nigrinus* beetles are synchronized with the overwintering HWA generation; adults emerge in fall to feed on developing nymphs, then lay eggs in late-winter on ovipositing HWA. Beetle larvae feed on HWA eggs and drop to the soil to pupate with minimal overlap with the spring–summer generation of HWA (Zilahi-Balogh et al. 2003) (Fig. 1). Reduced overwintering HWA densities from *La. nigrinus* predation leads to a density-dependent feedback of the spring–summer generation, where the parthenogenic HWA populations rebound (Crandall et al. 2020). These dynamics indicate that *La. nigrinus* alone cannot control HWA in the introduced range, highlighting the need for a complementary predator (Crandall et. al. 2020, 2022).

Leucotaraxis argenticollis and *Le. piniperda* are promising complementary predators that could enhance predation leading to effective management (Crandall et al. 2022, Mayfield et al. 2023). Their larvae feed on HWA eggs and have been observed

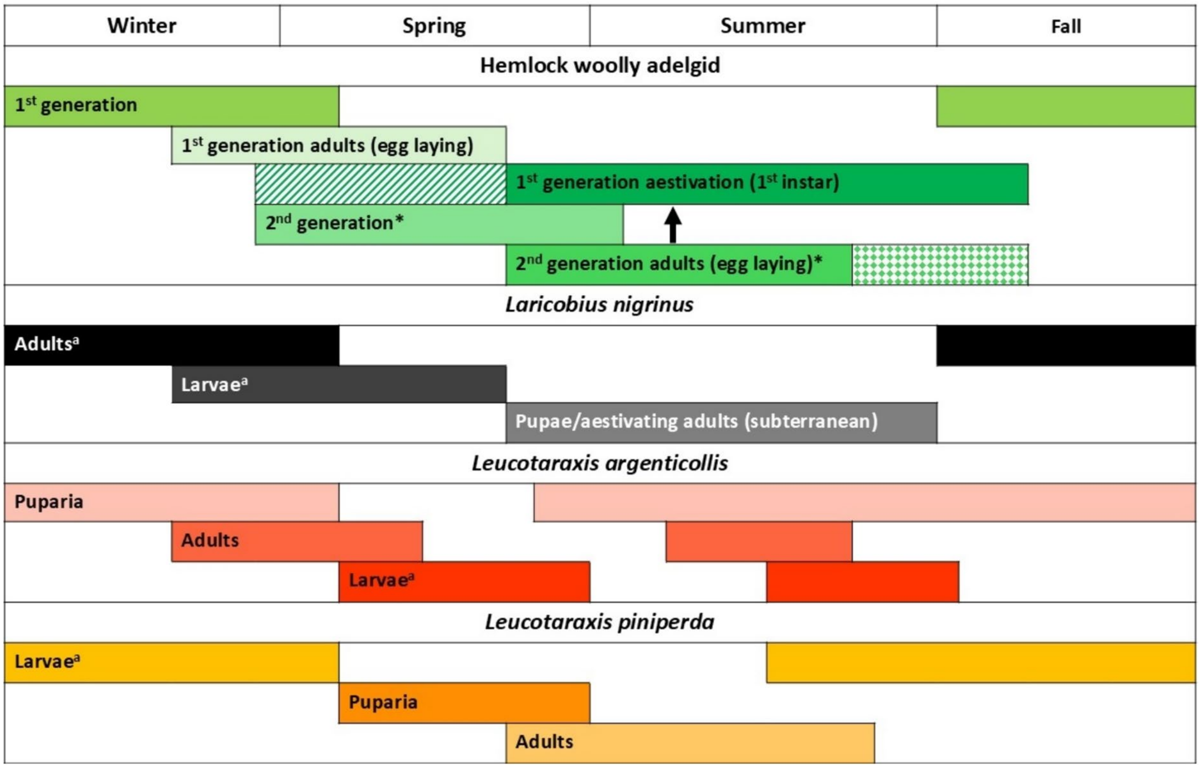


Fig. 1 The life cycle and synchrony of HWA and three specialist predators based on published information from western NA, results from this study, and experiments from eastern NA (Zilahi-Balogh et al. 2003; Grubin et al. 2011; Darr et al. 2018; Rose et al. 2020; Dietschler et al. 2021, 2023; Preston et al. 2023b). *2nd generation is facultative in the west. [a] represents predator feeding stages. Dashed lines represent facultative early diapause observed in western NA. Checkered box represents extended egg laying that has only been reported in western NA (Darr et al. 2018). Predator data reflects the pattern in the native western range. Thus far, *Laricobius nigrinus* appears to have the same phenology in eastern North America (Mausel et al. 2008)

during the oviposition period of both generations in western NA, suggesting they could fill predation gaps in the introduced range (Grubin et. al. 2011, Kohler et. al. 2016, Rose et. al. 2020) (Fig. 1). These species of *Leucotaraxis* have a broad geographic and adelgid species host range, with genetic differentiation by host, and collections from western hemlock being genetically distinct indicate specialization on HWA (Havill et al. 2023). Lacking distinguishing morphological features that limited earlier western NA research, *Leucotaraxis* larvae and puparia were identified using TaqMan-probe-based multiplex real-time qPCR with species and lineage specific primers, enabling rapid identification (see supplementary methods).

Study sites and sampling

Five sites naturally colonized by the native western lineage of HWA were selected in Washington State (WA, USA) in 2022 and 2023. In 2022, sites were in Edmonds, Port Townsend, and Kingston, and on Camano and Whidbey Islands. In 2023, the Camano Island, Whidbey Island, and Kingston sites were resampled while Lynnwood and Sequim were added due to HWA population crashes at the Edmonds and Port Townsend sites (Fig. S1). In 2022, three infested branches on each of three *T. heterophylla* trees per site were sampled. At each sampling, five twigs consisting of 15 cm of infested terminal growth were collected for destructive sampling, between one and three meters, for a total of 45 twigs per site. Twigs were categorized by site, tree, and branch. The same protocol was used in 2023 at Whidbey Island and Sequim but was modified due to lower HWA populations at other sites as follows: At Kingston, only one infested tree remained, so sampling was reduced to three branches. At Camano Island and Lynnwood, where infestations were more diffuse, branches were distributed more haphazardly across trees during sampling. All trees and branches were spatially discrete at each site, with twigs being destructively sampled within 1–2 m on each branch. Temperature was recorded at each site using a Tidbit MX400 (Onset HOBO, Bourne, MA).

Spatial and temporal niche partitioning—Field observations

Sampling periods were determined based on timing of specialist predator abundance, during the egg laying phase of HWA, from late February through June/July (Zilahi-Balogh et al. 2003; Grubin et al. 2011; Darr et al. 2018; Rose et al. 2020; Dietschler et al. 2021). Collections were made semi-monthly in 2022, from 21 February to 12 June. In 2023, twig samples were collected monthly to semi-monthly, between 25 March and 7 October. Twig samples were refrigerated no more than 48 h before being shipped overnight to Cornell University (Ithaca, NY) (USDA APHIS Permit #P526P-21-02017), and immediately frozen (− 20 °C) upon arrival for a minimum of one week prior to opening, ensuring all organisms had been killed. Ovisacs were destructively sampled, with HWA assigned to three developmental stages (aestivating nymphs, developing nymphs, and adults with eggs) and predators collected at each period to assess spatial and temporal occurrence.

Leucotaraxis spp. competition—laboratory assay

Laboratory rearing assays assessing competition between *Le. argenticollis* and *Le. piniperda* were set up with 12 adults, a maximum of two days post-emergence. *Leucotaraxis* spp. adults were reared from field-collected HWA infested western hemlock, collected from WA, in Cornell University's Sarkaria Arthropod Research Laboratory biocontainment facility (Ithaca, NY). Experimental rearing cage composition consisted of *Le. argenticollis* only ($n=12$), *Le. piniperda* only ($n=12$), or *Le. argenticollis* and *Le. piniperda* ($n=6{:}6$), at a 1:1 sex ratio. Adult flies were identified and sexed using external genitalia morphology (Dietschler et. al. 2021). Three treatments were set up to assess two variables of competition ($N=30$, $n=5$); *Le. argenticollis* only, *Le. piniperda* only, and combined *Le. argenticollis* and *Le. piniperda as treatments.* Cages were divided and tested for either (1) adult egg laying or (2) larval feeding competition. Cages (30.5 cm cubic insect cage) were held in laboratory conditions at room temperature (21–23 °C) under indirect natural lighting (Dietschler et al. 2023).

Adult *Leucotaraxis* spp. were provided bouquets of eastern hemlock infested with ovipositing overwintering generation of introduced Japanese lineage HWA collected from field locations in New York State (USA) with no biological control predator release history. Egg laying bouquets and supplemental feeding bouquets were made consisting of two heavily infested twigs, 15–25 cm of terminal growth, inserted into hydrated floral foam wrapped in parafilm (Dietschler et al. 2023). HWA density estimates (adelgids/cm) were made for all egg laying and supplemental feeding bouquets by counting HWA density on every third new growth twig segment moving clockwise. The bouquets were stored at 3 °C to slow HWA development and egg maturation.

Rearing cages were provided with an egg laying bouquet, and adult *Leucotaraxis* spp. were allowed to oviposit for four days. Egg laying bouquets were replaced after four days by aspirating adult flies from the cage. New egg laying bouquets were provided to adult flies for a total of 28 days (seven cage change intervals). Bouquets collected from cages assessing egg laying competition were immediately frozen at -20 °C for later processing. Bouquets collected from cages to assess larval competition were interspersed with a supplemental bouquet to provide additional food resources for developing larvae. Larval competition bouquets were held at room temperature (21–23 °C) for a total of 21 days to allow for larval development, before being frozen (− 20 °C) for later processing and genetic identification (see supplementary information).

Data analysis

Differences in predator distribution across sites were evaluated by Fisher's exact tests, due to small sample sizes of *Leucotaraxis* spp. at some sites. Predator distribution comparisons were limited to immature stages that interact directly with prey (larvae and puparia). Spearman rank correlations were used to evaluate relationships between predator and prey abundance, as assumptions of normality and homoscedasticity were not met. Assumptions were assessed by visualizing linear model residuals on both raw and log transformed data.

Due to the low sample size of *Le. argenticollis*, a Firth's binomial logistic regression was used to assess the temporal probability of immature predator occurrence in 2022 and 2023 data (Firth 1993). Sites were aggregated for each collection period, and sampled twig was treated as a binomial response (predators present = 1, and predators absent = 0, irrespective of density) for each predator species and immature stage (*Leucotaraxis* spp. larvae and puparia, and *La. nigrinus* larvae). Collection period was included as an interaction term and site as additive effect. Edmonds and Port Townsend in 2022 were excluded from temporal analysis due to the complete absence of *Leucotaraxis*. Model outputs were interpreted using the "emmeans" package in R, to assess the probability of predator occurrence and pairwise odds ratio comparison of temporal species stage co-occurrence (Lenth 2023). A non-parametric probabilistic co-occurrence model (Veech 2013) was used to evaluate the spatial relationships between predator species by developmental stage using the "cooccur" package (Griffith et al. 2016). Observations with predators present were grouped by site, tree, and branch, and tested at the twig level across collection periods. A threshold, of expected co-occurrence of < 1, was used to remove species-stage pairwise comparisons (i.e., species were not associated due to temporal separation, not expected to co-occur). Predator co-occurrence was treated as binomial, with each twig observation being present (1) or absent (0) for each predator, irrespective of density. Twig level co-occurrence was examined for pair-wise spatial niche separation for interactions between less mobile immature feeding stages; grouped at the site, tree, and branch for each sampling period. Temperature data was used to assess whether hypothesized thresholds were reached, triggering early-onset aestivation in the spring–summer generation. We evaluated the total number of days observed that reached a maximum temperature (Tmax) and mean temperature (Tmean) above the proposed threshold of 17 °C (Salom et al. 2001, Weed et al. 2016) between two developmental windows (peak egg laying from 1 April to 1 May, and settling of the spring–summer generation crawlers from 1 May to 15 June). Due to data logger malfunctions at Lynnwood, Camano Island, and Kingston in 2023, temperature data was acquired from the PRISM Group for these sites (PRISM Group 2023).

For the competition laboratory assay, an ANOVA was used to confirm provided prey density was equal between competition experiment treatments. *Leucotaraxis* spp. competition was analyzed using a negative binomial generalized linear mixed model (glmmTMB" package; Brooks et al. 2017) to estimate differences in egg or larval/puparial density by treatment and over time (four day intervals; cage change day as a categorical variable), including an offset for the number of live females. Post-hoc comparisons of treatment-species effects within each change level were conducted using estimated marginal means with Tukey-adjusted contrasts (emmeans), back-transformed to rate ratios on the response scale, accounting for the model offset. One of the *Le. piniperda* conspecific cages was found to be contaminated with *Le. argenticollis* and was removed from analysis. Akaike information criterion (AIC) model selection was used to determine which model was the best fit, using a ΔAIC of > 2.0 as a cutoff. The response variable was controlled for reproductive output per female fly and utilized as an offset in the model. All analysis was performed using R version 4.3.1 (R Core Team 2023), and all plots were created using ggplot2 (Wickam 2016).

Results

Leucotaraxis spp. immature distributions differed from *La. nigrinus* larvae across sites in 2022 and 2023 ($p < 0.001$), with *Leucotaraxis* spp. being 85% and 64% fewer, respectively. *Leucotaraxis piniperda* and *Le. argenticollis* distributions were different in both years ($ps < 0.001$) with *Le. piniperda* being consistently more abundant (Table S1). We found a positive correlation between HWA prey density and all stages of *La. nigrinus* (rho = 0.44, $n = 776$, $p = < 0.001$) and *Le. piniperda* (rho = 0. 14, $n = 221$, $p = 0.$ 049), but this relationship was non-significant for *Le. argenticollis* (rho = 0.28, $n = 26$, $p = 0.163$) (Fig. S2).

Temporal niche partitioning and competition-field observations

We report model estimated probabilities of predator occurrence to account for covariate effects and reduce bias in sparse data (using Firth's logistic regression) (Tables S2 and S4). Predators were present throughout the egg laying stage of HWA, ending mid-May in both years (Fig. 2), with probability of *La. nigrinus* larval occurrence synchronized with egg laying in both years and overlapping with both species of *Leucotaraxis* (Fig. 2A–F). Immature *Le. piniperda* exhibited temporal stratification with larvae appearing first (Feb-April) and puparia later (Apr–Jun), with larvae present as the likelihood of larval *La. nigrinus* increased during the onset of HWA oviposition (Fig. 2A, B). As HWA egg laying peaked, the occurrence of *Le. piniperda* puparia increased, with *La. nigrinus* larvae continuing to feed on the remaining eggs. The probability of *Le. argenticollis* puparia presence increased while *Le. piniperda* larvae were feeding, with greater odds of *Le. argenticollis* puparia when compared to *Le. piniperda* puparia (Feb–Apr), suggesting an inverse temporal relationship. As *Le.*

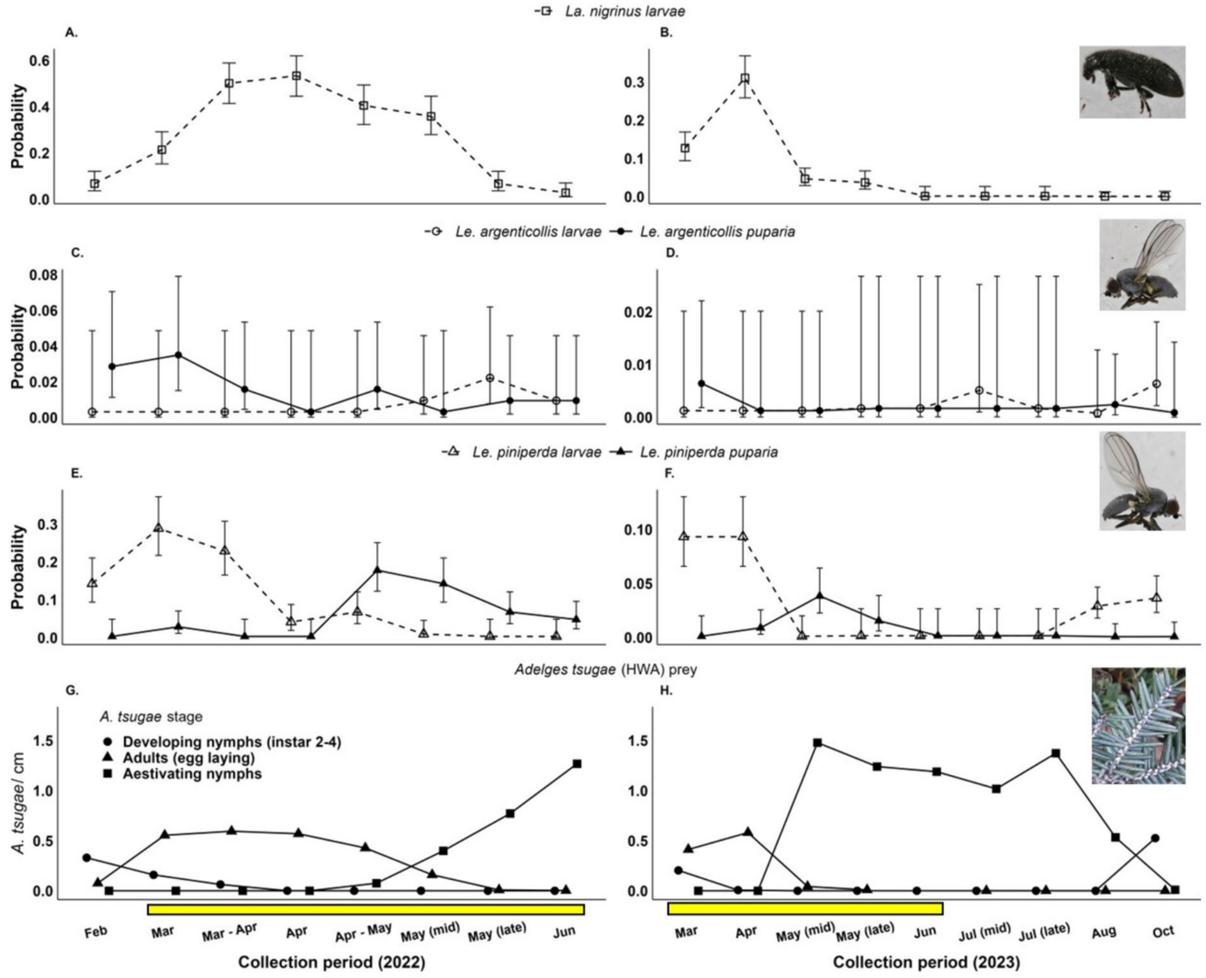


Fig. 2 Temporal niche separation and modeled probability of occurrence of *Laricobius nigrinus* (**A**, **B**), *Leucotaraxis argenticollis* (**C**, **D**), and *Le. piniperda* (**E**, **F**) during collection periods in 2022 (**A**, **C**, **E**) and 2023 (**B**, **D**, **F**). HWA density by developmental stage in 2022 (**G**) and 2023 (**H**). Site data is aggregated and modeled probability of the predator occurring on a twig with 95% confidence interval shown (**A**–**F**). Note the difference in date ranges between 2022 sampling (**A**, **C**, **E**, **G**) and 2023 sampling (**B**, **D**, **F**, **H**). Highlighted area under x-axis indicates seasonal overlap between the two sampling years. Specific dates for sampling are given in Tables S2 and S3

piniperda pupariated, the odds of detecting *Le. argenticollis* larvae increased when compared to *Le. piniperda* larvae (May–Jul) (Fig. 2A–F; Tables S3 and S5). *Leucotaraxis argenticollis* was relatively rare in both years of the study, and the probability of finding them on a twig was significantly lower than other predators (Fig. 2C, D; Tables S3 and S5). In 2023, a single *Le. argenticollis* larva was collected during the mid-July sampling (Fig. S3), with increased chances of *Le. piniperda* occurring during late-August and early-October collections, at higher odds than *Le. argenticollis* larvae in October (Fig. 2C–F; Tables S3 and S5). There was no difference between the probability of *La. nigrinus* and *Le. piniperda* larvae presence between February and March, indicating that these predators are equally widespread during early HWA egg laying (Fig. 2A, B, E, F; Tables S3 and S5). *Laricobius nigrinus* larvae had the highest probability of occurrence of all the predators from March–May in both years (Fig. 2). See Tables S3 and S5 for all pairwise comparisons, and Figure S3 for temporal separation of all species developmental stages.

In 2022 and 2023, HWA completed one generation by the end of May. Settled nymphs of a new generation were first observed at the end of April in 2022, and mid-May in 2023. This generation entered aestivation (i.e., summer dormancy) in both years and remained dormant through mid-June 2022 (when observations ended), and breaking dormancy in early-October in 2023. Developing HWA nymphs were observed feeding on the previous year's twig growth, with the youngest shoots being free of settled adelgids (Fig. 3AB). This pattern is contrary to that of the introduced eastern North American range where newest growth is preferred by the overwintering generation, with the spring–summer generation settling amongst their mothers (Fig. 3C). The range of Tmax recorded across sites from 1 April to 1 May were 15.3–20.6 °C and 15.3–25.5, and from 1 May to 15 June were 18.6 to 22.5 °C and 25.6–31.3 °C, in 2022 and 2023 respectively, showing that the proposed 17 °C threshold was regularly exceeded (Fig. S4 and Table S6).

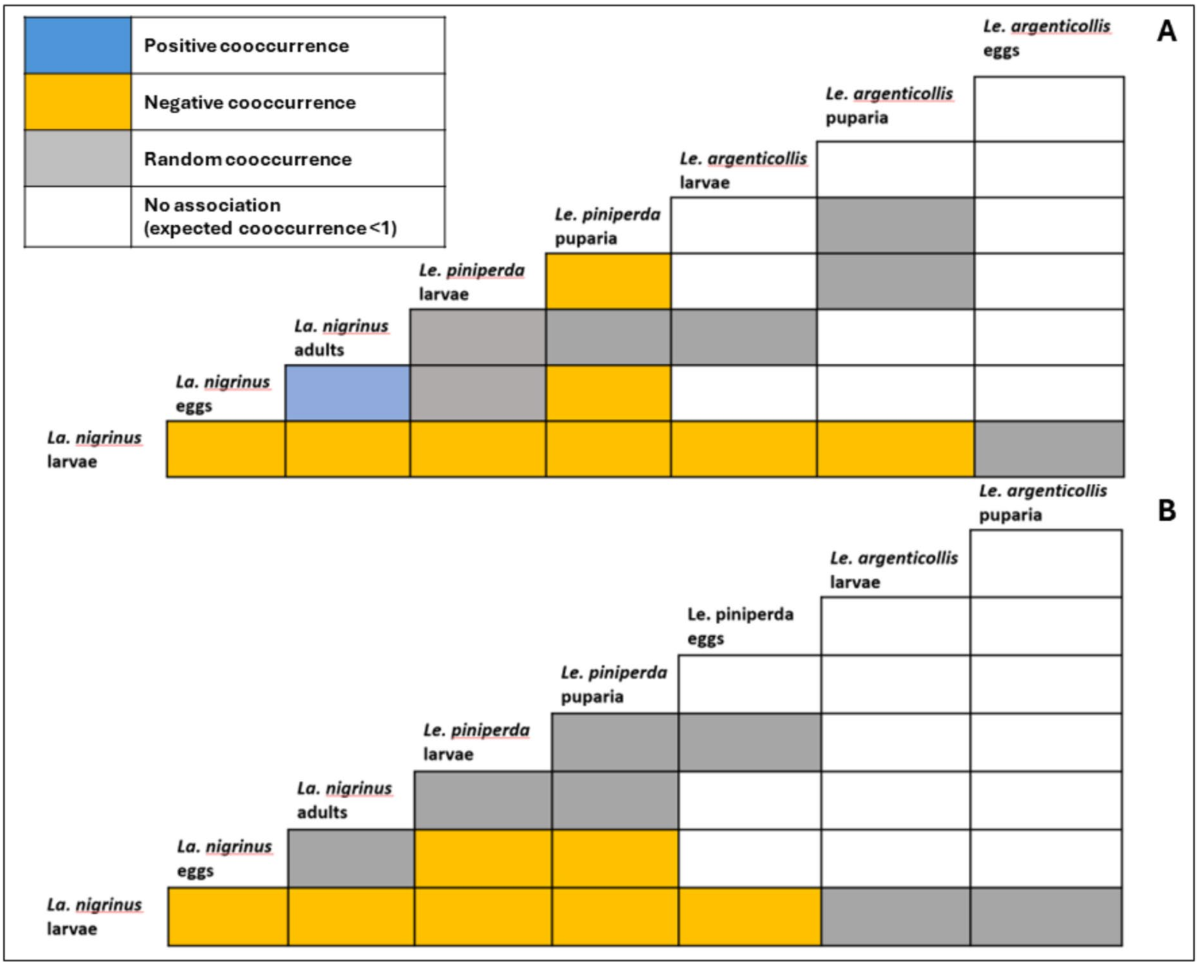
Spatial niche partitioning

All co-occurrence spatial analyses compared species developmental stage pair combinations at the twig level, with expected co-occurrence > 1, in 2022 and 2023 ($n = 28$ and 36 pairs, respectively). In 2022, 12 of the species-stage associations (43%) were removed because of the lack of expected co-occurrence; among

Fig. 3 Settling and feeding patterns of HWA. **A** In their native western NA range in 2022 **B** and 2023, aggregated on growth that is over one year old (see arrow and no HWA above the arrow on newer growth). **C** In the introduced eastern NA range, in addition to higher densities of HWA, they preferentially settle on the youngest foliage

the rest, one was positive, seven negative, and eight were randomly associated (Fig. 4A). During 2023, 22 species-stage pairs (62%) were removed; where none were positive, seven were negative, and seven random (Fig. 4B).

Across both years, *La. nigrinus* beetle larvae had the most interactions, showing significant negative co-occurrence with both *Leucotaraxis* spp. immatures in 2022, and *Le. piniperda* immatures in 2023 (Fig. 4). While *La. nigrinus* larvae were randomly associated with *Le. argenticollis* immatures in 2023 (Fig. 4B, Table S7), this was likely due to low samples size as they were never observed co-occurring. Adult *La. nigrinus* beetles, showed a positive association with their eggs in 2022, and negative co-occurrence with conspecific larvae, suggesting adults perform a single bout of egg laying on a twig. *Leucotaraxis piniperda* puparia were negatively associated with their own larvae in 2022. *Laricobius nigrinus* showed evidence of avoidance to *Le. piniperda* larvae, with eggs being negatively associated with *Le. piniperda* larvae (in 2023) and puparia (2022 and 2023) (Fig. 4). Very little spatial interaction was observed between *Leucotaraxis spp.*, and was either random, or excluded from analysis due to being below the expected co-occurrence threshold (< 1.0), supporting results of temporal niche separation between these species. All pairwise comparisons are given in Tabel S6.



🟦	Positive cooccurrence
🟨	Negative cooccurrence
▨	Random cooccurrence
⬜	No association (expected cooccurrence<1)

A

	La. nigrinus eggs	*La. nigrinus* adults	*Le. piniperda* larvae	*Le. piniperda* puparia	*Le. argenticollis* larvae	*Le. argenticollis* puparia	*Le. argenticollis* eggs
Le. argenticollis puparia							⬜
Le. argenticollis larvae						⬜	⬜
Le. piniperda puparia					⬜	▨	⬜
Le. piniperda larvae				🟨	⬜	▨	⬜
La. nigrinus adults			▨	▨	▨	⬜	⬜
La. nigrinus eggs		🟦	▨	🟨	⬜	⬜	⬜
La. nigrinus larvae	🟨	🟨	🟨	🟨	🟨	🟨	▨

B

	La. nigrinus eggs	*La. nigrinus* adults	*Le. piniperda* larvae	*Le. piniperda* puparia	Le. piniperda eggs	*Le. argenticollis* larvae	*Le. argenticollis* puparia
Le. argenticollis larvae							⬜
Le. piniperda eggs						⬜	⬜
Le. piniperda puparia					⬜	⬜	⬜
Le. piniperda larvae				▨	▨	⬜	⬜
La. nigrinus adults			▨	▨	⬜	⬜	⬜
La. nigrinus eggs		▨	🟨	🟨	⬜	⬜	⬜
La. nigrinus larvae	🟨	🟨	🟨	🟨	🟨	▨	▨

Fig. 4 Co-occurrence matrix depicting negative, positive, random, or no probability of co-occurrence for predators of HWA at all sites in 2022 (**A**) and 2023 (**B**) at the level of twigs. Designations are based on probabilistic co-occurrence models where negative or positive co-occurrence represents a $p < 0.05$, with only species-stages with interactions included. (see methods and Table S7)

Leucotaraxis spp. competition—laboratory assays

In the laboratory competition assay, HWA prey density was found to be equivalent for rearing bouquets ($F_{(6,7)} = 0.737$, $p = 0.597$) and supplemental bouquets ($F_{(6,7)} = 0.787$, $p = 0.458$) between treatments, indicating all treatments received equal prey. Akaike information criterion (AIC) model selection determined the model with a treatment-by-change interval interaction term, cage as a random effect, and offset for total living females was the best fit for egg laying comparisons ($\Delta AIC = 9.73$) (Table S8 and S9). *Leucotaraxis argenticollis* egg laying occurred at the highest rate during the first 12 days post-eclosion and was significantly greater than *Le. piniperda*, with a gradual decline; *Le. piniperda* egg laying did not peak until after 12 days post-eclosion. After day 12, differences in egg laying abundance were not significant between the two *Leucotaraxis* spp. (Fig. 4A). While *Le. argenticollis* laid significantly more eggs cumulatively than *Le. piniperda* in all treatment comparisons ($p = < 0.001$) (Table S10), no difference in egg laying abundance was detected when comparing *Leucotaraxis* conspecifics in single species versus competition treatments. See Table S10 for all pairwise comparisons.

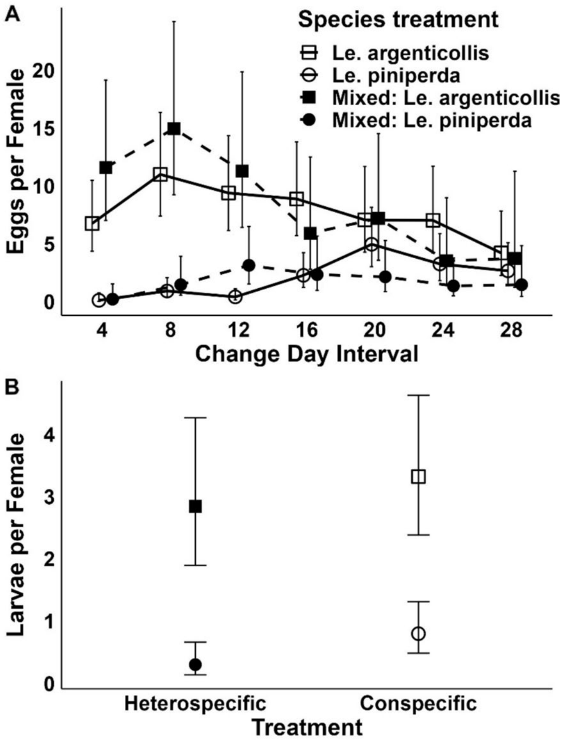


Fig. 5 Comparison of the abundance of congeneric *Leucotaraxis* fly predators of HWA in competition treatments. Adult *Le. argenticollis* (rectangles) *and Le. piniperda* (circles) mean eggs per female over cumulative four-day cage change intervals (**A**) in single species (open symbol/solid lines) and mixed species cages (filled symbols/dashed lines). Comparison of larval *Le. argenticollis* (rectangles) *and Le. piniperda* (circles) mean larval survival per female across sampling periods (**B**) in single species (open symbol) and interspecies competition cages (filled symbols). Estimated marginal mean and 95% confidence intervals shown

AIC model selection determined that the treatment-by-change interval additive model, with cage as a random effect, was the best fit for larval/puparial survival comparisons ($\Delta AIC = 24.65$) (Table S8 and S11). *Leucotaraxis* conspecific larval abundance was not significantly different between competition treatments. While not significant, we did observe a > 30% reduction in mean larval survival per female in the heterospecific competition treatment for *Le. piniperda* ($p = 0.1286$) and 14.4% for *Le. argenticollis* ($p = 0.9336$). There was a significant difference between *Le. argenticollis* and *Le. piniperda* larval abundance in all pairwise treatment comparisons ($p = < 0.001$) (Fig. 4B), indicating *Le. piniperda* was less fecund than *Le. argenticollis* in our assays (all pairwise comparisons in Table S12).

Discussion

A common feature of species invasions is higher abundance in the introduced versus native range, and HWA follows that pattern, with populations generally occurring at lower densities in western NA compared with the east, often attributed to natural enemy control in the native range (Hierro et al. 2005, see; McClure 1991, Crandall et al. 2020) (Fig. 2GH). Beyond locating suitable specialist biocontrol agents, understanding the predator–prey synchrony and multi-predator niche specialization are key, and these interactions in the native range can offer insight into implementation and effectiveness of classical biological control (Kenis et al. 2017; Fischbein and Corley 2022). Interactions of closely related natural enemies sharing resources can occur through multiple avenues, leading to impacts on population growth or prey suppression. In western NA, three specialists make up the most abundant predators of HWA (Kohler et al. 2008), with their relative abundance being highly variable among sites and years, suggesting no individual species is likely most important (Rose et al. 2020; Dietschler et al. 2021) (Table S1). Examples from aphid systems, close relatives of adelgids, show prey suppression increases with specialist predator diversity, while increased generalist diversity has little impact, supporting the efficacy of multi-predator communities (Finke and Snyder 2008; Northfield et al. 2010). Accordingly, one of the most important issues in HWA population dynamics is understanding the potential effectiveness of the suite of specialist predators feeding throughout the HWA life cycle.

Temporal niche separation and phenological synchrony

We found evidence that *Le. argenticollis* and *Le. piniperda* predatory flies divide resources temporally, with no observed overlap in larval feeding during winter-spring HWA oviposition (Fig. 2C–F); this result contrasts with earlier findings of temporal overlap among the same species, which were based on less intensive sampling over a single year and across a broader geographic range (Rose et al. 2020). Asynchrony among predators, combined with variation in site-level predator composition and abundance (Table S1), can offer temporal refuges for prey that help stabilize host-predator interactions (Fischbein and Corley 2022), potentially facilitating the coexistence of multiple sympatric predators. Laboratory and field data from eastern NA show *Le. argenticollis* overwinter as puparia and suggests *Le. piniperda* overwinter as larvae, a pattern further supported by this study and one that helps explain earlier records of overwintering *Leucotaraxis* larvae, now tentatively attributable to *Le. piniperda* (Grubin et al. 2011; Dietschler et al. 2023; Preston et al. 2023b) (Fig. 2C–F). In both years, *La. nigrinus* larvae overlapped with both *Leucotaraxis* spp. during February-May. Although *La. nigrinus* beetles were more abundant than *Leucotaraxis*, they were also more gregarious, while *Leucotaraxis* appeared more solitary; this behavioral difference helps explain their comparable likelihood of late winter occurrence on a twig despite contrasting overall abundance (Fig. 2; Tables S1 and S3, and S5). Synchrony between *La. nigrinus* and HWA was previously shown in both the native western and introduced eastern range, feeding entirely on the overwintering generation and their eggs (Zilahi-Balogh et al. 2003; Mausel et al. 2008) (Fig. 1).

Phenological synchrony with prey is critical for effective predation and prey suppression. A bivoltine HWA life-history has been widely observed in the introduced eastern range (McClure 1989; Mausel et al. 2008, Limbu et al. 2018) and reported in the native western range (Zilahi-Balogh et al. 2003; Kohler et al. 2008, 2016; Grubin et al. 2011; Rose et al. 2020). Nonetheless, western HWA has also been recorded as univoltine (Weed et al. 2016) and with extended egg-laying or multi-voltinism (Darr et al. 2018) (Fig. 1). Our observations provide two additional cases of univoltinism in the west (Fig. 2G, H). These observations imply that variation in HWA phenology could be more common than previously thought, with temperature being implicated as a major influence (Weed et al. 2016). A critical temperature threshold of 17 °C has been proposed for the early onset of aestivation in the introduced Japanese lineage of HWA (Salom et al. 2001) and was suggested as the cause of univoltinism in western HWA (Weed et al. 2016). Indeed, we observed max daily temperatures reaching this threshold at eight of ten sites during HWA egg laying, and all the sites during crawler settlement (Fig. S4 and Table S6). While our data supports previous observations that temperature could be influencing HWA population dynamics in western NA, further research is needed to confirm causation. Fluidity of voltinism is common in the Adelgidae (Havill and Foottit 2007), with variation in voltinism reported in *Pineus strobi* on eastern white pine based on latitude (Raske and Hudson 1964; Wantuch et al. 2017). Such variation in life-history strategies between herbivore populations or among cryptic species can influence biological control effectiveness (Schröder et al. 2020).

In the current study, developing overwintering HWA was only observed feeding on the previous years' tree growth in 2022 and 2023 (Fig. 3A, B), which is consistent with univoltinism since shoot elongation occurs later in the season. Furthermore, the absence of developing HWA on the youngest shoots during 2022 collections implies HWA displayed univoltinism in 2021, or potentially plant-mediated defenses of the newest growth. A univoltine life-history would alleviate the density-dependent intergenerational competition between the overwintering HWA generation and their daughters that is observed in the introduced eastern range (McClure 1991), leaving the youngest growth open for settling the following year. The second spring–summer generation of HWA has great reproductive potential in eastern NA, even leading to complete recovery from *La. nigrinus* predation on experienced by the previous generation (Crandall et al. 2020). The fly predator, *Le. argenticollis*, was found to have a facultative diapause in field experiments in the introduced eastern range, which could be a bet hedging strategy to cope with variable prey phenology (Dietschler et al. 2023), and the lack of the spring–summer generation has unknown consequences on predator–prey population dynamics. The cause of variation of HWA voltinism in the native range is unknown, but climate change is showing signs of increasing phenological mismatch in many systems impacting both predators and prey, leading to reduced predator efficacy in some instances (Damien and Tougeron 2019; Ferracini et al. 2022).

In eastern NA, heavy predation on the overwintering HWA generation by *La. nigrinus* can lead to significant reductions in prey population densities (Jubb et al. 2020), but HWA can recover within a single year due to their density dependent parthenogenic life-history (Crandall et al. 2020). The presence of a diverse predator community occupying unique niches increases prey consumption leading to more effective control (Finke and Snyder 2008; Northfield et al. 2010), with diverse complementary predators being able to exploit more of their preys' vulnerabilities. While our data shows phenological overlap between *La. nigrinus* and *Leucotaraxis* spp., there is evidence of complementary predation, supporting their combined use in eastern NA. *Leucotaraxis piniperda* larvae are most likely to occur early in HWA oviposition, reducing overlap with *La. nigrinus* larvae, which peak later; as *Le. piniperda* begin to pupariate, *Le. argenticollis* larvae were observed, while the probability of observing *La. nigrinus* larvae declined (Fig. 2). Species with overlapping phenologies, like emerald ash borer parasitoids (*Spathius galinae* and *Tetrastichus planipennisi*) (Quinn et al. 2022), exhibit alternate strategies like spatial separation facilitating co-occurrence, leading to reduced herbivore density and increased tree health (Duan et al. 2021; Morris et al. 2023, 2024).

Spatial niche separation

Temporal niche separation facilitates the co-occurrence of *Leucotaraxis* spp., but *La. nigrinus* overlaps with feeding stages of both flies during the overwintering HWA generation, suggesting another mechanism driving feeding specialization. Spatial niche partitioning can be influenced through distributions in host resources, predator behavior, avoidance of intraguild predation and cannibalism (Duan et al. 2021; Kajita et al. 2006; Schellhorn and Andow 1999). Negative co-occurrence of *La. nigrinus* larvae with conspecifics, *Leucotaraxis spp.* immatures (Fig. 4), suggest avoidance or intraguild predation. Adult *La. nigrinus* were positively associated with conspecific eggs but negatively associated with larvae, indicating adults leave twigs after oviposition, reducing intergenerational competition for prey. Negative associations between *La. nigrinus* larvae and conspecific eggs may reflect synchronous hatching or cannibalism, a self-limiting behavior that may reduce *La. nigrinus* abundance at low prey densities, indirectly facilitating *Leucotaraxis* spp. and enhancing HWA suppression (Flowers et al. 2005; Schellhorn and Andow 1999). Natural enemies of the cottony cushion scale (*Icerya purchasi*) segregate at the landscape scale, with vedalia beetles (*Novius cardinalis*) preferring the California interior, and a parasitoid (*Crytochetum iceryae*) favoring coastal areas. These scale enemies effectively regulate populations independently, and can co-exist in intermediate areas with abundant prey, but out-compete each other when prey are scarce (Caltagirone and Doutt 1989).

Intraguild predation can prevent establishment of species if heterospecific predators preferentially prey on them (Kajita et al. 2006). Larval *La. nigrinus* had a negative association with all immature stages of *Leucotaraxis* spp., indicating beetle larvae were being preyed upon or are avoiding fly larvae. Our results suggest avoidance because at that stage, flies were puparia, incapable of predation (Fig. 4, Appendix 9), thus supporting spatial niche partitioning as opposed to intraguild predation. Chemical fecal cues of both hetero and conspecific lady beetles have been shown as a mechanism facilitating avoidance behavior (Agarwala et al. 2003). With *La. nigrinus* being widely established in eastern NA (Mayfield et al. 2023), *Leucotaraxis* spp. will need to establish in environments with existing beetle populations, and spatial resource partitioning may aid in this establishment. Spatial niche partitioning of biological control agents occupying the same feeding guild, at the local scale, is proving successful in improving prey suppression through complementary feeding in the emerald ash borer (*Agrilus planipennis*) system (Duan et al. 2021; Morris et al. 2023), adding evidence that predators occupying unique niche space can increase overall predation (Finke and Snyder 2008; Northfield et al. 2010).

Competition between Leucotaraxis spp.

Field releases of biological controls in an introduced range aim to match their phenological synchrony from the native populations. While our results indicate little temporal competition between *Leucotaraxis* spp. larvae in their native range, and adults having temporally disjunct emergence patterns that inform release timing in eastern NA (Dietschler et al. 2021), the adults can live for over one month (in the lab, Dietschler et al. 2023) suggesting the potential for interactions in the field. Our laboratory assay put the two *Leucotaraxis* spp. into direct competition, offering insight into their life-history strategies that influence coexistence and inform release methods. We observed varying oviposition strategies, with earlier emerging *Le. argenticollis* ovipositing almost immediately, and the later emerging adult *Le. piniperda* one week post emergence (Fig. 5A), making their divergent egg laying strategies complementary. Rapid egg laying in *Le. argenticollis* could be a strategy to exploit the remaining HWA eggs, as *La. nigrinus* larvae are present feeding throughout *Le. argenticollis* emergence (Zilahi-Balogh et al. 2003; Dietschler et al. 2021) (Figs. 1 and 2A–D). As *Le. argenticollis* egg laying is waning, *Le. piniperda* egg laying will start and peak after a week post emergence, limiting larval overlap and competition. Temporal separation of oviposition in parasitoids has been found to reduce competitive interactions between sympatric species sharing resources through a reduction in priority advantage, with success often observed in the species that oviposits first (Hood et al. 2021). These observations of divergent oviposition strategies emphasize how variation in life-history traits can offset the potential for competition, even if released simultaneously, and provide a framework for optimizing release timing based on species-specific reproductive phenology.

We found no significant evidence of interspecies competition for egg laying space, or between larvae. While *Le. piniperda* laid significantly fewer eggs than *Le. argenticollis* overall, with the main differences concentrated in the first 12 days post-emergence, there was no difference of eggs laid in either species under a competitive scenario (Fig. 5A, Table S5). Predator chemical cues such as those in feces can influence avoidance behavior, or prey abundance can influence interference competition with egg laying adults (Schellhorn and Andow 1999; Agarwala et al. 2003), but we found no evidence suggesting these interactions between the two *Leucotaraxis* spp. While larval abundance did not show a significant difference between single species and competition treatments, there was a trend of lower larval abundance for both species when in competition (Fig. 5B), which may warrant further investigation. Intraguild predation between larvae can lead to direct impacts on predator performance, or scramble competition for prey could influence predator abundance (Polis et al. 1989). Relatively low abundances of *Le. piniperda* compared to *Le. argenticollis* in the lab, with the inverse often being true in the native range, suggests *Le. piniperda* may not perform well in the lab or on the introduced lineage of HWA on eastern hemlock. Nonetheless, our results indicate that these *Leucotaraxis* spp. would show little competition if released together in the invaded eastern NA range.

Conclusion

Research on native natural enemy interactions beyond species identity and prey specificity can inform more effective biological control programs when pests are introduced. Mounting evidence suggests that the introduced HWA and climate in eastern NA are suitable for *Leucotaraxis spp.*, in addition to *La. nigrinus* which is already established (Dietschler et al. 2023, Mayfield et al. 2023, Preston et al. 2023b). Laboratory experiments showing no strong competition between *Leucotaraxis* spp. and temporal niche separation in the native range suggests they can be released in sympatry. Previous research has shown releasing *Le. argenticollis* just prior to *La. nigrinus* larval drop, and *Le. piniperda* immediately after larval drop aligns with adult *Leucotaraxis* emergence (Dietschler et al. 2021); the current findings of temporally stratified phenology support those recommendations. Evidence of spatial separation between *La. nigrinus* and *Leucotaraxis* spp. supports releasing predators in sympatry, even where *La. nigrinus* are established. Nonetheless, variability in HWA life-history and settling patterns in the western NA range emphasize the importance of understanding an organism's native ecology when implementing management. Some invasive pests are controlled by individual natural enemies, such as winter moth (*Operophtera brumata*) by *Cyzenis albicans* (Elkinton et al. 2021), with others requiring multiple complimentary agents, like emerald ash borer (Duan et al. 2021; Morris et al. 2023). Our work adds to the growing evidence that the western NA suite of HWA predators can offer complimentary control, co-existing and dividing prey over space and time, with implications for improved hemlock health (Mayfield et al. 2023, Preston et al. 2023a). More generally, ecological research conducted in a pest's native range can bridge knowledge gaps in its invasive range, ultimately enhancing management outcomes.

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Data availability Data will be deposited in Dryad prior to publication.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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