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RESEARCH ARTICLE

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Host–enemy interactions provide limited biotic resistance for a range-expanding species via reduced apparent competition

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Abstract

Aim: As species' ranges shift poleward in response to anthropogenic change, they may lose antagonistic interactions if they move into less diverse communities, fail to interact with novel populations or species effectively, or if ancestral interacting populations or species fail to shift synchronously. We leveraged a poleward range expansion in a tractable insect host–enemy community to uncover mechanisms by which altered antagonistic interactions between native and recipient communities contributed to 'high niche opportunities' (limited biotic resistance) for a range-expanding insect.

Location: North America, Pacific Northwest.

Methods: We created quantitative insect host–enemy interaction networks by sampling oak gall wasps on 400 trees of a dominant oak species in the native and expanded range of a range-expanding gall wasp species. We compared host–enemy network structure between regions. We measured traits (phenology, morphology) of galls and interacting parasitoids, predicting greater trait divergence in the expanded range. We measured function relating to host control and explored if altered interactions and traits contributed to reduced function, or biotic resistance.

Results: Interaction networks had fewer species in the expanded range and lower complementarity of parasitoid assemblages among host species. While networks were more generalized, interactions with the range-expanding species were more specialized in the expanded range. Specialist enemies effectively tracked the range-expanding host, and there was reduced apparent competition with co-occurring hosts by shared generalist enemies. Phenological divergence of enemy assemblages interacting with the range-expanding and co-occurring hosts was greater in the expanded range, potentially contributing to weak apparent competition. Biotic resistance was lower in the expanded range, where fewer parasitoids emerged from galls of the range-expanding host.

Main Conclusions: Changes in interactions with generalist enemies created high niche opportunities, and limited biotic resistance, suggesting weak apparent competition may be a mechanism of enemy release for range-expanding insects embedded within generalist enemy networks.

KEYWORDS
gall wasps, interaction networks, parasitoids, phenology, *Quercus*, range-expansion, traits

1 | INTRODUCTION

Human activity is causing the reorganization of Earth's biota as species are transported around the globe and shift their ranges in response to climate and land-use change (Carey et al., 2012; Root et al., 2003; Ruiz & Carlton, 2003). When species move into new locations, interacting species may not move synchronously due to differences in dispersal or niche requirements (Gilman et al., 2010; Hellmann et al., 2012; Parmesan, 2006). As a result, coevolved or coadapted interactions are lost, and novel associations can be formed in new locations. This biogeographic flux disrupts complex networks of biotic interactions with cascading effects in ecosystems (Gilman et al., 2010; Hellmann et al., 2012; Pecl et al., 2017). Here, we examine how changes in biotic interactions in networks of interacting species contribute to the dynamics of species' range expansions, which is pressing given the extent and pace of anthropogenic change.

Net changes in direct and indirect biotic interactions between species' native and expanded ranges affect the population dynamics of species as they move into new regions. For example, if antagonistic interactions with predators or competitors are lost or reduced, range-expanding species experience 'high niche opportunities' (Shea & Chesson, 2002; that is, reduced competition leading to increased resources, or reduced predation) that may lead to demographic release or increased fitness or population growth (i.e. 'ecological release') (Gilman et al., 2010; Keane & Crawley, 2002; Shea & Chesson, 2002). If net changes in interactions provide greater population control of range-expanders, they experience 'biotic resistance' with lower fitness or population growth in the expanded range (Gilman et al., 2010; Mitchell et al., 2006; Shea & Chesson, 2002).

The above-described community ecology framework explains why some introduced species become invasive (Colautti et al., 2004; Prior et al., 2015; Shea & Chesson, 2002). It is recently applied to species undergoing shorter-distance range expansions, including in response to climate change (Gilman et al., 2010; Hellmann et al., 2012; Van Der Putten et al., 2010; Wallingford et al., 2020). It is predicted that differences in biotic interactions will be more significant and outcomes of those altered interactions more severe when species are moved over long distances (i.e. inter-continental introductions) into communities with which they share little or no coevolutionary history (Mitchell et al., 2006; Mueller & Hellmann, 2008). Yet, there are growing examples of short-distance expanders (i.e. intra-continental expanders) experiencing ecological release (Battey, 2019; Carey et al., 2012; Prior & Hellmann, 2013). Short-distance expanders may experience release not just from coevolved or coadapted species but also from coadapted populations (Engelkes et al., 2008; Menéndez et al., 2008; Thompson, 2005) and under poleward expansions, if they encounter low-diversity communities and weaker interactions, due to latitudinal diversity gradients (Cronin et al., 2015; Jones et al., 2022; Menéndez et al., 2008; Pecl et al., 2017; Prior & Hellmann, 2013). Short-distance expansions are also particularly tractable for testing hypotheses about the consequences of altered biotic interactions, as the similarity of ecosystems and species in networks allows for more direct comparisons of the biotic interactions affecting the focal species. We leverage a short-distance poleward expansion of a phytophagous insect in a tractable host–enemy community to uncover the community dynamics of short-distance expansions.

Parasitoid wasps are primary enemies of phytophagous insects and often interact in antagonistic networks (Kaartinen et al., 2010; Smith et al., 2008; Wirta et al., 2014). Species undergoing poleward range expansions may encounter less diverse communities in higher latitudes with weaker antagonistic interactions (Hillebrand, 2004; Schemske et al., 2009; Willig et al., 2003). If networks are also less specialized in poleward locations (Dyer et al., 2007), recipient communities may provide limited biotic resistance as specialized antagonistic networks with high trophic complementarity are predicted to have high 'function' or host control (Gagic et al., 2011; Montoya et al., 2003; Poisot et al., 2013). Alternatively, networks that are more generalized (with high connectance) may provide greater biotic resistance if they are more difficult to infiltrate (Romanuk et al., 2019, Smith-Ramesh et al., 2017). In addition to moving into less diverse networks, range-expanding insects may lose ancestral specialist enemies that fail to shift or lag behind range-expanding hosts ('enemy release'), or they may escape generalist enemies if generalists fail to follow, if fewer are in the recipient species pool, or if they fail to effectively switch from co-occurring hosts to the novel host ('release from apparent competition') (Cornell & Hawkins, 1993; Menéndez et al., 2008; Prior & Hellmann, 2013; Schönrogge et al., 1996; Schönrogge & Crawley, 2000). Previous studies suggest that range-expanding or introduced insects lose specialist enemies from their native range, and even if generalist enemies attack novel hosts, that apparent competition may be weak due to reduced effectiveness (Allen et al., 2021; Cornell & Hawkins, 1993; Gröbler & Lewis, 2008; Menéndez et al., 2008; Prior & Hellmann, 2013; Schönrogge et al., 1996; Schönrogge & Crawley, 2000).

Trait variation in one trophic level influences community assembly in interacting trophic levels (Bailey et al., 2009; Petchey et al., 2008). A lack of biotic resistance may result from recipient communities possessing divergent traits from range-expanding species that prevent effective host switching or sharing by enemies (Bailey et al., 2009, Minoarivelo & Hui, 2016). Selection favours the evolution of defensive traits of hosts that reduce the success of parasitoids. At the same time, selection favours parasitoid traits that help evade host defences (Bailey et al., 2009; Luz et al., 2021; Singer & Stireman, 2005). Traits include morphological features such as body size that can facilitate host defence or ovipositor size that can facilitate parasitoid attack (Luz et al., 2021; Singer & Stireman, 2005). Phenology is also essential to interactions between insect hosts and parasitoids, as successful development for parasitoids requires that they attack hosts during specific time windows (Godfray et al., 1994; Stone & Schönrogge, 2003). In this study, we explore mechanisms of altered interactions under a poleward expansion, including how traits of interacting species may contribute to high niche opportunities and ecological release (Figure 1).

Oak gall wasp-enemy communities are tractable multi-trophic communities that are excellent systems for uncovering direct and indirect trophic interactions and how interactions are altered under anthropogenic change (Csóka et al., 2017; Jones et al., 2022; Prior & Hellmann, 2010, 2013; Schönrogge et al., 1996). Oak gall wasps induce structures (galls) on plant tissues. That galls vary in traits, including size, shape and texture are considered defensive adaptations to evade attack from natural enemies (Hayward & Stone, 2005; Stone & Schönrogge, 2003). Host gall morphology and phenology influence enemy assemblages (Bailey et al., 2009; Hayward & Stone, 2005; Zhang et al., 2022). In North American western oak ecosystems, a community of oak gall wasps (Hymenoptera: Cynipidae: Cynipini) co-occur on a dominant oak, *Quercus garryana* (Douglas ex. Hook (Fagaceae)). A community of natural enemies interacts with this *Q. garryana* gall wasp community. One oak gall wasp species, *Neuroterus saltatorius* (Edwards), is expanding poleward, occurring at higher abundances in its expanded range and causing damage to *Q. garryana* (Duncan, 1997; Prior & Hellmann, 2013; Smith, 1995).

To reveal how direct and indirect interactions among co-occurring hosts and natural enemies are altered and if altered interactions contribute to limited biotic resistance under a short-distance poleward range expansion, we performed systematic surveys of oak gall wasps co-occurring on *Q. garryana* and their interacting natural enemies in the native and expanded range of *N. saltatorius*. We created quantitative oak gall wasp-enemy interaction networks, measured traits of interacting species and calculated parasitoid emergence rates of the range-expanding host. Our objectives were to uncover mechanisms of altered interactions and if altered interactions contributed

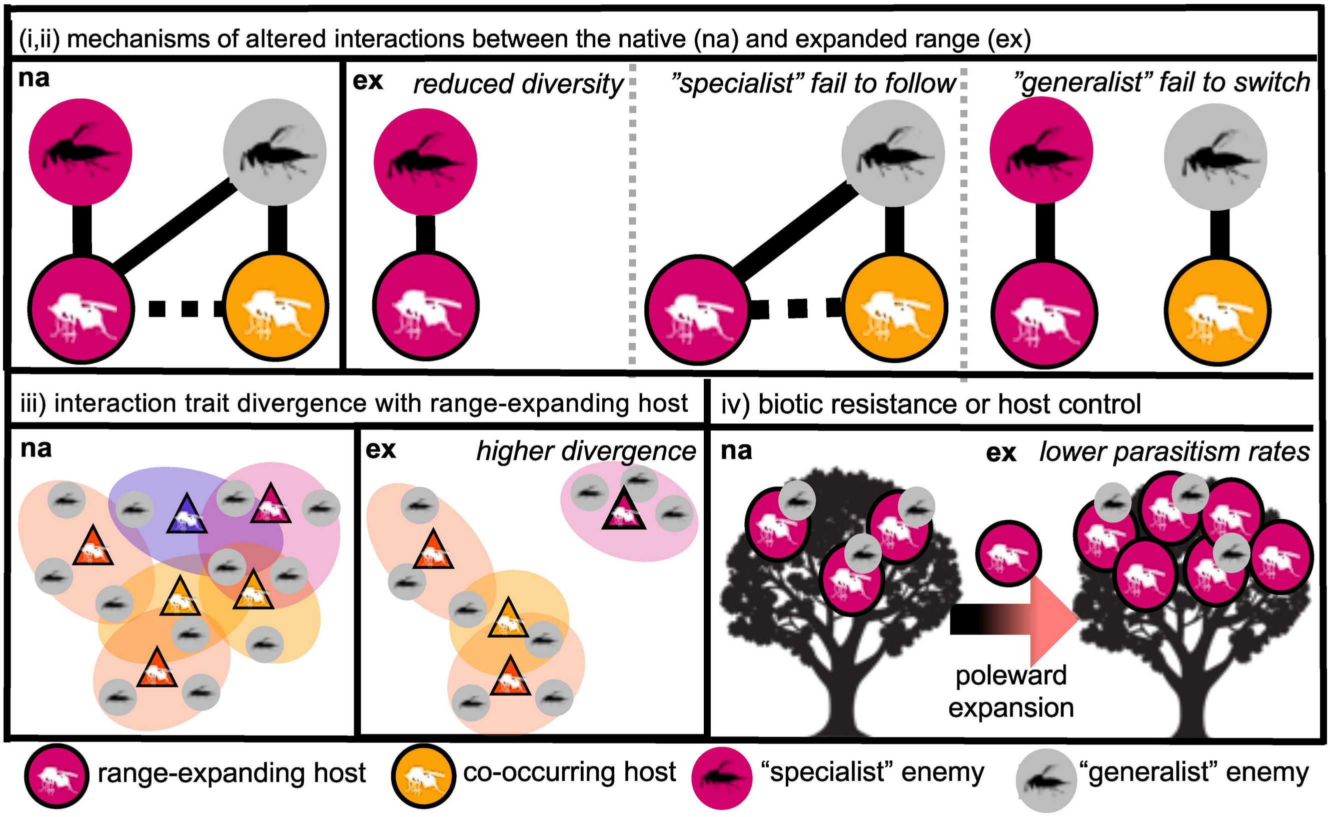

FIGURE 1 Conceptual figure outlining objectives and predictions. Objectives (*i-ii*) Loss of antagonistic interactions between the range-expanding host (*Neuroterus saltatorius*) and co-occurring hosts (other gall wasp species on *Quercus garyanna*) and 'specialist' and 'generalist' enemies (parasitoid wasps) are expected between the native (na) and expanded range (ex). Mechanisms leading to loss of interactions include: *N. saltatorius* moving into low diversity communities at higher latitudes, 'specialist' enemies failing to follow the range-expanding host, or 'generalist' enemies in the expanded range failing to interact with *N. saltatorius* effectively. Solid and dashed lines represent direct and indirect antagonistic interactions, respectively. Objective (*iii*) Greater trait (morphology, phenology) divergence between parasitoid assemblages attacking co-occurring hosts and *N. saltatorius* in the expanded range may be a mechanism of failed host switching by generalists. Circles represent parasitoid species mapped in their trait space (i.e., an ordination biplot), and triangles represent host species mapped in the centre of traits of interacting parasitoid species. Hosts further apart in trait space interact with parasitoid assemblages with more divergent traits. Objective (*iv*) Lost antagonistic interactions (measured as lower parasitoid emergence) may contribute to limited biotic resistance and ecological release (increased performance in the expanded range).

to limited biotic resistance in recipient communities (Figure 1). We predict that the range-expanding species may lose antagonistic interactions if: (i) networks in poleward recipient communities are less diverse with fewer interactions; (ii) enemies from the native range failed to track the range-expanding host; or if generalist enemies already present in the expanded range failed to effectively interact with the range-expanding host, which may be a result of (iii) greater trait divergence between the range-expanding host and co-occurring hosts. We also predict that (i-iii) may contribute to (iv) limited biotic resistance or host control of the range-expanding species in its expanded range. Uncovering how complex networks of biotic interactions are altered under anthropogenic change and how altered interactions contribute to biotic resistance is essential given the extent and pace of species' range changes under anthropogenic change (Tylianakis et al., 2007, 2008).

2 | METHODS

2.1 | Study system

Quercus garryana Douglas ex. Hook (Fagaceae) is a dominant oak in North American western oak ecosystems, ranging from northern California to Vancouver Island, British Columbia (BC), and is the only oak from Oregon northwards. *Quercus garryana*-ecosystems occur in the rain shadow of the coastal mountain ranges as savannahs, grasslands, deep soil woodlands or on rocky outcrops and become patchier at higher latitudes in northern Washington and at the edge of its northern range, which is on Vancouver Island, BC (Vellend et al., 2008).

Oak gall wasps (Hymenoptera: Cynipidae: Cynipini) are phytophagous insects that deposit their eggs in the plant tissue of Fagaceae (oaks), inducing gall formation. Galls house and provide nutritive tissue to larvae (Stone et al., 2001; Stone & Schönrogge, 2003). The majority of oak gall wasps have two generations, a gamic (sexual) and an agamic (asexual) generation, that form distinct galls (Hood et al., 2018). Gall structures vary and occur in various plant tissues (Hayward & Stone, 2005; Stone & Schönrogge, 2003). There are approximately 1000 oak gall wasp species, with the Nearctic having ~700 species (Russo, 2021; Ward, Bagley et al., 2022). Oak gall wasps support a rich community of natural enemies, predominantly parasitoid wasps in the superfamily Chalcidoidea. These wasps attack a narrow range of hosts (specialists) to multiple hosts (generalists) (Askew, 1980; Askew et al., 2014; Ward, Busbee et al., 2022). Parasitoid wasps that emerge out of galls directly attack gall wasps or inquilines (other organisms that live inside galls or gall tissue) or are hyperparasitoids of parasitoids (Ward, Busbee et al., 2022).

Neuroterus saltatorius (Edwards) induces galls on white oaks in western North America, including *Q. garryana* (Russo, 2021). The native range of *N. saltatorius* is restricted to mainland North America. In the early 1980s, it expanded onto Vancouver Island, BC (Duncan, 1997; Smith, 1995), and to the northernmost range of *Q. garryana* (Prior & Hellmann, 2010, 2013). *Neuroterus saltatorius*'s early-spring gamic generation is a clustered integral leaf gall, and its agamic generation occurs in the summer and is a detachable leaf gall (Smith, 1995). The detachable galls drop from the leaves in mid-late summer, remaining in the leaf litter for the winter, with adults emerging the following spring (Smith, 1995). *Neuroterus saltatorius* occurs at higher abundance on *Q. garryana* in its expanded range, especially noticeable in the agamic generation with a higher frequency of trees infested in the expanded range. Some trees are infested in the native range but at lower frequency (Jones et al., 2022; Prior & Hellmann, 2013). Particularly high abundances of the agamic generation cause foliar scorching with adverse effects on oaks and species that interact with oaks (Duncan, 1997; Prior & Hellmann, 2010, 2013; Smith, 1995).

2.2 | Oak gall wasp and parasitoid enemy surveys

In 2017, we chose four sites in *N. saltatorius*'s native range that were the largest oak patches closest to the expanded range and six sites in the expanded range (Jones et al., 2022; Prior & Hellmann, 2013) (Figure 2). Sites were oak grasslands or savannahs with *Q. garryana* as the dominant tree, ranging from 6 to 130 ha and separated by at least 10 km in a matrix of rural agriculture, residential areas and *Pseudotsuga menziesii* forests (Figure 2, Table S1).

At each study site, we performed surveys of oak gall wasps on *Q. garryana* during four separate sampling periods, coinciding with the two generations (gamic and agamic) of *N. saltatorius* (mid-May to late-July) (Figure 2; Table S1). We surveyed 10 trees during each period, for a total of 40 trees per site. Trees were chosen haphazardly, spread out throughout sites and were at least 10 m apart. Selected trees were larger than 2 m, and we needed to have observed a gall wasp species within 5 min of searching branches, using a 1.5 m ladder (up to ~3 m). On 10 branches, we searched 10 leaf clusters for leaf galls and 1 m of branches for stem galls. All oak gall wasp individuals were identified via gall morphology, contacting experts in some cases (Gallformers.org, 2021; Russo, 2021) (Table S2). We identified all gall morphotypes to species, except for *Disholcaspis mamillana* and *D. simulate* that we lumped together as they are only distinguishable by opening up the galls.

Mature galls were collected and stored in rearing containers, separated by gall morphotype, site and survey date. For 1 year, galls were kept in environmental chambers set to summer Pacific northwest conditions (25°C, 14:10). These conditions were chosen because optimal environmental rearing conditions for all species were unknown. Since parasitoids emerged out of all gall morphotypes, except for those collected in small numbers (<~20 galls), was evidence that conditions were suitable. Once a week, containers were checked for emergents, which were stored at −80°C.

We identified emergent wasps to family. Then for wasp families with known parasitoids, we identified individuals to the lowest taxonomic level using keys (Gibson et al., 1997) and experts' help (Prior & Hellmann, 2013). Inquiline wasps (i.e. cynipids that are not parasitoids but feed on gall or plant tissue) also emerged, but we did

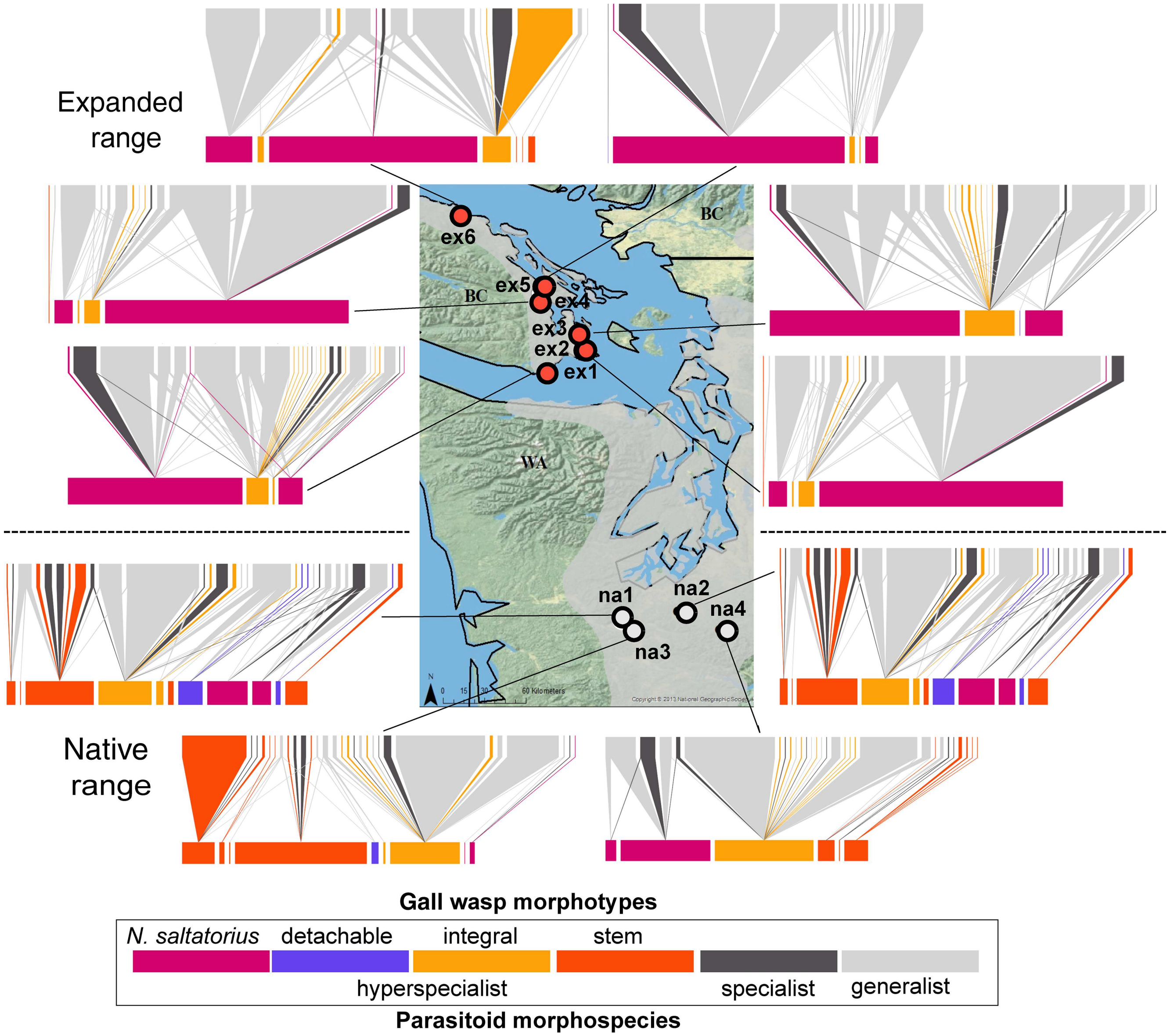

FIGURE 2 Range of *Quercus garryana* (shaded grey) in Washington State and Vancouver Island, BC (full range extends to California and further up the Island). Bipartite quantitative networks at study sites in the native range of *N. saltatorius* (light symbols) and expanded range (red/shaded symbols) galls. Shown are interactions (links) between gall wasp hosts (bottom bars) and emerged parasitoids (top bars). Blocks represent species, and their width represents the relative abundance of hosts and parasitoids that emerged from each host. Networks represent data that were combined over survey periods. Pink bottom bars represent *N. saltatorius* (each bar represents a generation), and pink links represent parasitoid morphospecies that only emerged (hyperspecialists) from *N. saltatorius*. Other coloured bottom bars represent host morphotypes in different gall type groups (leaf detachable, leaf integral and stem), and coloured links and top bars represent hyperspecialist parasitoid morphospecies that only emerged from a single gall species in that group. Dark grey and light links and top bars represent specialist (emerged from 1 to 3 host morphotypes) or generalist (>3 hosts) parasitoid morphospecies (Tables S2 and S3).

not include them in networks as they may not all act as enemies of hosts (see Supplementary Methods). While we included morphospecies in families with wasps that are known parasitoids, not all wasps may have direct interactions with gall wasp hosts, and they could be parasitoids of inquilines or hyperparasitoids. Given that many associations of parasitoids are undescribed, we were conservative. We included all morphospecies from families with known parasitoids, assuming that most caused deaths (direct or indirect) of gall wasp hosts. Over 99% of individuals reared were from taxonomic groups known to directly associate with gall wasps (see Appendix S1 for details) (Gibson et al., 1997; Ward, Busbee et al., 2022).

2.3 | Host–parasitoid interaction networks

We created gall wasp host and parasitoid quantitative interaction networks using R's 'bipartite' package (Dormann et al., 2022). The width of the bottom bars represents the relative abundances of host morphotypes (Figure 2, Figure S1). For multilocular galls (that contain multiple host individuals) (*N. washingtonensis*, *A. quercuscalifornicus*) (Table S2), we multiplied each gall by an estimated number of wasp larvae in galls. We estimated individuals by opening 25–50 galls of each species and counting larval chambers. We treated generations of *N. saltatorius* separately, given that they occur at different times and have different parasitoid assemblages, as with other oak gall wasps (Bailey et al., 2009). *Neuroterus saltatorius* was the only species we collected two known generations for, and both generations for the vast majority of species in our collection are unknown (Russo 2021). The width of the top bars and links represent the relative parasitoid emergence frequency of each parasitoid morphospecies from each host morphotype. We characterized gall wasps by gall type groups: detachable leaf galls (including the agamic generation of *N. saltatorius*), integral leaf galls (gamic generation of *N. saltatorius*) and stem/woody galls; and parasitoids by interactions: hyperspecialist (reared out of one host morphotype), specialist (1–3) and generalist (>3), following (Bailey et al., 2009).

We created bipartite quantitative interaction networks for each study site by pooling interactions among survey periods (Figure 2). We created site-level rather than survey-level networks, as survey-level networks were not independent. Several host species (including *N. saltatorius*) occurred throughout the four survey periods, and parasitoid interactions were linked over time. We created regional networks (pooling sites within regions) and a metanetwork (pooling all sites) to perform network and trait analyses (Figure S1).

2.3.1 | Comparing host–enemy interaction network structure between ranges

We calculated trophic-level and network-level metrics to describe differences in network structure between the native and expanded range. We focused on metrics that describe the 'diversity' of species and interactions (i.e. richness, evenness, diversity) and the 'distribution' of interactions (i.e. specialization or generalization) as these components relate to communities' potential to provide biotic resistance (as discussed above). For several metrics, we calculated weighted metrics by including interaction frequencies, as weighted metrics represent functional importance of species and their interactions and are more robust to sampling biases (Bersier et al., 2002; Vázquez et al., 2005; Dormann et al., 2022) (see Table S4 for list of all metrics calculated).

First, we estimated host morphotype and parasitoid morphospecies richness by calculating abundance-based *Chao 1* estimates using the 'vegan' package in R (Oksanen et al., 2022). We also estimated interaction richness using *Chao 1* (number of unique interactions between hosts and parasitoids) (Jordano, 2016) (see Appendix S3; Figures S4 and S5, Table S7). We calculated network size as the estimated number of hosts x parasitoids and included this as a factor in models (see below). We also calculated network interaction diversity (Shannon Entropy, H_2) and interaction evenness using weighted interaction diversity across networks (Tylianakis et al., 2007).

We calculated several metrics that represent network 'distribution' (i.e. specialization). First, we calculated the proportion of specialist parasitoid morphospecies (attacking <3 hosts in the metanetwork; (Bailey et al., 2009); Figure S1) out of all parasitoid morphospecies in each site network. As a weighted metric of network-level specialization, we calculated H_2', which represents the uniqueness of host–parasitoid interactions relative to each other (Blüthgen et al., 2006). Next, we calculated weighted connectance, a commonly measured metric that represents the frequency of realized interactions out of potential interactions or the linkage density (the number of interactions per species weighted by the frequency of interactions) divided by the number of species in the network (Bersier et al., 2002), with high connectance reflecting more generalized networks.

We performed linear (LM) or generalized linear models (GLM) to compare metrics between regions at the site level. For linear models, we log-transformed some metrics (listed in Table S4). For GLMs, we used Poisson and negative binomial distributions in some instances to correct for overdispersion (Table S4). Given that network size correlates with network metrics and properties (Pellissier et al., 2018), we ran all analyses with and without network size (as an interaction term) to uncover if network size contributes to differences in network structure or if mechanisms other than network size (i.e. changes in re-wiring of interactions) are influencing differences (Pellissier et al., 2018).

2.3.2 | Altered enemy interactions with the range-expanding host

We calculated *N. saltatorius* species-level metrics to uncover potential mechanisms of enemy loss, including the loss of *N. saltatorius* specialist parasitoids and weaker apparent competition by generalists (Figure 1). We estimated the richness of parasitoid morphospecies emerged from *N. saltatorius* by calculating *Chao 1* (see Appendix S3). To compare specialists interacting with *N. saltatorius*, we calculated the proportion of specialist parasitoids out of all parasitoids that emerged from *N. saltatorius* (see above). Also, as a weighted metric of species-level specialization, we calculated *d'* for *N. saltatorius*, which represents how specialized parasitoid interactions with *N. saltatorius* are given interaction frequencies of all parasitoid species in the network (Blüthgen et al., 2006).

To assess if parasitoids potentially fail to switch from alternative hosts in the expanded range effectively, we estimated the potential for apparent competition, *PAC*, from co-occurring hosts to *N. saltatorius* as Muller's index, d_{ij} (Müller et al., 1999). This index calculates the likelihood that parasitoid k attacking host i developed in host j for all shared parasitoid species between host i and j. The effect of host species j on i is as follows:

$$d_{ij} = \sum_k \left[\frac{\alpha_{ik}}{\sum_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right]$$

The d_{ij} value summarizes interactions between two hosts, with 0 representing no shared parasitoids and 1 high competition from host *j* to host *i*. The α_{ik} value represents the strength of the link between host *i* and parasitoid *k*, with the first quantity in the bracket representing the fraction of parasitoids of host *i* (out of all parasitoid species, *l*) belonging to species k, and the second quantity representing the fraction of parasitoids of species *k* that develops on host species *j* (out of all host species, *m*) (Muller et al. 1999). We treated *N. saltatorius* as host *i*, reflect the strength of *PAC* from co-occurring hosts to the novel host and calculated *PAC* as the sum of d_{ij} all gall wasp morphotypes interacting with *N. saltatorius* (for generations separately and pooled). We performed LMs and GLMS as described above (see Table S5).

2.3.3 | Divergence in traits and phenology of enemies interacting with hosts

We calculated peak parasitoid attack timing for each host morphotype at each site as a mean Julian date weighted by the number of parasitoids that emerged from that host morphotype collected on different sampling dates. Weighted mean parasitoid attack timing reflects when the host is vulnerable to parasitoids and the timing in which parasitoid morphospecies attack hosts. To compare parasitoid attack timing between *N. saltatorius* and other hosts, we calculated effect sizes (as absolute values) as the log-response ratio (*ln R*) between each host morphotype and each generation of *N. saltatorius*. High effect sizes reflect phenological divergence in parasitoid attack timing between *N. saltatorius* and other gall morphotypes. For each generation, we calculated the average effect sizes of *N. saltatorius* interactions with each gall morphotype at each site and calculated mean effect sizes of sites within regions ±95% confidence intervals (CI). When CIs do not overlap zero phenological divergence occurs between the host community and *N. saltatorius*. We ran LMs to compare effect sizes between regions for each *N. saltatorius* generation.

We measured morphological traits related to the ability of parasitoids to attack hosts and hosts to defend parasitoids. We measured 1–3 individuals per host morphotype per region for each parasitoid morphospecies. We measured body size from the tip of the thorax to the end of the abdomen, the wing's area, the external ovipositor's length, the thorax's width and the size of the tibia (all in mm) (Luz et al., 2021). Body size correlates with other traits, so we divided trait measurements by body size. Some parasitoids have internal ovipositors (Gibson et al., 1997) that we were unable to measure, and we performed the trait analysis (see below) without ovipositors and found no differences (see Appendix S1 for details). We measured gall morphotype traits important in defence, such as gall size, internal traits (e.g. woody, fleshy or hollow) and external traits (e.g. nectar-producing, woolly, textured) using our observations and other resources (see Appendix S1 for details) (Gallformers.Org, 2021; Russo, 2021).

We performed a Principal coordinates analysis (PCoA) on the full (metanetwork) parasitoid community and the entire host community using Gower's dissimilarity, which is useful for a mix of continuous and binary or categorical variables (Laliberte & Legendre, 2010). We calculated functional (or 'interaction') trait spaces by plotting host morphotypes onto parasitoid morphospecies trait space (Dehling et al., 2016, 2020). Specifically, for each study site, we calculated weighted interaction centroids as the weighted (by frequency of interaction) mean position of assemblages of parasitoid morphospecies that a host morphotype interacts with in parasitoid trait space for each host morphotype. We calculated the distance of each host morphotype in interaction trait space to each generation of the focal species for each site (Dehling et al., 2016, 2020). We calculated the mean morphological distance of each host morphotype with *N. saltatorius* (each generation separately) at each location and then the mean (±95% CI) of sites for each region. We compared morphological divergence between areas using a LM, with higher averages representing higher morphological divergence in parasitoid assemblages interacting with other hosts compared to the focal host. Also, to examine which parasitoid traits influence interactions with hosts and which host traits influence interactions with parasitoids, we plotted PCoA biplots reflecting parasitoid trait space, host trait space and interaction trait spaces, along with traits of gall morphotypes and parasitoid morphospecies (see Appendix S1 and Figures S2 and S3 for biplots). Analyses were performed using the vegan package in R (Oksanen et al., 2022).

2.3.4 | Relationship between mechanisms of altered interactions and biotic resistance

We calculated trophic complementarity (*TC*) as a proxy for network function, or the ability of interactions in the network to provide control of the lower trophic level (Peralta et al., 2014; Philpott et al., 2020; Poisot et al., 2013). Trophic complimentary defines the degree to which parasitoids are shared among hosts of each host morphotype relative to other host morphotypes based on parasitoid assemblages. We calculated *TC* as the inverse of weighted *NODF* (nestedness), $TC = \left(\frac{100 - NODF}{100}\right)$ (as in Poisot et al., 2013).

To assess the potential for biotic resistance against *N. saltatorius*, we estimated parasitism rates by calculating parasitoid emergence rates from agamic galls. In 2021, we returned to sites in this study (along with three additional sites) and collected 500 agamic *N. saltatorius* galls with no emergence holes over their development (100 galls over five sampling periods). Each gall was placed in an individual gel capsule and kept in environmental chambers. For 1 year, we counted the number of parasitoids that emerged in capsules. We combined this data with collections using the same approach in 2007 and 2008 (Prior & Hellmann 2013, see SI). We focused on the agamic generation for feasibility and because it has higher parasitism rates than the gamic generation (Smith 1995). We also focused on this generation to combine this dataset with previous collections that took the same approach (Prior & Hellmann 2013). We performed a linear mixed model comparing parasitoid emergence rates (log-transformed) between the native and expanded range, including year and site as random effects, using the 'lme4' package in R (Bates et al., 2015).

To examine how variation in network structure, function and traits are related, we performed a correlation analysis among select representative network metrics, *N. saltatorius*-specific metrics relating to mechanisms of enemy loss, and morphological and phenological trait divergence. Since *TC* is linked to function in antagonistic networks (Poisot et al., 2013), correlations between other metrics and *TC* reflect how structure relates to function. We standardized all factors by calculating a z-score and then performed a correlation analysis using 'corrplot' in R (Taiyun Wei et al., 2021), reporting which interactions were significant ($p<.05$).

Code for analyses and figures are in Appendix S4.

3 | RESULTS

3.1 | Comparing host–enemy network structure between ranges

We identified 63 parasitoid morphospecies and 14 host morphotypes (12 of which parasitoids emerged from). Parasitoids belong to 11 families in Superfamilies Chalcidoidea, Ichneumonoidea and Platygastroidea (Table S3). Host–parasitoid networks were 52% larger in size in the native range than in the expanded range (*Chao 1*: $p<<0.001$; Figure 2); see full statistical results in Table S4, with 39% more host morphotypes (*Chao 1*: $p=.035$; Figure 3a) and 23% more parasitoid morphospecies ($p=.025$; Figure 3b) (observed richness for host morphotypes and parasitoid morphospecies showed similar results, see Appendix S3). However, there was no difference in the number of interactions (*Chao 1*: $p=.956$), in network Shannon's diversity ($p=.781$), or interaction evenness ($p=.186$) between regions.

Networks had a 26% higher proportion of specialist parasitoids attacking hosts in the native range (including network size as a covariate ($p=.040$; Figure 3d; Table S4)). However, there was no difference in network specialization H_2' between regions ($p=.169$). Weighted connectance was 26% higher in the expanded range ($p<.001$; Figure 3c), with more shared partners for both host morphotypes ($p=.001$) and parasitoid morphospecies ($p=.007$) (see Table S4).

3.2 | Altered enemy interactions with range-expanding host

Neuroterus saltatorius had 26% higher parasitoid specialization *d'* in the expanded range compared to the native range ($p=.007$; Figure 3e), along with higher *N. saltatorius* parasitoid richness (*Chao 1*: $p=.002$, S3). The potential for apparent competition (*PAC*) was 58% lower in the expanded range for hosts competing with *N. saltatorius* through shared parasitoids ($p=.007$, Figure 3f).

3.3 | Divergence in traits and phenology of enemies interacting with hosts

Mean effect size of parasitoid attack timing (phenological divergence) was higher in the expanded range compared to the native range

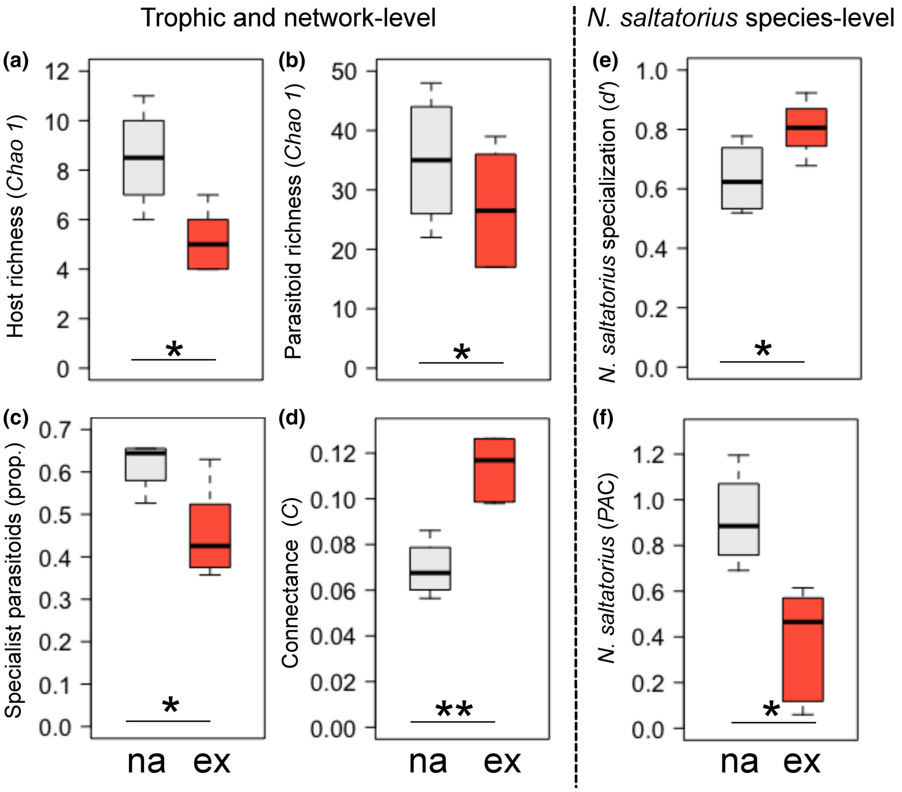

FIGURE 3 Host–parasitoid (a-d) trophic and network-level metrics and (e, f) species (*Neuroterus saltatorius*)-level metrics. (a) Estimated (*Chao 1*) number of host morphotypes and (b) parasitoid morphospecies, (c) proportion of specialist (1–3 hosts) parasitoid morphospecies, (d) weighted connectance, (e) *N. saltatorius* specialization *d'*, (f) potential for apparent competition *PAC* with *N. saltatorius* in the native (na) ($n=4$, grey boxes) and expanded (ex) range ($n=6$, orange). Box plots show median + 5th, 10th and 25th percentiles. Statistics are shown in Tables S4 and S5 in Appendix S2. *$p<.05$, **$p<.001$, ***$p<.001$.

for the spring gamic generation of *N. saltatorius* by 86% ($p = .029$; Figure 4a; Table S5). There was no difference in the mean effect size of parasitoid attack timing between other hosts and the agamic generation of *N. saltatorius* between regions ($p = .654$; Figure 4b). Both generations of *N. saltatorius* were, on average, further from other hosts in interaction trait space (morphological divergence) in the native range compared to the expanded range (gamic: $p < .001$; agamic: $p = .0003$; Figure 4c,d). Hosts are attacked by parasitoids with different body sizes, with more overlap in small and medium parasitoids attacking shared hosts (Figure S2). Parasitoids attack hosts of different gall sizes, with different internal gall tissue (woody, hollow or fleshy). External gall traits do not seem to strongly influence parasitoid assemblages (Figure S3).

3.4 | Relationship between mechanisms of altered interactions and biotic resistance

Trophic complementarity (*TC*) was 21% higher in the native range ($p < .001$), including when accounting for network size, showing less overlap in parasitoid assemblages among host morphotypes (Figure 5a). Parasitoid emergence rates from *N. saltatorius* agamic galls were 50% higher in the native range ($p << .005$) (Figure 5b).

Trophic complementarity (*TC*) had a significant negative correlation with connectance ($R = .95$, $p < .001$; Figure 6; Table S6). There was no relationship between specialization of *N. saltatorius d'* and *TC* ($R = .38$, $p = .279$). There was a positive trend between the potential for apparent competition *PAC* and *TC* ($R = .59$, $p = .07$). Morphological divergence was negatively correlated with *TC*, showing the opposite of what we predicted, that trait matching between hosts and parasitoids is related to decreased function ($R = .92$, $p < .001$). There was a negative non-significant relationship between phenological divergence and *TC* ($R = .53$, $p = .16$), influenced by a greater divergence of the gamic population with co-occurring hosts in the expanded range.

4 | DISCUSSION

Neuroterus saltatorius moved into recipient oak gall wasp-parasitoid communities that were less diverse, with fewer host morphotypes and parasitoid morphospecies. Networks in the expanded range were also more generalized, with fewer specialist parasitoids and co-occurring hosts having less complementarity or turnover in parasitoid assemblages. Diverse, specialized host–parasitoid networks with higher complementarity are predicted to have higher function or host control (Cardinale et al., 2006; Poisot et al., 2013). Despite whole networks being more generalized in the expanded range, interactions between co-occurring hosts and *N. saltatorius* were more specialized. Greater specialization of parasitoid assemblages on *N. saltatorius* may result from more specialist parasitoids or lower potential for apparent competition. That is, putative generalist parasitoids that attack multiple hosts may be more specialized (i.e. have unequal attack rates) on *N. saltatorius* and co-occurring hosts in the expanded range. Our results suggest that differences in the network structure of poleward recipient communities and altered interactions with the novel host by putative generalist parasitoids may contribute to limited biotic resistance (Figure 1). These findings support that oak gall wasp-parasitoid communities are composed mainly of putative generalist parasitoids with broad host ranges that specialize (i.e. have high attack rates) on hosts with different morphological or spatio-temporal niches (Askew et al., 2014; Bailey et al., 2009; Godfray, 1994). The morphological divergence of parasitoid assemblages attacking co-occurring hosts and the range-expanding host was not greater in the expanded range, reflecting that generalist parasitoids with similar traits attacked *N. saltatorius* and co-occurring hosts. Phenological divergence was greater in the expanded range, suggesting that altered timing of interactions could contribute to weaker apparent competition and low biotic resistance in the expanded range.

4.1 | Comparing host–enemy network structure between ranges

Poleward range-expanding species may experience weaker biotic interactions when they move into low-diversity communities at the poles (Jones et al., 2022; Menéndez et al., 2008) except see (Morris et al., 2014). We found fewer host and parasitoid species in the poles and expanded range. The most significant decline in diversity resulted from a loss of detachable leaf galls (*N. saltatorius* is a detachable gall) with high diversity of this group further south in the range (Jones et al., 2022). Sites are smaller and patchier at the edge of the ecosystem's range, and limited recruitment after the last glacial maximum could be one mechanism by which diversity decreases (Jones et al., 2022; Marsico et al., 2009). Despite lower diversity in both trophic levels towards the poles and the expanded range, there was a similar number of interactions. Networks were more connected with more overlap in parasitoid assemblages attacking co-occurring hosts. Higher network specialization of parasitoid assemblages in the native range could be driven by higher host diversity, with parasitoids specializing on hosts with differences in morphology, spatio-temporal niches, host immunity or evolutionary divergence (Bailey et al., 2009). While the expanded range is on an island, *Q. garryana*-ecosystems become naturally patchy at higher latitudes and on the mainland, with unsuitable habitats acting as a barrier between oak patches. Latitudinal patterns in diversity in *Q. garryana*-oak gall wasp and parasitoid communities follow similar trends on the mainland and when extended to the Island (Chen, 2022; Jones et al., 2022).

4.2 | Enemy interactions with the range-expanding host

In addition to *N. saltatorius* moving into less diverse and more generalized recipient communities, range-expanding species often

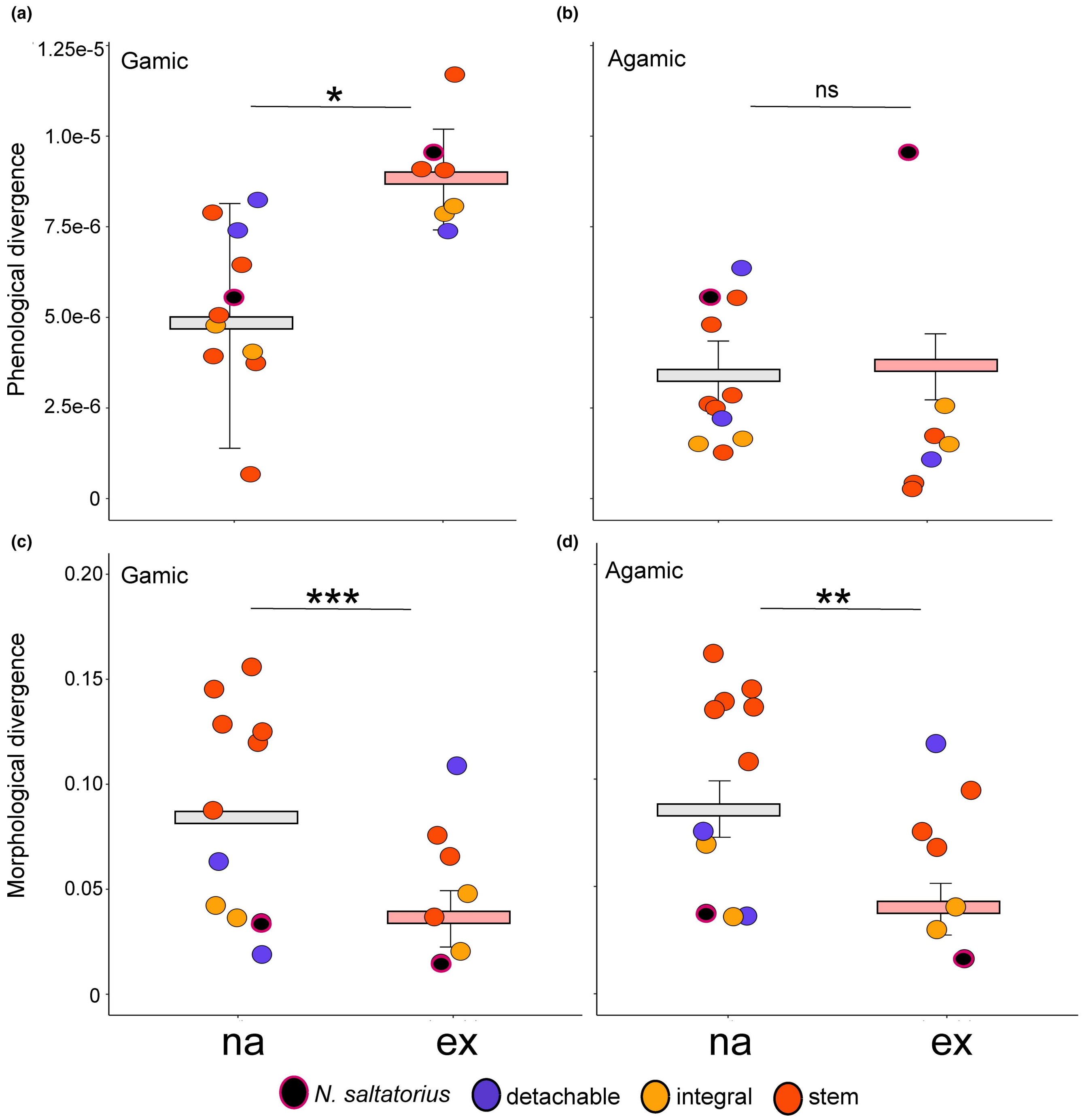

FIGURE 4 Host and parasitoid phenology (a, b) and morphology (b, c). (a, b) Effect sizes *ln*(*R*) of peak parasitoid attack timing for each host morphotype relative to (a) *Neuroterus saltatorius* (gamic) and (b) *N. saltatorius* (agamic) at each study site in the native (na) and expanded (ex) range. Mean (±95% CI) of average attack times of sites in the native range (light bars) and expanded range (red/shaded bars). (c, d) Differences between centroids of each host species to focal species (a) *N. saltatorius* (gamic) and (b) *N. saltatorius* (agamic) of interacting parasitoids in parasitoid morphological trait space at each site. Mean (±95% CI) of average differences of sites in the native range and expanded range are shown. Each circle represents the difference between *N. saltatorius* and another gall wasp morphotype, and colours represent different gall type groups (see Figure 2). Black circles outlined in pink represent differences between generations of *N. saltatorius*.

lose interactions when enemies (including specialist parasitoids) from the native range fail to shift (Menéndez et al., 2008; Nicholls et al., 2010). Opposite to this prediction, we found more putative specialist parasitoid species attacking *N. saltatorius* in the expanded range. However, this could result from higher collections of *N. saltatorius*, where it is outbreaking. <*Amphidicous shickae*> (Pteromalidae) is the most abundant specialist of *N. saltatorius* that was initially described from *N. saltatorius* and has not been recorded in any other samples of oak gall wasps (Chen, 2022; Duncan, 1997; Prior & Hellmann, 2013; Smith JL, 1995), including

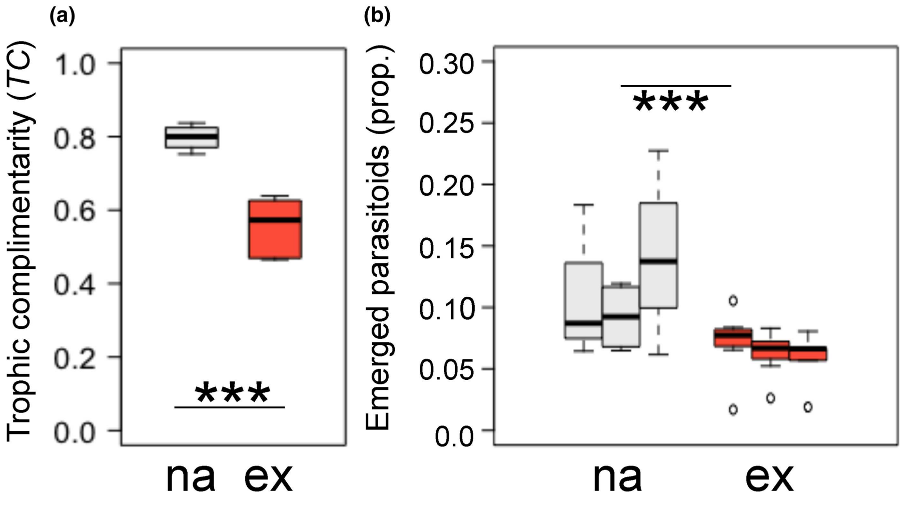

FIGURE 5 Network function and biotic resistance. (a) Trophic complementarity *TC* of networks at sites in the native (na) (grey boxes) and expanded (ex) (orange) range. (b) Proportion of emerged parasitoids from the agamic generation of *Neuroterus saltatorius* galls collected in 2007, 2008, 2021 (three bars) Box plots depict the median + 5th, 10th and 25th percentiles. Statistics are shown in Table S5 *$p < .05$, **$p < .001$, ***$p < .001$.

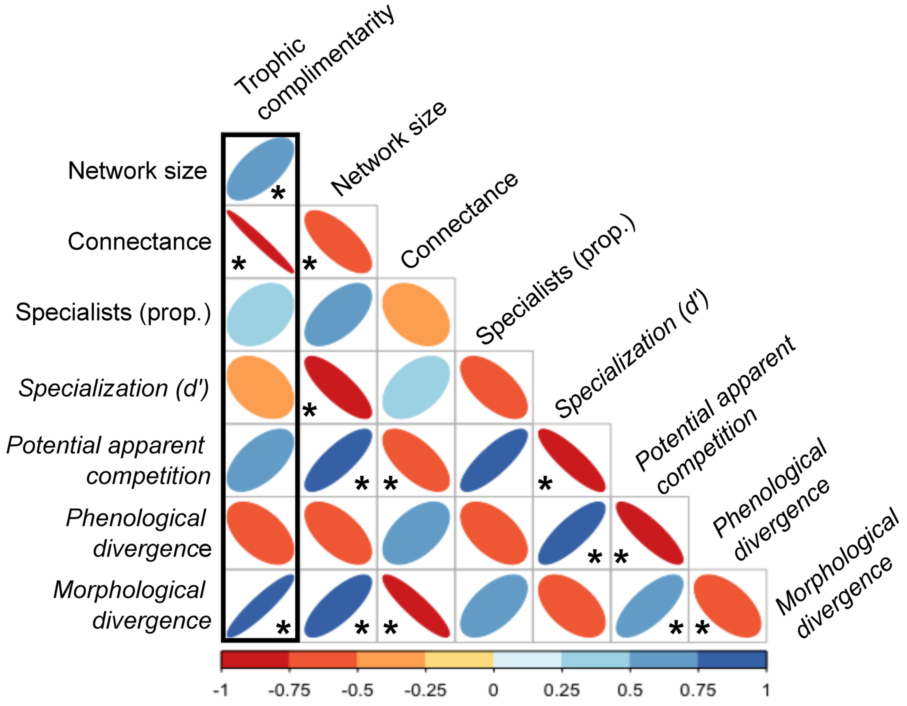

FIGURE 6 Relationships among network structure, interactions with *Neuroterus saltatorius*, trait divergence and function. Shown are correlations among standardized factors. Blue ellipses show positive relationships, and red negative relationships, with the width and shade of ellipses reflecting the strength of relationships (*$p < .05$) (Table S6).

in this study. This result suggests that *A. schickae* followed *N. saltatorius* when it expanded its range to BC. In a different study, *A. schickae* emergence rates were similar between regions (Prior & Hellmann, 2013). Here, we found higher emergence rates in the expanded range, suggesting this species is equally effective at attacking *N. saltatorius* in both regions (Torchin et al., 2003). Therefore, losing specialist parasitoids from the native range might not be a mechanism leading to weak biotic interactions in the expanded range.

Even though whole networks were more generalized in the expanded range, interactions with *N. saltatorius* were more specialized. Greater specialized interactions, *d'* with *N. saltatorius* may be partially a result of higher *N. saltatorius* attack rates by specialist parasitoids. However, generalist parasitoids are also more specialized because they have a greater asymmetrical frequency of attack between *N. saltatorius* and other hosts in the expanded range. To this end, we found lower *PAC* between co-occurring hosts and *N. saltatorius* in the expanded range, not due to fewer shared generalist parasitoid species but rather greater niche separation (unequal frequency of attack) between host species that shared parasitoids. This suggests that while generalist parasitoids can switch to attack *N. saltatorius*, they may not do so effectively. Lower attack rates by generalist parasitoids could result from ineffective host switching or sharing between other hosts and *N. saltatorius* when interactions are novel. Several mechanisms might lead to ineffective attack of novel hosts by locally adapted parasitoids, such as behavioural failure, physiological incompatibilities or altered or novel parasitoid–parasitoid interactions (Van Nouhuys

& Tay, 2001; Vos & Vet, 2004). Other study of range-expanding insects found lower attack rates by generalist parasitoids where species have expanded their range (Menéndez et al., 2008; Schönrogge & Crawley, 2000).

One of the most abundant generalist parasitoids attacking *N. saltatorius*, <*Aprostoceus pattersonae*> (Eulophidae), had lower attack rates on *N. saltatorius* in the expanded range (Prior & Hellmann, 2013). We do not know if generalist parasitoids attacking *N. saltatorius* in the expanded range are native range populations that moved with *N. saltatorius* or expanded range populations from other hosts (as some generalists were found in both regions). This information is critical to interpreting if lower attack rates by generalists result from ineffective switching by locally adapted populations or populations from the native range having lower efficacy in novel environments. These mechanisms of lower attack rates by putative generalists have occurred for introduced or range-expanding species (Menéndez et al., 2008; Torchin et al., 2003). Uncovering pathways of parasitoid assembly on *N. saltatorius* (as in Nicholls et al., 2010) would be useful for future studies to uncover mechanisms of reduced generalist attack.

Our findings suggest that niche specialization by generalist parasitoids rather than loss of *N. saltatorius* specialists might be important in determining variation in biotic resistance under range expansions. This finding supports that niche specialization by generalist parasitoids with broad host ranges is common in oak gall wasp-parasitoid communities, with richness in parasitoid communities maintained by partitioning generalist parasitoids among different gall phenotypes (Askew, 1980; Bailey et al., 2009; Hayward & Stone, 2005). However, molecular studies of parasitoid wasp communities and their interactions reveal more putative specialists originally described as generalists (Hrcek et al., 2011; Kaartinen et al., 2010; Sheikh et al., 2022; Wirta et al., 2014; Zhang et al., 2022). Identifying parasitoids via morphological features is challenging, and rearing out parasitoids from hosts may lead to incomplete information about associations. Future studies will use molecular approaches to resolve interactions more accurately. Additionally, when creating networks, we likely miss interactions due to the window in which we made observations. We chose to sample the gall community when *N. saltatorius* was developing on trees, but we could not capture associations for parasitoids emerging during other times in the season.

4.3 | Divergence in traits and phenology of enemies interacting with hosts

One mechanism of failed host sharing or switching may result from parasitoids in recipient communities lacking morphological adaptations to attack the novel host. We predicted that morphological trait divergence of parasitoid assemblages attacking other hosts and *N. saltatorius* might be higher in the expanded range if trait mismatching influences weak biotic resistance. However, we found that morphological divergence was lower in the expanded range, with traits of assemblages of parasitoids attacking co-occurring hosts and *N. saltatorius* being similar. This result is unsurprising as networks were more generalized in the expanded range. The native range has more stem gall species that are large with woody tissue. Parasitoids attacking these species have different traits, and their assemblages have little overlap with *N. saltatorius*. Oak gall morphotypes that shared parasitoids with *N. saltatorius* included fleshy integral leaf galls, *N. washingtonensis* and *A. opertus*, which are present in both regions and small leaf detachable species, such as *A. kingi*, that are not (Jones et al., 2022). Here, we found that small generalist parasitoids in the families Pteromalidae and Eulophidae were common in these morphotypes.

Phenological divergence of assemblages of parasitoids attacking hosts was higher in the expanded range for the earlier agamic generation. Greater phenological divergence of parasitoid attack timing was due to the gamic generation of *N. saltatorius* being more apparent to parasitoids earlier than co-occurring species in the expanded range but not in the native range. Parasitoid attack timing is important for successful parasitism (Godfray et al., 1994; Van Nouhuys & Tay, 2001), and greater divergence between co-occurring hosts that share parasitoids could be a mechanism of low *PAC* in the expanded range.

4.4 | Relationship between mechanisms of altered interactions and biotic resistance

Lower trophic complementarity of parasitoid assemblages on hosts decreases host function (Cardinale et al., 2006; Poisot et al., 2013). While low trophic complementarity (redundancy in parasitoid assemblages among hosts) is predicted to promote network stability or low variation in function, it is predicted to result in lower overall function or host control (Gagic et al., 2011; Montoya et al., 2003; Poisot et al., 2013). Previous studies of antagonistic networks have found higher trophic complementarity leads to greater host control in networks (Gagic et al., 2011; Montoya et al., 2003; Poisot et al., 2013), except see (Philpott et al., 2020). We found lower *TC* in the expanded range and lower emergence rates of parasitoids from *N. saltatorius* galls collected over 3 years, suggesting the parasitoids are less effective at host control (Prior & Hellmann 2013). Several metrics were related to *TC*, suggesting that altered interactions driven by *N. saltatorius* moving into less diverse and specialized recipient communities at the poles and less effective generalists mediated by altered phenology may be mechanisms leading to decreased biotic resistance (Figure 1).

4.4.1 | Considerations and conclusions

Our snapshot natural experiment approach prevents us from comparing post to pre-expansion networks. As a result, we do not know if *N.saltatorius* moved into less diverse, generalized networks or is creating less diverse, generalized networks. However, records of oak gall wasps on *Q.garryana* before the introduction of *N.saltatorius* do not include many host species recorded in the native range (Evans, 1985; Smith, 1995), and oak gall wasp diversity decreases from southern to northern latitudes on *Q.garryana* (Jones et al., 2022), strongly suggesting *N.saltatorius* moved into a less diverse gall wasp community.

As species expand their range, they move into structurally different networks in recipient communities and may lose interactions with coadapated or coevolved species or populations. While the number of interactions was resilient to network diversity changes, the distribution of interactions was not. Networks shifted from more specialized to generalized interactions between the lower latitude native range and higher latitude expanded range, which may result from lower species diversity at the poles. Moving into less diverse, generalized networks might be typical for range-expanding species infiltrating recipient poleward communities. Additionally, interactions with range-expanding species may be lost, and we found that less effective interactions with putative generalist parasitoids might contribute to limited biotic resistance. Thus, variation in niche specialization by putative generalists, not interactions with specialists, might be important in creating high niche opportunities for range-expanding insects embedded within generalist enemy networks. This work provides novel insights into how population-level differences might create open niches in short-distance-range expansions. Even when species move into similar nearby habitats with similar species compositions, subtle differences in interaction networks may still have important consequences for population dynamics, potentially contributing to outbreaks and invasions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are available on Dryad https://doi.org/10.5061/dryad.sqv9s4n8m.

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BIOSKETCH

Kirsten M. Prior is a community ecologist who studies how biodiversity and biotic interactions are influenced by anthropogenic change and how altered diversity and interactions influence community and ecosystem processes. Kirsten works on antagonistic and mutualistic interactions in plant and insect communities. Kirsten is an Associate Professor at Binghamton University with a PhD from the University of Notre Dame and was a postdoctoral fellow/associate the University of Toronto and at the University of Florida.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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