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Warm temperatures increase population growth of a non-native defoliator and inhibit demographic responses by parasitoids

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Abstract

Changes in thermal regimes that disparately affect hosts and parasitoids could release hosts from biological control. When multiple natural enemy species share a host, shifts in host-parasitoid dynamics could depend on whether natural enemies interact antagonistically versus synergistically. We investigated how biotic and abiotic factors influence the population ecology of larch casebearer (*Coleophora laricella*), a non-native pest, and two imported parasitoids, *Agathis pumila* and *Chrysocharis laricinellae*, by analyzing (i) temporal dynamics in defoliation from 1962-2018 and (ii) historical, branch-level data on densities of larch casebearer and parasitism rates by the two imported natural enemies from 1972-1995. Analyses of defoliation indicated that, prior to the introduction of parasitoids (1962 to ~1980), larch casebearer outbreaks occurred in 2 to 6 year cycles. This pattern was followed by a >15-year period during which populations were at low, apparently stable densities undetectable via aerial surveys, presumably under control from parasitoids. However, since the late 1990s and despite the persistence of both parasitoids, outbreaks exhibiting unstable dynamics have occurred. Analyses of branch-level data indicated that growth of casebearer populations, *A. pumila* populations, and within-casebearer densities of *Ch. laricinellae* – a generalist whose population dynamics are likely also influenced by use of alternative hosts – were inhibited by density-dependence, with high intraspecific densities in one year slowing growth into the next. Casebearer population growth was also inhibited by parasitism from *A. pumila*, but not *Ch. laricinellae*, and increased with warmer autumnal temperatures. Growth of *A. pumila* populations and within-casebearer densities of *Ch. laricinellae* increased with casebearer densities but decreased with warmer annual maximum temperatures. Moreover, parasitism by *A. pumila* was associated with increased growth of within-casebearer densities of *Ch. laricinellae* without adverse effects on its own demographics, indicating a synergistic interaction between these parasitoids. Our results indicate that warming can be associated with opposing effects between trophic levels, with deleterious effects of warming on one natural enemy species potentially being exacerbated by similar impacts on another. Coupling of such parasitoid responses with positive responses of hosts to warming might have contributed to the return of casebearer outbreaks to North America.

Keywords: climate, *Coleophora laricella*, defoliator, host-parasitoid, invasion, population dynamics, spatial synchrony, weather

Introduction

Global climate change can influence the population dynamics of insect herbivores through a variety of mechanisms (Bale et al. 2002), including effects on natural enemies (Hance et al. 2007). Shifting climatic regimes can have disparate impacts by trophic level (Harrington et al. 1999, Voigt et al. 2003), potentially facilitating outbreaks of insect herbivores and complicating their management (Harrington et al. 2001, Castex et al. 2018). Cross-trophic climatic effects may be particularly important for non-native herbivores, which are frequently combatted via the importation of natural enemies from their native range, termed importation, or "classical", biological control. Following introduction, both invasive species and natural enemies must contend with novel climatic and photoperiodic regimes that can directly or indirectly mediate their distributions and abundances (Van der Putten et al. 2010).

Importation biological control can be an effective long term management technique for non-native forest insects and provide long-lasting control across spatial extents not feasible with insecticides or silvicultural treatments (Pschorn-Walcher 1977, Kenis et al. 2017). After the initiation of a biocontrol program, monitoring the population dynamics of target pests and their natural enemies, as well as interactions among natural enemy species, can provide insight into drivers of program efficacy (Murdoch et al. 1985). Several complex interactions can influence efficacy, such as intraguild predation among natural enemies (Rosenheim et al. 1995), evolution of pests and/or natural enemies (Simberloff and Stiling 1996, Goldson et al. 2014), and/or intraspecific and interspecific competition between natural enemies (Denoth et al. 2002, Kidd and Amarasekare 2012). Multiple species of natural enemies sharing prey, for example, might result in competitive exclusion (Ehler and Hall 1982), or conversely, additive effects on prey mortality (Snyder and Ives 2003, Stiling and Cornelissen 2005). Interactions between prey and one or more natural enemies may also be context dependent, varying across space and time due to novel or changing climatic regimes (Hance et al. 2007, Jeffs and Lewis 2013).

The larch casebearer, *Coleophora laricella* Hübner (Lepidoptera: Coleophoridae), is a non-native defoliator of larch (*Larix* spp; Pinaceae) in North America. Adult casebearers oviposit eggs singly onto larch needles and larvae hatch through egg bases and into underlying needles in which larvae feed through the second or third instar. Typically during the third instar, larvae render the

mined needle as a case, continue feeding, and then overwinter by attaching cases near dormant larch buds. In spring, larvae molt into fourth instars, detach their cases, and begin to forage for foliage – termed "activation" – and, after feeding on several needles, eventually pupate inside cases. Spring feeding larvae can substantially reduce plant vigor, and so an importation biological control program against larch casebearer was established and eventually deemed a success by the 1990s in forests of both eastern larch, *L. laricina* (Du Roi) K. Koch, and western larch, *L. occidentalis* Nutt. (Graham 1948, Webb and Quednau 1971, Otvos and Quednau 1981, Ryan et al. 1987, Ryan 1990, 1997).

Efficacy of the program was mostly attributed to parasitism from introduced populations of *Agathis pumila* Ratzeburg (Hymenoptera: Braconidae) and *Chrysocharis laricinellae* Ratzeburg (Hymenoptera: Eulophidae) (Quednau 1970b, Ryan 1997), although the former was considered to be the primary driver underlying the collapse of casebearer outbreaks in western larch (Ryan 1997). The initial invasion by larch casebearer and its biological control in western larch were well documented; a time series of larch casebearer abundance concurrent with the introduction and spread of *A. pumila* and *Ch. laricinellae* was recorded from 1972-1995 across 13 release and/or monitoring sites in Oregon and southeastern Washington (Fig. 1a) (Ryan 1990, 1997). Imported parasitoids were released in the 1970s at several locations in western larch forests and multiple investigations of ensuing casebearer population dynamics were conducted (Fig. 2) (Ryan 1983, 1986, 1997). By the mid-1980s, parasitoids had reached all 13 sites and the region-wide, combined parasitism rate by *A. pumila* and *Ch. laricinellae* was above 10% (Ryan 1997). Previous analyses of the 13 monitoring and release sites were conducted on a site-by-site basis and concluded that density dependence – high intraspecific densities in one year affecting population growth into the next – and parasitism from *A. pumila*, but not *Ch. laricinellae*, significantly decreased casebearer population growth (Ryan 1986, 1990, 1997). Drivers of population dynamics of *A. pumila* and/or the within-casebearer dynamics of *Ch. laricinellae*, and interactions between these two parasitoids, were not investigated.

Studies on eastern larch provide a foundation for hypotheses on how these two parasitoids might interact, however. Field data collected across two years in Quebec, Canada at one eastern larch site suggested that *A. pumila* may increase parasitism rates by *Ch. laricinellae* (Quednau 1970b). *Agathis pumila* is a specialist and solitary endoparasitoid that attacks needle mining second instars in summer but emerges from fourth instars the following spring (Quednau 1970a). *Chrysocharis*

laricinellae can use alternative hosts (Quednau 1967a, 1967b) and is a solitary endoparasitoid that attacks casebearing stages (second-fourth instars and pupae) in both spring and autumn. Foraging *Ch. laricinellae* in autumn, however, emerge several weeks earlier, such as in late spring to early summer, and need to survive until autumnal casebearing stages are available for oviposition (Quednau 1967a, 1967b). *Chrysocharis laricinellae* will parasitize hosts containing *A. pumila* and is a superior within-host competitor. The potential facilitation of *Ch. laricinellae* by *A. pumila* has been attributed to delayed development of casebearer larvae parasitized by *A. pumila* (Quednau 1970b), which results in increased synchrony of fourth instar casebearers with foraging *Ch. laricinellae* females in spring (Quednau 1970b). Multiparsitism by *Ch. laricinellae* invariably results in mortality for *A. pumila*, although the latter appears better at dispersing and locating hosts (Quednau 1970b, Ismail and Long 1982). This interaction, where a superior within-host competitor is an inferior forager, can prevent competitive displacement and promote persistence of multiple parasitoid species on a shared host (Lei and Hanski 1998). However, the role of *A. pumila* in facilitating parasitism by *Ch. laricinellae* across larger areas, and effects of *Ch. laricinellae* on population dynamics of *A. pumila*, remains unknown but could have important implications for the efficacy of biological control of larch casebearer.

We investigated the spatiotemporal dynamics of larch casebearer and the two imported parasitoid species to gain insight into patterns of landscape-scale outbreaks of larch casebearer, drivers of efficacy of biological control, and the effects of weather on different trophic levels. Our specific aims were to (i) examine potential temporal shifts in the dynamics of casebearer populations using data collected via aerial surveys before, during, and after the introduction of parasitic wasps (ii) investigate biotic and abiotic drivers of population dynamics of larch casebearer and *A. pumila* and within-casebearer dynamics of *Ch. laricinellae*, emphasizing previously uninvestigated interactions between *A. pumila* and *Ch. laricinellae* and (iii) quantify spatial variation in abundances of each species by investigating intraspecific spatial synchrony.

Materials and Methods

Defoliation data

We obtained aerial survey data for Region 6 (Oregon and Washington) from the USDA Forest Service (www.fs.usda.gov/detail/r6/forest-grasslandhealth/insects-

diseases/?cid=stelprd3791643, accessed 20 January 2020). Annual surveys were conducted in fixed-wing aircrafts by forest health experts from the Washington Department of Natural Resources, Oregon Department of Forestry, and USDA FS Forest Health Protection. Spatially referenced polygons indicating defoliation of western larch by larch casebearer were compiled using the geographic information system (GIS) capabilities of R statistical software. Specific packages used included rgdal (Bivand et al. 2019), raster (Hijmans 2020), geosphere (Hijmans 2019), and tidyverse (Wickham et al. 2019). Analyses throughout were conducted using R statistical software v.3.5.0 (R Core Team 2020) and all data supporting the results are archived in the Purdue University Research Repository (see Data Availability).

We included polygons (i) for which larch casebearer was listed as the first (95.7% of polygons), second (3.8%), or third (<1%) agent of disturbance and (ii) from all defoliation intensities (e.g., trace, moderate, heavy). We also assumed that, based on the presence of data for at least one forest disturbance agent in each year of our time series, that damage from casebearer would have been detected if present. However, we could not confirm that all sites/areas were surveyed in all years.

To assess shifts in population dynamics of larch casebearer – using mapped defoliation as a proxy for abundance –through time, hectares defoliated per year was $\ln(x+1)$-transformed and plotted against year. To further examine patterns in the vicinity of historical sampling sites, we also plotted defoliation within a convex hull polygon with a 10 km buffer that enclosed our sites (Fig. 1a). We note that some unknown percentage of defoliation is attributable to needle diseases, but ground surveys confirmed the widespread abundance of larch casebearers in Oregon and Washington (see Ward and Aukema (2019b) for details).

Periodicity of defoliation and changes therein were quantified using wavelet analysis following the approach Klapwijk et al. (2018) employed to examine oscillatory dynamics of several forest insects. Briefly, wavelet analysis estimates the fit of wavelets (oscillating periodic functions) to a time series (Cazelles et al. 2008). We used the continuous Morlet wavelet transform (Farge 1992, Grenfell et al. 2001) to calculate the wavelet spectrum of $\ln(x+1)$-transformed casebearer defoliation. Periodicity through the times series was assessed using a contour plot of the wavelet power spectrum, a matrix of period (number of years) by time (year) (Torrence and Compo 1998). Statistical significance of wavelet power at $\alpha = 0.05$ was determined by comparison with a first-order

autoregressive (AR(1)) process. Wavelet analyses were conducted via the biwavelet package in R (Gouhier et al. 2019).

Historical branch-level data

We analyzed data documenting population dynamics of larch casebearer and parasitism rates by *A. pumila* and *Ch. laricinellae* at 13 sites from 1972-1995. For a detailed description of sampling methods used to collect these data, see Ryan (1983, 1997). Briefly, four terminal branches 45 cm in length were clipped from the lower (1 branch), mid (2 branches) and upper crowns (1 branch within reach of a 12.2 m pole-pruner) of 5 or 10 western larch trees (height range: 6 to 25 m) per site across 13 sites in Oregon and southern Washington (Fig. 1). Sampling was conducted twice per year, once in December-March (winter) and again in June (spring). Larch casebearer densities were recorded as the number of casebearing larvae (winter and spring sampling) or adults (spring sampling only) per 100 buds per site. Parasitism rates were determined from these samples as described below.

Prior to 1981, percent parasitism by *A. pumila* was determined using June samples. From 1981 onward, parasitism by *A. pumila* was estimated via dissection of overwintering hosts from winter samples. Parasitism rates by the first generation of *Ch. laricinellae* were estimated by dissection of winter samples whereas parasitism rates during the second generation were estimated by rearing wasps from hosts collected in spring (% parasitism = no. of adult *Ch. laricinellae* / [no. of adult parasitoids + no. of adult casebearers]). Before 1983, when overwintering larvae were extremely abundant and parasitoid populations were building, a subsample of cases were obtained to determine percent parasitism. After 1983, all cases were processed. Combined parasitism for *Ch. laricinellae* was expressed on a site by site basis as $1 - (s_1 s_2)$, where s_1 is the proportion of unparasitized larvae surviving during winter and s_2 is the proportion of unparasitized larvae in spring (Ryan 1997).

Host-parasitoid dynamics

For larch casebearer, the mean numbers of overwintering larvae and adults per 100 buds in year t were expressed as O_t and N_t, respectively. Abundances for *A. pumila* (A_t) and *Ch. laricinellae* (C_t) (Quednau 1967a, 1967b) were calculated as the percent of overwintering larvae parasitized × no. of overwintering larvae per 100 buds, given that *A. pumila* is solitary (Quednau 1970a) and that only one adult wasp typically emerges from hosts parasitized by *Ch. laricinellae* (Quednau 1967a, 1967b). Given that *Ch. laricinellae* can use alternative hosts, the interannual fluctuations in densities of this

wasp we investigated relate strictly to patterns within larch casebearer populations, and are not necessarily reflective of region-wide dynamics. Thus, we refer to such fluctuations as "within-casebearer", rather than "population", dynamics of *Ch. laricinellae*. Spring parasitism rates by *Ch. laricinellae* were not included in models characterizing the within-casebearer dynamics of *Ch. laricinellae* to focus on a single rather than composite (e.g., summing abundances from two generations) measure of wasp density and to facilitate parallel analyses between parasitoid species.

We calculated population growth rates for hosts in year *t* as $\ln(O_{t+1} + 0.001) - \ln(O_t + 0.001)$, represented as R_t^O for larch casebearer. Growth rates for *A. pumila* populations (R_t^A) and within-casebearer densities of *Ch. laricinellae* (R_t^C) were defined in a manner equivalent to R_t^O. Analyses of interannual population change focused on overwintering larvae (O_t) to maintain consistency with parasitoid analyses, which evaluated winter samples. We used a linear mixed-effects model framework to investigate region-wide trends in interannual fluctuations for each species as a function of biotic and abiotic (weather) variables while accounting for variation due to site. For each model, a random intercept was fit for each site. Mixed effects models were constructed using the lme4 package (Bates et al. 2015) and degrees of freedom were estimated using Satterthwaite's approximation via the lmerTest package (Kuznetsova et al. 2017) and rounded down to the nearest integer for presentation. Two "biotic" models – those with only predictors such as conspecific densities and parasitism rates (Berryman 1991, 1996) – were first constructed for larch casebearer, one each for 1972-1980 (Model 1) and 1981-1995 (Model 2). Analyzing these time periods enabled us to investigate changes in the dynamics of casebearer populations after the build-up of parasitoid populations. Regression frameworks have been used to model growth rates of other forest insects as a function of intraspecific densities and attack rates from natural enemies (Berryman 2003, Weed et al. 2017).

We then constructed similar biotic models to quantify dynamics of *A. pumila* (Model 3) and *Ch. laricinellae* (Model 4) across 1981-1995 and reduced models using backwards elimination procedures such that only predictors with $P < 0.05$ remained. Analyses focused on 1981-1995 because (i) by 1981 both parasitoids were considered established in the region (ii) this permitted us to analyze parasitism data sampled in a consistent manner (see sampling protocols above) and (iii) high resolution weather data were available beginning in January 1981. Adult density (N_t) rather than O_t was fit as a predictor in models of parasitoid dynamics given that wasps would most likely respond to

abundances of adults. That is, not all overwintering larvae necessarily activate to become hosts for spring foraging *Ch. laricinellae* or survive to adults that oviposit eventual hosts for foraging *A. pumila* later in the growing season. Site × year observations preceded and followed by zero values – strings of zeros not reflective of changes in densities – were excluded from analyses of insect dynamics, resulting in time series of variable lengths for each site. For the 1972-1980 model, only intraspecific densities (O_t, O_{t-1}) were considered due to extremely low densities of parasitoids across the region during this period (Fig. 2) and the absence of daily weather data needed to construct a bioclimatic model (see below).

Species specific, inverse distance weighted (IDW) averages of growth rates were developed in an equivalent manner to Walter et al. (2015) and included in corresponding models to account for spatial autocorrelation in model residuals. For a given site *i*, weights were calculated as

$$w_{ij} = \frac{1}{d_{ij}^2}$$

where *d* is the distance (km) between site *i* and *j* in a UTM Zone 11 projection. A histogram of pairwise distances is provided in Appendix S1: Fig. S1. The IDW mean growth rate in year *t* for species *X* was calculated as

$$IDX_t = \frac{\sum_{j=1}^{n} w_{ij} R_{jt}^X}{\sum_{j=1}^{n} w_{ij}}$$

and expressed as IDO_t, IDA_t, and IDC_t, for casebearer larvae, *A. pumila*, and *Ch. laricinellae*, respectively. Spatial autocorrelation in residuals of final, reduced models with and without the IDW terms was compared using nonparametric spatial covariance functions fit with the ncf package in R (Bjørnstad and Falck 2001, Bjørnstad 2020). IDW predictors sufficiently reduced spatial autocorrelation (Appendix S1: Fig S2) and were retained in models irrespective of statistical significance. Definitions of all biotic variables are provided in Table 1.

Once best fitting biotic models were developed, we quantified the utility of weather predictors for explaining variation in insect dynamics (bioclimatic models). Weather predictors were developed using the Parameter-elevation Regressions on Independent Slopes Model (PRISM 2019). For larch casebearer, we extracted two suites of weather variables to evaluate (i) predictors based on laboratory assays of casebearer development (Ward et al. 2019b) and bioclimatic analyses of larch casebearer

outbreaks in Minnesota in which degree-day accumulation during the growing season, minimum temperatures in autumn, and spring precipitation were positively correlated with the incidence of defoliation of eastern larch (Ward and Aukema 2019a) and (ii) generic bioclimatic predictors (e.g., temperature means and extremes, precipitation totals) to account for potential differences in the thermal biology of casebearer populations on western vs. eastern larch (Ward et al. 2020). The generic bioclimatic predictors were developed using the dismo package in R (Hijmans et al. 2017) on PRISM climate data spanning 1 January to 31 October of each year. Thus, generic bioclimatic predictors were based on weather experienced by casebearer from the overwintering stage (F_0 generation) to the casebearing stage the following autumn (F_1 generation). Bioclimatic predictors from analyses of eastern larch (el-bioclimatic) and generic predictors (gen-bioclimatic) are described in Table 2. Parasitoid dynamics were modeled as a function of gen-bioclimatic predictors.

Bioclimatic models were developed using a two-step approach. We first fit each weather predictor individually into reduced biotic models. All weather predictors with $P < 0.15$ – the threshold for entry into models aimed at protecting against overfitting and reducing inclusion of potentially collinear terms – during this step were then added simultaneously into the reduced biotic model and backwards elimination was again used to obtain a final "el-bioclimatic" model for larch casebearer (Model 5a) and "gen-bioclimatic" models for larch casebearer (Model 5b), *A. pumila* (Model 6), and *Ch. laricinellae* (Model 7). Only weather predictors were considered for elimination during this step. Temporal trends for bioclimatic predictors occurring in final, reduced models are provided in Appendix S1: Fig. S3. Parasitism terms for the parasitoid not represented in the response variable were included in models to evaluate negative effects of *Ch. laricinellae* on *A. pumila* due to multiparasitism and positive effects of *A. pumila* on *Ch. laricinellae* arising from delayed development of hosts parasitized by *A. pumila*. Model structures for each full biotic and bioclimatic model are provided in Table 3. Final models (reduced versions of Models 1-2, 5a, and 6-7) are presented in the main text, whereas results from all full models and reduced versions of Models 3-4 and 5b are presented in Appendix S1. Statistical significance for all modeling was determined using a Type I error rate of $\alpha = 0.05$.

Spatial dynamics

There was considerable variation in host densities and parasitism rates both within and between sites (Fig. 2). To gain insight into variability in interannual fluctuations, we quantified intraspecific spatial synchrony in densities of each species as well as parasitism rates by the two wasps. Synchrony – the correlation between intraspecific abundances through time as a function of distance – was estimated using nonparametric spatial covariance functions fit with the ncf package in R (Bjørnstad and Falck 2001, Bjørnstad 2020). For hosts, densities of larvae and adults were analyzed and densities of all three species were ln(x+0.001)-transformed. Casebearer densities were analyzed across two time periods (1972-1980 and 1981-1995) to investigate synchrony before and after widespread establishment of parasitoids, whereas analyses for parasitoids were again limited to data from 1981-1995. Mean synchrony and associated confidence intervals were estimated from 1000 bootstrapped samples.

Results

Defoliation dynamics

Analysis of defoliation data indicated that historical population dynamics could be approximately categorized into three phases: (i) outbreak levels in the early 1960s to early 1980s prior to parasitoid establishment, (ii) endemic levels from the early 1980s to the late 1990s following widespread parasitoid establishment, and (iii) outbreak levels from the late 1990s onward (Fig. 1b) despite the persistence of parasitoids. Defoliation was cyclical during the first phase with dominant periodicity of 2-3 years and 4-6 years (Fig. 1c). During the second phase, no defoliation was detected in the vicinity of our study area (Fig. 1b) and thus no periodicity was detected across the region (Fig. 1c). During the third phase, defoliation exhibited seemingly unstable dynamics with no detectable periodicity (Fig. 1c).

Host-parasitoid dynamics

From 1972-1980, there was an average of 64.9 ± 4.3 overwintering casebearer larvae and 51.5 ± 3.6 SE adults per 100 buds. From 1981-1995, there were 19.0 ± 2.1 SE overwintering larvae and 8.4 ± 1.3 SE adults per 100 buds (Fig. 2a). From 1981-1995, mean (±SE) parasitism rates by *A. pumila* were 39.4 ± 2.0 % (range: 0 – 100; Fig. 2b) and combined parasitism rates by *Ch. laricinellae* were 4.2 ± 0.7 % (range: 0 – 63; Fig. 2c). Parasitism rates by *Ch. laricinellae* during winter sampling were

1.32 ± 0.3 % compared to 3.5 ± 0.6 % during spring sampling. When evaluating the earlier time period prior to widespread establishment of biocontrol agents (1972-1980), analyses indicated that larch casebearer growth rates were inhibited by density dependence (Table 4a). Analysis of data from 1981-1995 indicated that population growth of casebearer was still moderated by current year densities, but that parasitism from *A. pumila* also significantly reduced host population growth (Table 4b). Casebearer dynamics were not mediated by parasitism from *Ch. laricinellae* (Appendix S1: Table S1b), although parasitism from this wasp could be influenced by its dispersal to or from alternative hosts.

Population dynamics of larch casebearer and *A. pumila* as well as within-casebearer dynamics of *Ch. laricinellae* were influenced by weather (Table 5). Similar to the biotic model for larch casebearer, the bioclimatic model indicated that population growth was negatively correlated with conspecific densities in the current year and current year parasitism from *A. pumila* while unveiling positive associations of population growth with warmer minimum temperatures in October (Table 5a). None of the generic bioclimatic predictors were associated with casebearer population growth, however (Appendix S1: Table S4). The bioclimatic models for *A. pumila* (Table 5b) and *Ch. laricinellae* (Table 5c) indicated that growth rates of both wasps increased with host densities in the current year but decreased with densities of conspecifics in the current year and warmer annual maximum temperatures. There was also evidence of a synergistic interaction between parasitoid species, given that within-casebearer densities of *Ch. laricinellae* increased with current year parasitism by *A. pumila* (Table 5c) but no negative effects of *Ch. laricinellae* parasitism on population growth of *A. pumila* were detected (Table 5b; Appendix S1: Table S2). We caution that dynamics of *Ch. laricinellae* quantified here may not reflect region-wide dynamics of this wasp given its ability to use alternative hosts.

Spatial dynamics

Within each of the two time periods analyzed (1972-1980 and 1981-1995), patterns of spatial synchrony in larch casebearer larvae and adult populations were approximately equivalent (Fig. 3a,b). Prior to 1980, however, densities of larvae and adults were synchronous up to ~20 km (Fig. 3a). From 1981-1995, adults did not exhibit spatially synchronous fluctuations at any distance whereas larvae were spatially synchronous at distances from ~10-45 km (Fig. 3b). The absence of synchrony for

larvae at distances <10 km might have been due to the dearth of pairs of sites spaced 0-10 km apart (Appendix S1: Fig. S1); that is, sample size at shorter pairwise distances was low. Parasitism rates by *A. pumila* (Fig. 3c) and *Ch. laricinellae* (Fig. 3d) were synchronous beyond 80 km, whereas parasitoid densities exhibited no statistically significant synchrony at lag distances of zero. The absence of synchrony in parasitoid densities could be due in part to variability in casebearer densities, given that the latter were used to estimate the former.

Discussion

Climate can have disparate effects on the distribution and abundance of herbivores and their natural enemies (Jeffs and Lewis 2013). These dynamics are further complicated when multiple species of natural enemies interact to mediate herbivore population growth (Denoth et al. 2002, Stiling and Cornelissen 2005). Our study indicates that warmer autumnal minimum temperatures increased growth rates of casebearer populations (Table 5a) while warmer maximum temperatures inhibited growth *of A. pumila* populations and within-casebearer densities of *Ch. laricinellae* (Table 5b). Furthermore, negative impacts of weather on one parasitoid species might cascade to moderate efficacy of the other, given that prior parasitism from *A. pumila* was associated with increased growth of within-casebearer densities of *Ch. laricinellae* (Table 5c). Taken together, our results suggest that climatic warming might have contributed to recent outbreaks of the non-native larch casebearer by exerting opposing influences at different trophic levels.

Analyses of aerial survey data indicated that casebearer populations exhibited cyclical oscillations prior to parasitoid establishment but shifted into a period of low, endemic population levels and, eventually, into unstable dynamics without detectable periodicity. During time periods in which defoliation was not detected, low density casebearer populations could have undergone cyclical fluctuations but failed to surpass a discoloration threshold, thus escaping detection from aerial surveys (Büntgen et al. 2020). Depending on the functional responses (e.g, Type II vs. III) of natural enemies to host densities and resource enrichment for prey (e.g., increases in larch susceptibility to or suitability for casebearer), cyclical dynamics could emerge or be lost (Uszko et al. 2017), but such factors are currently unknown in this system. Loss of cycles have been observed in other taxa (Williams et al. 2004, Ims et al. 2008) and, in some instances, climatic warming has been implicated

in driving such losses (Johnson et al. 2010, Cornulier et al. 2013). Warming could be a plausible cause for the loss of cycles here (e.g., temperature driving the system across a stability boundary (Uszko et al. 2017)), but any effects are somewhat confounded with the abundance of parasitoids in this system and disentangling any contributions from these factors to changes in casebearer cycles, especially without continued larval sampling from 1996 onwards, is challenging. Moreover, recent defoliation patterns might not be driven by host-parasitoid interactions and could be attributable to casebearers irrupting to densities above their carrying capacity and subsequently collapsing, for example, due to resource depletion.

Warmer minimum temperatures in October –potentially associated with decreased mortality from acute cold exposure – appeared to benefit casebearer populations on western larch. The incidence of casebearer defoliation on eastern larch increased with both warmer minimum temperatures in autumn and warmer growing seasons (Ward and Aukema 2019a), as the latter likely results in higher proportions of larvae successfully developing into the overwintering stage (Ward et al. 2019a). We did not detect a relationship between casebearer population growth and degree-day accumulation (Appendix S1: Table S4a). Casebearers residing on western larch activate over 100 degree-days earlier than those on eastern larch when exposed to the same environmental conditions (Ward et al. 2020), potentially relaxing any constraints on population growth arising from insufficient degree-day accumulation. That is, earlier activation of the F_0 generation (i.e., overwintering larvae) would provide more time for the F_1 generation to reach the overwintering stage. Moreover, when feeding on western larch, casebearers could exhibit faster development rates during other larval stages, further moderating the influence of insufficient degree-day accumulation.

Growth of *A. pumila* populations and within-casebearer densities of *Ch. laricinellae* decreased with warmer annual maximum temperatures (Table 5b,c), indicating that warmer temperatures might have compounding effects on casebearer outbreaks by (i) increasing casebearer growth rates and (ii) reducing growth rates of natural enemies. The timing of warming (spring vs. autumn) may have distinct influences on host and/or parasitoid ecology, although both October minimum temperatures and annual maximum temperatures have increased across our study region (Appendix S1: Fig. S3). Warmer temperatures significantly accelerated mortality of adult *A. pumila* in laboratory assays (Quednau 1970a), but ecological importance of adult longevity for *A. pumila* remains unknown.

Given the positive effects of *A. pumila* on within-casebearer densities of *Ch. laricinellae* (Table 5c), negative impacts of temperature on *A. pumila* performance could have cascading effects. Warmer summers have been implicated in decreasing efficacy of *Ch. laricinellae* (Ryan 1986), likely because time to adult mortality accelerates with temperature (Quednau 1967a) and females emerging in summer need to await casebearers in autumn to reproduce when alternative hosts are not available (Quednau 1970b). Thus, increased frequency and/or intensity of damaging warm temperatures might impact efficacy of one or both parasitoids by accelerating mortality of foraging females. There remain several other potential mechanisms, such as changes in parasitoid fecundity, parasitoid size, and/or host-parasitoid phenological synchrony (Hance et al. 2007) as well as parasitoid attack rates (Meisner et al. 2014) through which warmer temperatures could influence parasitoid efficacy.

Growth of *A. pumila* populations and within-casebearer densities of *Ch. laricinellae* increased in response to host densities (Table 5b,c), indicating the potential ability of both species to mount a numerical response. *Chrysocharis laricinellae* can use other hosts, and thus any numerical or functional response by this species might be influenced by the availability and abundance of alternative hosts. For example, *Ch. laricinellae* might rely on alternative hosts to sustain its population growth (Quednau 1970b) or wasps could disperse away from casebearer populations in search of alternative hosts when (i) only needle mining larch casebearers are present in mid-summer or (ii) intraspecific competition reaches a certain threshold, a mechanism that could contribute to the density dependent inhibition of within-casebearer growth rates (Table 5c). *Chrysocharis laricinellae* could undergo a shift in host use when *A. pumila* parasitism rates are high, preferentially attacking casebearers vs alternative hosts. This latter mechanism is consistent with our findings but would indicate a shift in host preference (i.e., increased abundance on casebearer vs. other hosts) rather than a region-wide increase in abundance. Nonetheless, *Chrysocharis laricinellae* has been implicated in controlling populations of casebearer in northeastern Washington and on eastern larch (Quednau 1970b, Ryan 1997), but factors underlying the apparent inability of *Ch. laricinellae* to slow host population growth (Table 4b) in our study region remain unknown.

Intraspecific spatial synchrony was detected within-casebearer larvae and adults prior to 1980 and in parasitism rates from 1981-1995. Natural enemies are hypothesized to induce spatial synchrony in prey populations (Liebhold et al. 2004); however, synchrony was nearly absent in larval and adult

casebearer populations from 1981-1995 when parasitoids were abundant. Although our analyses were not aimed at elucidating the effects of parasitoids on temporal patterns of host synchrony, theoretical models indicate that dispersal by natural enemies (i) to avoid intraspecific competition and (ii) into areas of high prey density can reduce spatial synchrony (Li et al. 2005). Climate has been implicated in driving synchrony in defoliation by larch casebearer, which was synchronous up to 321 km in western larch forests and 79 km in eastern larch forests (Ward and Aukema 2019b). Larval and adult abundances may be more prone to sampling error than defoliation and our investigations were at a different spatiotemporal scale than Ward and Aukema (2019b), which could influence results.

Despite the large variability in parasitism rates across our study period (Fig. 2b,c), parasitism was synchronous in both wasp populations at distances >80 km. Parasitoid abundances (vs. parasitism rates) were not spatially synchronous, potentially owing to the variability in host abundances used in their calculation. Density-independent parasitism rates could have resulted in stronger synchrony among rates vs. abundances; that is, density-dependence would result in parasitism rates tracking host densities, and the latter had high variability (Fig. 3b). Indeed, parasitism rates by either wasp species were not associated with densities of overwintering larch casebearer larvae (Appendix S1: Fig. S4). Host abundance might be more likely to drive synchrony in specialist parasitoids, given that generalists might be influenced by densities of multiple host species. Conversely, if climate was the main driver, then synchrony might not be influenced by diet breadth, a pattern consistent with our finding that synchrony was similar between the specialist *A. pumila* and generalist *Ch. laricinellae* (Fig. 3c,d). Nonetheless, identifying drivers of synchrony, of which there may be several, is challenging and beyond the scope of this study.

Outbreaks in both western and eastern larch forests have occurred since the late 1990s despite the continued presence of both introduced parasitoids (Miller-Pierce et al. 2015, Ward and Aukema 2019b). While both parasitoid species are still known to be present in casebearer populations, their functional responses, which could mediate their responses to warming (Uszko et al. 2017), numerical responses, or population dynamics have not recently been investigated. It is not clear why this once successful biological control might be undergoing a prolonged lapse in efficacy, but there are several factors that could contribute to such a change (Goldson et al. 2014). Our re-analysis of historical data from the 13 western larch sites identified positive and negative effects of warm temperatures on larch

casebearer vs. *A. pumila*, respectively. Given that *A. pumila* was considered the main controlling factor after its widespread establishment – a finding supported by our region-wide analyses –it is possible that longer-term climatic change has contributed to the recent return of casebearer outbreaks. We caution that (i) consideration of generic bioclimatic predictors indicated that casebearer dynamics were not significantly influenced by weather, potentially indicative of casebearer sensitivity to temperatures in smaller windows of time (e.g., late autumn), (ii) drivers of insect dynamics can be highly context-specific, varying across space and through time (i.e., key drivers could have changed or might not have been considered), and (iii) nonlinear effects of density-dependent and density-independent factors on population dynamics were likely present (Higgins et al. 1997) but not considered.

Competition (May and Hassell 1981) or hyperparasitism (Rosenheim et al. 1995, Rosenheim 1998, Schooler et al. 2011) from other parasitoids, of which there are many associated with larch casebearer (Miller-Pierce et al. 2015), or evolved host resistance (e.g., parasitoid encapsulation) (Muldrew 1953) could drive decreases in parasitism. There were other factors, such as spring disappearance of larvae and mortality of needle miners, that were key mortality factors for casebearer prior to widespread parasitism (Ryan 1986). Relaxation of these and other mortality factors not compensated for by increased parasitism could lead to outbreaks. The effects of weather on insect dynamics detected here could also be acting indirectly (Barton and Ives 2014a, 2014b). Tree susceptibility can change with altered temperature and precipitation regimes (Zavala et al. 2008, Jamieson et al. 2012), and, in addition to herbivores, altered host plant chemistry can influence performance of natural enemies (Havill and Raffa 2000, Ode et al. 2004). Thus, recent casebearer outbreaks may not necessarily be due to a reduction in parasitoid efficacy, but rather facilitated by changes in several abiotic and/or biotic factors. Such changes underscore the challenges of making demographic predictions of population trends by non-native herbivores under changing thermal regimes.

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Data Availability

Data are available from the Purdue University Research Repository (PURR) at:

https://doi.org/10.4231/P800-NM47

Tables

Table 1 Response and predictor variables considered in linear mixed-effects models investigating the population ecology of larch casebearer and two imported parasitoids, *Agathis pumila* and *Chrysocharis laricinellae*, across 13 western larch sites in Oregon and Washington (1972-1995).

Variable	Description
Biotic	
O_t	Density of overwintering larch casebearers per 100 buds in year t
N_t	Density of larch casebearer adults per 100 buds in year t
P_t	Proportion of overwintering larvae parasitized by *A. pumila* in year t
s_{1t}	Proportion of larvae not parasitized by *Ch. laricinellae* in winter of year t
s_{2t}	Proportion of larvae not parasitized by *Ch. laricinellae* in spring of year t
Q_t	Combined parasitism by *Ch. laricinellae* in year t $(1- s_{1t} \times s_{2t})$
A_t	Density of *A. pumila* per 100 buds in year t $(=P_t \times O_t)$
C_t	Density of *Ch. laricinellae* in casebearers per 100 buds in year t $(= [1- s_{1t}] \times O_t)$
R_t^N	Growth rate of larch casebearer in year t; $\ln(N_{t+1}/N_t)^*$
R_t^A	Growth rate of *A. pumila* in year t; $\ln(A_{t+1}/A_t)^*$
R_t^C	Growth rate of *Ch. laricinellae* in casebearers in year t; $\ln(C_{t+1}/C_t)^*$
IDW_t	Inverse distance weighted average for R_t^N
IDA_t	Inverse distance weighted average for R_t^A
IDC_t	Inverse distance weighted average for R_t^C

*Casebearer and wasp densities had a small constant (0.001) added to them prior to growth rate calculations.

Table 2 Weather predictor variables calculated for each year from 1981-1995. Bioclimatic predictors were calculated using PRISM climate data (PRISM 2019) with the dismo package in R (Hijmans et al. 2017).

Variable	Description
el-bioclimatic	Each variable was positively correlated with the incidence of casebearer defoliation of **e**astern **l**arch in Minnesota (Ward and Aukema 2019a).
GDD_t	Degree-days, $(T_{max} + T_{min})/2 - 5$ °C, accumulated between 20 February and 30 November in year t
$OctMinTemp_t$	Minimum temperature (°C) in October of year t
$SepMinTemp_t$	Minimum temperature (°C) in September of year t
$MayPPT_t$	Total precipitation (mm) in May of year t
gen-bioclimatic[*]	**Gen**eric predictors potentially associated with performance of non-native insects (e.g., Lantschner et al. 2014).
MAT	Annual mean of daily mean temperatures (daily mean = $[T_{max} + T_{min}]/2$)
$MaxT$	Annual maximum temperature (°C)
$MinT$	Annual minimum temperature (°C)
I-therm	Mean monthly diurnal range (= [monthly maximum – monthly minimum[/[$MaxT$ – $MinT$])
TAP	Total annual precipitation (mm)
PPT-CV	Coefficient of variation for monthly precipitation totals

[*]Annual weather data used to develop gen-bioclimatic predictors spanned 1 January – 31 October in each year.

Table 3 Summary of linear mixed-effects models investigating the population ecology of larch casebearer and two imported parasitoids, *Agathis pumila* and *Chrysocharis laricinellae*, across 13 western larch sites in Oregon and Washington. Variables are described in Tables 1 and 2.

Model	Time	Response	Predictors*	Table locations† Reduced	Table locations† Full
1‡	1972-1980	R_t^O	O_t, O_{t-1}, IDO_t,	4a	S1a
2	1981-1995	R_t^O	O_t, O_{t-1}, P_t, Q_t, IDO_t,	4b	S1b
3	1981-1995	R_t^A	N_t, A_t, A_{t-1}, Q_t, IDA_t,	S2a	S2b
4	1981-1995	R_t^C	N_t, C_t, C_{t-1}, P_t, IDC_t,	S3a	S3b
5a	1981-1995	R_t^O	O_t, P_t, IDO_t, el-bioclimatic	5a	S4a
5b	1981-1995	R_t^O	O_t, P_t, IDO_t, gen-bioclimatic	‡	S4b
6	1981-1995	R_t^A	N_t, A_t, IDA_t, gen-bioclimatic	5b	S5
7	1981-1995	R_t^C	N_t, C_t, P_t, IDC_t, gen-bioclimatic	5c	S6

*Density predictors (e.g., N_t, A_t, C_t) were $\ln(x+0.001)$-transformed

†Locations of tables that report summary statistics from reduced or full models. Tables with "S" accompanying numbers are in Appendix S1.

‡No gen-bioclimatic predictors occurred in the reduced model (all $P > 0.05$), and so reduced versions of Models 2 and 5b were equivalent.

Table 4 Linear mixed-effects models predicting population growth rates of overwintering larch casebearer larvae across 13 western larch sites in Oregon and Washington before (1972 – 1980) and after (1981-1995) two imported parasitoids, *Agathis pumila* and *Chrysocharis laricinellae*, were widely established. Variables are described in Table 1.

Term	Estimate	SE	t	df	P
a. Larch casebearer growth rate (R_t^O, 1972 – 1980; Model 1)					
Intercept	1.46	0.24	6.02	92	<0.0001
O_t	-0.36	0.06	-5.87	92	<0.0001
IDO_t	0.48	0.11	4.43	92	<0.0001
b. Larch casebearer growth rate (R_t^O, 1981 – 1995; Model 2)					
Intercept	0.68	0.13	5.33	178	<0.0001
O_t	-0.18	0.04	-5.12	178	<0.0001
P_t	-1.26	0.23	-5.56	178	<0.0001
IDO_t	0.64	0.08	8.54	178	<0.0001

Table 5 Linear mixed-effects models predicting annual growth rates of larch casebearer adults and two imported parasitoids, *Agathis pumila* and *Chrysocharis laricinellae*, across 13 western larch sites in Oregon and Washington (1981-1995). Variables are described in Tables 1 and 2.

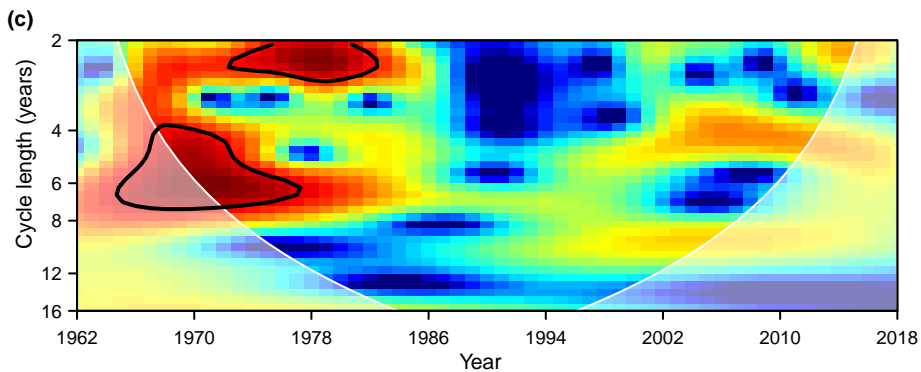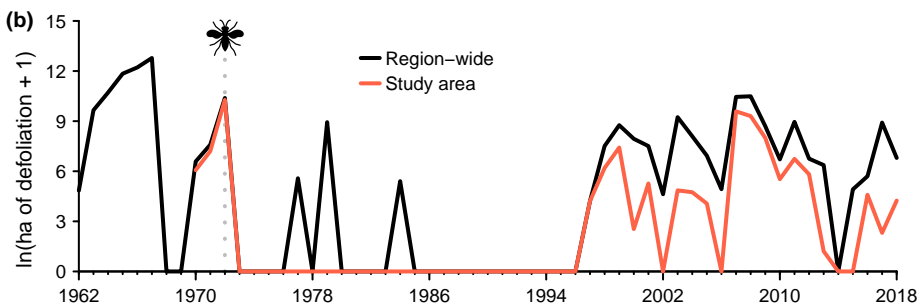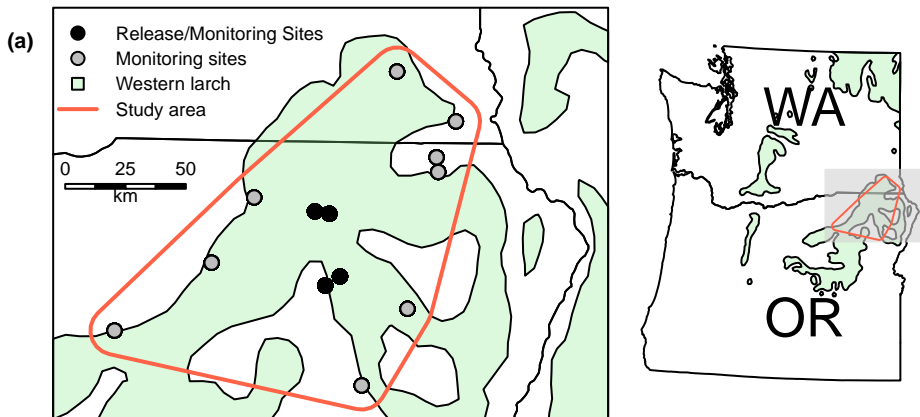| Term	Estimate	SE	t	df	P
a. Larch casebearer growth rate (R_t^O; Model 5a)*					
Intercept	1.14	0.18	6.38	177	<0.0001
O_t	-0.19	0.03	-5.53	177	<0.0001
P_t	-1.37	0.22	-6.18	177	<0.0001
IDO_t	0.54	0.08	6.87	177	<0.0001
$OctMinTemp_t$	0.07	0.02	3.55	177	0.0005
b. *Agathis pumila* growth rate (R_t^A; Model 6)					
Intercept	4.38	1.88	2.33	37	0.0256
N_t	0.47	0.06	8.09	126	<0.0001
A_t	-0.72	0.06	-12.81	160	<0.0001
IDA_t	0.27	0.08	3.48	169	0.0006
$MaxT$	-0.13	0.06	-2.32	37	0.0256
c. *Chrysocharis laricinellae* growth rate (R_t^C, Model 7)					
Intercept	4.52	4.47	1.01	48	0.32
N_t	0.40	0.13	3.03	66	0.0035
C_t	-1.27	0.09	-13.70	64	<0.0001
P_t	2.87	1.04	2.77	67	0.0073
IDC_t	0.01	0.09	0.15	67	0.88
$MaxT$	-0.32	0.13	-2.49	47	0.0164

*Model 5b is not presented because no gen-climatic predictors occurred in final models after backwards selection. Thus, the reduced versions of Model 2 (Table 4) and Model 5b (Appendix S1: Table S4b) were equivalent.
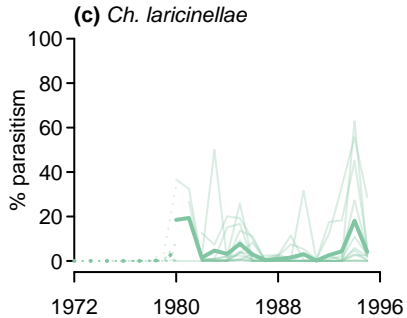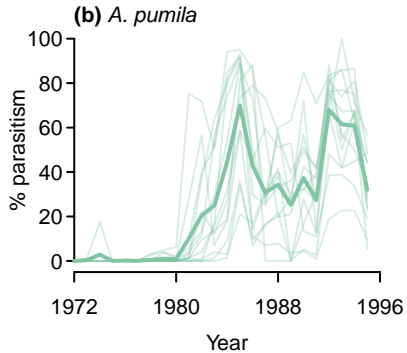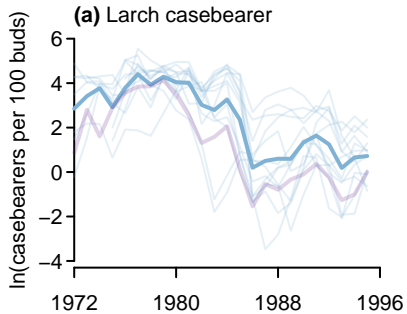
Figure legends

Fig. 1 (a) Map of 13 sites in Oregon (OR) and Washington (WA) where densities of larch casebearer and parasitism rates by *Agathis pumila* and *Chrysocharis laricinellae*, two imported hymenopteran parasitoids, were tracked from 1972-1995. Sites are similarly mapped and described in Ryan (1990). (b) Time series of defoliation of western larch by larch casebearer in Oregon and Washington (1962-2018). Dashed vertical line indicates onset of biological control releases and red line indicates defoliation within a convex hull polygon surrounding sites with a 10 km buffer (red polygon in maps of panel a). Data are from aerial detection surveys conducted by the USDA Forest service and state cooperators. Wasp graphic by Ben Davis from the Noun Project. (c) Wavelet analysis of defoliation data in panel b quantifying periodicity in population fluctuations. The colors of the contour indicate the power of the wavelet spectrum, with "red" indicating high power and increasingly "colder" colors indicating reduced power. The white shaded areas indicate the "cone of influence", in which time-series edge effects become influential (Torrence and Compo 1998). The black lines in the graph enclose areas where the power of the spectrum was found to be significant
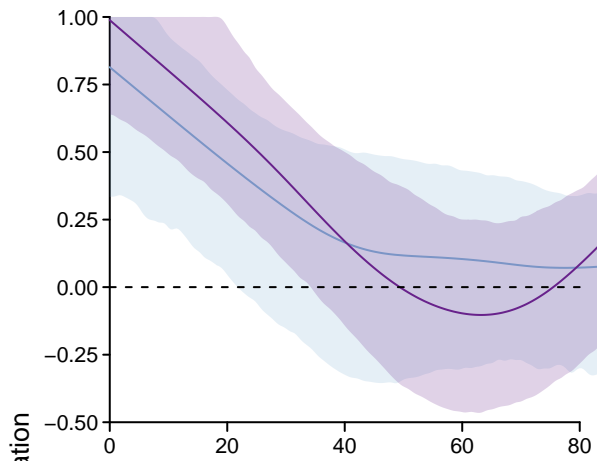
Fig. 2 Time series of the (a) number of larch casebearer larvae (blue line) and adults (purple line) per 100 buds and parasitism rates by (b) *Agathis pumila* and (c) *Chrysocharis laricinellae* (c) across 13 western larch sites in Oregon and Washington (1972-1995). Dark lines are cubic smoothing splines fit to mean values for all sites whereas lighter lines connect annual values at each site (site level lines not provided for casebearer adults). Corresponding dotted lines in panel (c) indicate spring parasitism rates prior to 1981, as winter parasitism rates, assumed to be approximately zero, were not available for several sites prior to 1981. A similar depiction of the data appear in Ryan (1997).

Fig. 3 Spatial synchrony quantified by spatial covariance functions of $\ln(x + 0.001)$-transformed densities (no. per 100 buds) of larch casebearer larvae (blue) and adults (purple) from (a) 1972-1980 and (b) 1981-1995 and of *A. pumila* (c; yellow), and *Ch. laricinellae* (d; yellow) from 1981-1995 across 13 western larch sites in Oregon and Washington. Panels (c) and (d) also contain synchrony in parasitism rates pictured in green. Solid lines indicate mean synchrony in density or parasitism and shaded areas are 95% confidence intervals. When confidence intervals include the dashed line, no statistically significant synchrony within insect densities was detected at the corresponding distance.
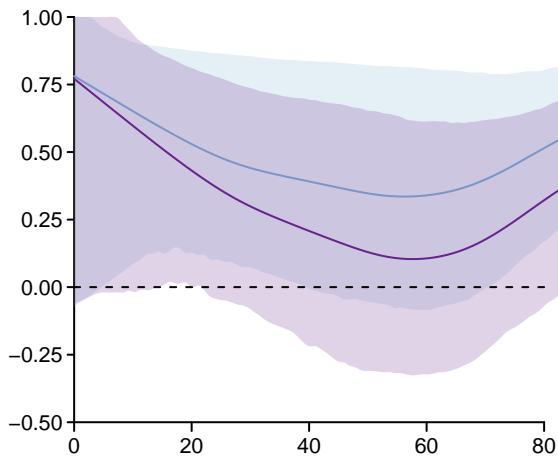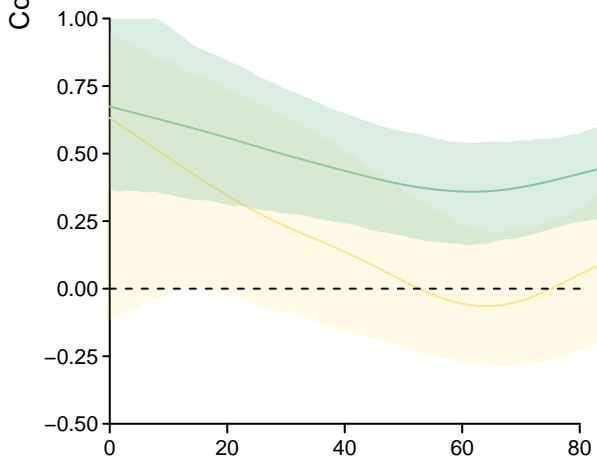
(a)

- ● Release/Monitoring Sites
- ● Monitoring sites
- ◻ Western larch
- — Study area

0 25 50
km

WA

OR

(b)

ln(ha of defoliation + 1)

— Region−wide
— Study area

(c)

Cycle length (years)

Year

(a) Larch casebearer

(b) *A. pumila*

(c) *Ch. laricinellae*

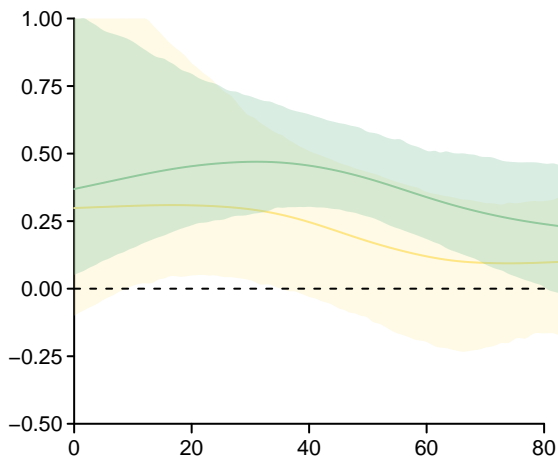**(a)** Larch casebearer (1972–1980)

(b) Larch casebearer (1981–1995)

(c) *A. pumila*

(d) *Ch. laricinellae*

Distance (km)

Correlation