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RESEARCH ARTICLE

Latitudinal gradient in species diversity provides high niche opportunities for a range-expanding phytophagous insect

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Abstract

1. When species undergo poleward range expansions in response to anthropogenic change, they likely encounter less diverse communities in new locations. If low diversity communities provide weak biotic interactions, such as reduced competition or predation, range-expanding species may experience high niche opportunities.
2. Here, we investigated if oak gall wasp communities follow a latitudinal diversity gradient (LDG) and if lower diversity communities provide weaker interactions at the poles for a range-expanding community member, *Neuroterus saltatorius*.
3. We performed systematic surveys of gall wasps on a dominant oak, *Quercus garryana*, throughout most of its range, from northern California to Vancouver Island, British Columbia. On 540 trees at 18 sites, we identified 23 oak gall wasp morphotypes in three guilds (leaf detachable, leaf integral, and stem galls). We performed regressions between oak gall wasp diversity, latitude, and other abiotic (e.g. temperature) and habitat (e.g. oak patch size) factors to reveal if gall wasp communities followed an LDG. To uncover patterns in local interactions, we first performed partial correlations of gall wasp morphotype occurrences on trees within regions). We then performed regressions between abundances of co-occurring gall wasps on trees to reveal if interactions are putatively competitive or antagonistic.
4. *Q. garryana*-gall wasp communities followed an LDG, with lower diversity at higher latitudes, particularly with a loss of detachable leaf gall morphotypes. Detachable leaf gall wasps, including the range-expanding species, co-occurred most on trees, with weak co-occurrences on trees in the northern expanded region. Abundances of *N. saltatorius* and detachable and integral leaf galls co-occurring on trees were negatively related, suggesting antagonistic interactions. Overall, we found that LDGs create communities with weaker associations at the poles that might facilitate ecological release in a range-expanding community member.
5. Given the ubiquity of LDGs in nature, poleward range-expanding species are likely moving into low diversity communities. Yet, understanding if latitudinal diversity pattern provides weak biotic interactions for range-expanding species is not well explored. Our large-scale study documenting diversity in a related community of phytophagous insects that co-occur on a host plant reveals that

LDGs create high niche opportunities for a range-expanding community member. Biogeographical patterns in diversity and species interactions are likely important mechanisms contributing to altered biotic interactions under range-expansions.

KEYWORDS
biotic interactions, Cynipidae, ecological release, latitudinal diversity gradient, niche opportunity, range expansion, species diversity

1 | INTRODUCTION

Anthropogenic change leads to species range shifts in response to human-mediated dispersal, including to higher latitudes and elevations (Parmesan & Yohe, 2003). Species experience range shifts at different rates due to variation in thermal tolerances and dispersal capabilities (Hellmann et al., 2012; Parmesan & Yohe, 2003). As a result, range-expanding populations may lose interactions and form novel interactions in new communities (Gilman et al., 2010; Hellmann et al., 2012). Depending on the net effects of lost or gained antagonistic and facilitative interactions, range-expanding species may experience increased resources due to reduced competition or reduced predation/parasitism, 'high niche opportunities' (sensu Shea & Chesson, 2002) that results in higher performance in new locations, 'ecological release' (Gilman et al., 2010; Shea & Chesson, 2002).

One of the most ubiquitous patterns in nature is that species diversity declines towards the poles or higher elevations (latitudinal diversity gradient, LDG; Fitt & Lancaster, 2017; Gaston, 2000; Hillebrand, 2004; Willig et al., 2003; Zvereva & Kozlov, 2021). This pattern has been observed across many taxa, including phytophagous insects (Cuevas-Reyes et al., 2003; Galiana et al., 2019; Kerr et al., 1998; Willig et al., 2003). LDGs are linked with latitudinal gradients in biotic interactions, with stronger interactions among competitors or with predators resulting from and contributing to higher diversity towards the tropics (Pennings et al., 2009; Schemske et al., 2009; Zvereva & Kozlov, 2021; except see Moles et al., 2011). Low-diversity communities are predicted to have high niche opportunities if there are weak interactions among competitors or with predators (Gilman et al., 2010; Schemske et al., 2009; Shea & Chesson, 2002; Willig et al., 2003). As a result, poleward communities may provide weak biotic resistance, making high latitude communities susceptible to colonization by range-expanding species and invaders (Gilman et al., 2010; Wallingford et al., 2020). This study aims to uncover if patterns in LDGs create weak biotic resistance for poleward range expansions and contribute to ecological release. Few studies have investigated range expansions in the context of LDGs (except see Menéndez et al., 2008, Fitt & Lancaster, 2017; Wallingford et al., 2020), despite LDGs likely being an important mechanism of altered biotic interactions under poleward expansions.

While LDGs result from regional-scale processes, uncovering whether gradients provide high niche opportunities requires linking regional and local scale patterns and processes (Fitt & Lancaster, 2017; Shea & Chesson, 2002; Wallingford et al., 2020). Patterns in species diversity occur through a series of 'filtering' processes. Across a geographic range, regional species pools are determined by large-scale processes, including gradients in abiotic conditions and dispersal after historic geographical events (Bello et al., 2013; Deák et al., 2018; Gaston, 2000; Willig et al., 2003). Local species pools are determined by a combination of processes, including dispersal from regional pools, suitability of abiotic conditions, and biotic interactions (Chase & Myers, 2011; Cornell & Harrison, 2014). Ecological release in response to high niche opportunities depends on release from antagonistic interactions or reduced competition or predation at local scales (Bello et al., 2013; Shea & Chesson, 2002).

Phytophagous insects do not often compete directly, but more commonly via indirect interactions mediated by interactions with host plants or enemies (Frank van Veen et al., 2006; Holt & Bonsall, 2017; Kaplan & Denno, 2007; Prior & Hellmann, 2010). Lower phytophagous insect diversity (richness and abundance) at the poles may create high niche opportunities on host plants by relaxing plant-mediated competition, leading to susceptible host plants with more available resources or low defences (Więski & Pennings, 2014; Woods et al., 2012). Release from 'apparent competition' (competition via shared enemies) for range-expanding populations moving poleward could result from lower richness or abundances of hosts at the poles, or if enemies fail to effectively switch to attacking novel hosts (Menéndez et al., 2008; Shea & Chesson, 2002). There is evidence for patterns of weaker biotic interactions between phytophagous insects and host plants at the poles, with studies finding lower host plant damage or defences or higher foliar nutrients (Pennings et al., 2009; Więski & Pennings, 2014). Previous studies of range-expanding phytophagous insects have also found evidence for weaker apparent competition in expanded regions (Menéndez et al., 2008; Prior & Hellmann, 2013; Schönrogge et al., 2012).

Here we leverage a poleward range expansion of a phytophagous oak gall wasp, *Neuroterus saltatorius* (Hymenoptera: Cynipidae) (cynipid) that occurs on a dominant oak in western North America, *Quercus garryana*. The native range of *N. saltatorius* on *Q. garryana* spans from California to Puget Sound, Washington (Prior & Hulcr, 2017; Russo, 2006) while *Q. garryana* ranges from California into select parts of British Columbia (Figure 1, highlighted grey). *Neuroterus salatatorius* recently expanded its range poleward to Vancouver Island, BC and now occurs at the most northern locations of *Q. garryana* (Duncan, 1997; Prior & Hellmann, 2013). In its expanded range, it occurs at higher abundances on a higher proportion of trees compared with its native range (Prior & Hellmann, 2013). *Q. garryana* also hosts a community of cynipid wasps that co-occur with *N. saltatorius* that are attacked by a community of parasitoid wasps (Prior & Hellmann, 2013; Smith, 1995; Ward, Busbee, et al., 2022).

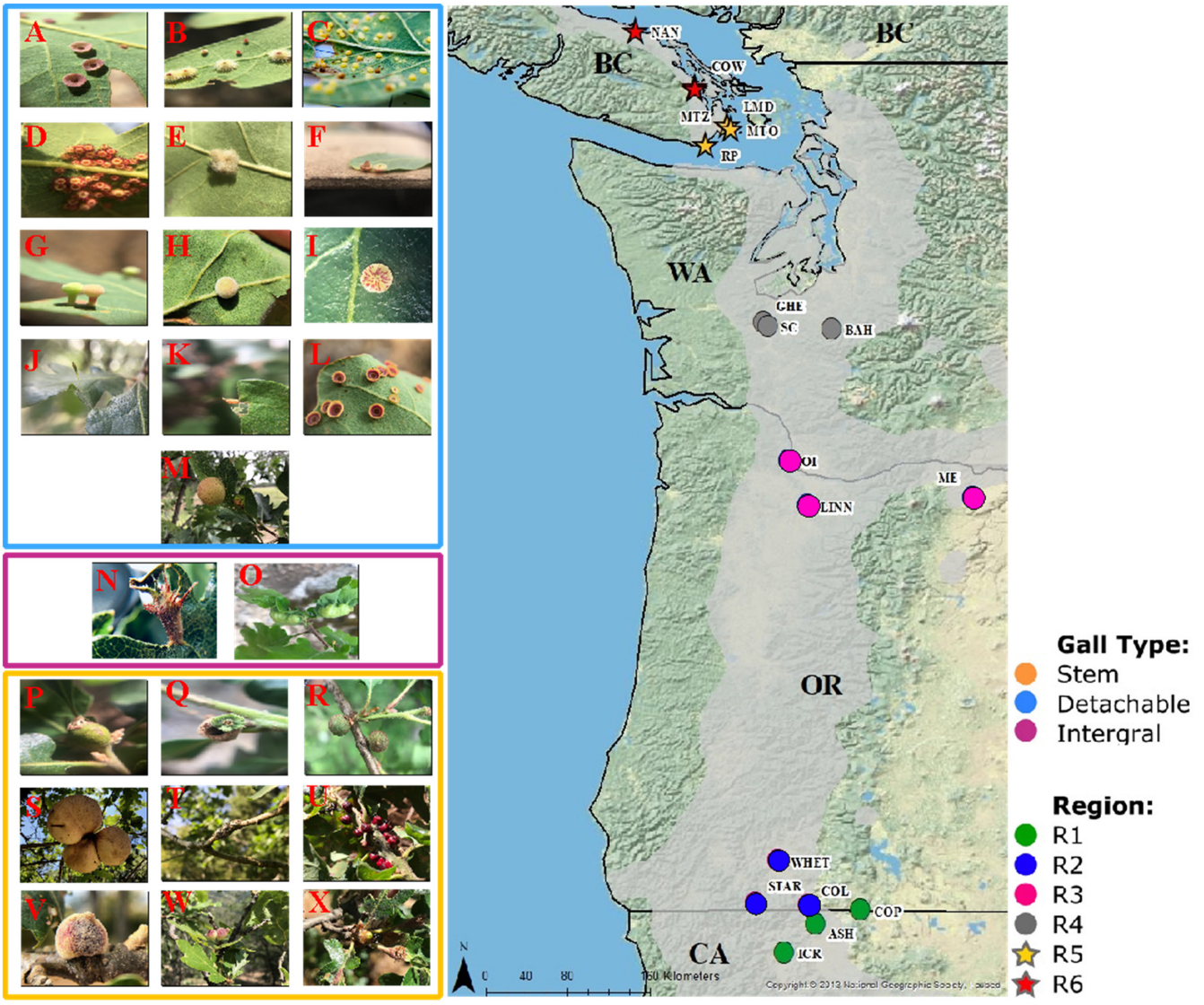

FIGURE 1 Cynipid morphotypes found on *Quercus garryana*: Row 1) *Andricus gigas* (*AG*), *A. stellaris* (*AS*), *Neuroterus saltatorius* (agamic, *NSA*), row 2) *A. tubifaciens* (TT), *A. confertus* (*ACF*), *A. kingi* (agamic, *AKA*), row 3) *Xanthoteras teres* (*XT*), *A. fullawayi* (*AF*), *A. parmula* (AP), row 4) *A. pedicellatum* (*DP*), *A. kingi* (gamic, *AK*), unknown sp. (pink bowtie, *PB*), row 5) *Besbicus mirabilis* (*BMI*), *A. opertus* (*AO*), *N. washingtonensis* (*NW*), row 6) *A. coortus* (*AC*), unknown sp. (acorn cap, *ACG*), *Burnettweldia washingtonensis* (*DW*), row 7) *A. quercuscalifornicus* (*AQ*), *A. chrysolepidicola* (*ACH*), *Disholcaspis mellifica* (*DME*), row 8) *D. canescens* (*DC*), *D. mamillana/simulata* (*DM/DS*), *unknown* sp. (acorn gall, *ACO*). Morphotypes coloured by gall-type guild (blue = detachable leaf, purple = integral leaf, orange = stem). Y) Map showing range of *Quercus garryana* (grey) and study sites grouped into six regions represented by different colours, circles represent sites in the native range, stars expanded range (see Table S1 for site acronyms).

The objective of this study is to test whether the *Q. garryana*-cynipid community follows an LDG, and if lower diversity leads to weak interactions for the range-expanding species. To this end, we measure cynipid diversity throughout the range of *Q. garryana* to uncover if diversity follows an LDG, and if other abiotic or habitat factors contribute to patterns in regional diversity. Next, we examine how regional species pools influence local patterns of cynipids that co-occur and putatively interact on individual host plants. Finally, we uncover if co-occurring cynipids interact with *N. saltatorius* as evidence that release from local antagonistic interactions contribute to ecological release. We predict that *Q. garryana*-cynipid communities follow an LDG and that regional species pools create variation in local niche opportunities, with higher niche opportunities at the northern extent of range via reduced interactions on host plants.

2 | MATERIALS AND METHODS

2.1 | Study system and sites

Q. garryana var. *garryana* Douglas ex. Hook (Fagaceae), Garry/Oregon white oak, ranges from central California to southwestern BC (Figure 1, highlighted grey). *Q. garryana* occurs in semi-arid woodlands or savannas and is often the predominant overstory vegetation

(Stein, 1990). *Q. garryana* is the only oak species from central Oregon to BC but overlaps with several oak species in the southern portion of its range (Stein, 1990). Oak ecosystems occur in rain shadows of coastal mountains, and their distribution becomes patchier (surrounded by *Pseudotsuga menziesii* forests) with increasing latitude, due to decreased suitable abiotic conditions (Stein, 1990; Vellend et al., 2008).

Cynipid wasps are a specialized group of phytophagous insects that deposit their eggs in living plant tissue of Fagaceae (beech and oaks), eliciting the formation of a gall structure that houses larvae while it feeds on plant tissue (Hayward & Stone, 2005; Stone et al., 2002). Cynipids often have two generations; a gamic (sex-ual) generation and an agamic (asexual) generation that form dis-tinct galls. Cynipid galls vary significantly in morphology among species and among generations and occur on various plant tissues (Hayward & Stone, 2005; Russo, 2006; Stone et al., 2002; Ward, Bagely, et al., 2022). There are ~700 described oak cynipid species in North America, with western oak ecosystems being a hotspot of diversity (Burks, 1979; Russo, 2006; Weld, 1957). Cynipid wasps are attacked by a suite of parasitoids wasps, largely in the Superfamily Chalcidoidea, that specialize on one or more cynipid species (Askew et al., 2013; Bailey et al., 2009; Forbes et al., 2016; Hayward & Stone, 2005; Ward, Busbee, et al., 2022).

N. saltatorius (Edwards), the jumping gall wasp, is one of several cynipid wasps on *Q. garryana* in western North America (Prior & Hulcr, 2017; Russo, 2006). *N. saltatorius*'s native range on *Q. garryana* occurs from northern California to Puget Sound, Washington. This species is absent in historical records (Evans, 1985), and its first appearance and spread in BC was tracked by the Canadian Forest Service starting in 1983 around the city of Victoria (Duncan, 1997), and Prior and Hellmann (2013) noted that it occurred at the northern most intact *Q. garryana* site in BC on Hornby Island by 2007.

N. saltatorius forms small galls (1–2 mm), with clustered integral leaf galls produced by the gamic spring generation and detachable leaf galls formed by the summer agamic generation (Smith, 1995). The detachable agamic galls drop from the leaves in mid-late summer where the galls remain in the leaf litter for the winter until the following spring (Smith, 1995). The agamic generation occurs at high abundances on *Q. garryana* in its expanded range, with more infested trees. There are infested trees in the native range, but they are usually isolated (Prior & Hellmann, 2013). High abundance causes foliar scorching with putative effects on oaks and documented effects on native oak insects (Duncan, 1997; MacDougall et al., 2010; Prior & Hellmann, 2010).

We selected *Q. garryana* study sites based on if oaks were the dominant tree species, patch size, and accessibility. Sites were delineated into six regions (three sites per region), determined based on oak distribution, and access to sites. This ecosystem is more continuous in California and Oregon but becomes naturally patchier up in Washington State and on Vancouver Island at the edges of this ecosystem's range. Our regions reflected turnover in regional diversity (see below). Sites in regions were separated on average 44.67 km, with the closest sites being 3 km from one another. All oak patches were >1.5 ha (Figure 1; Table S1). Sites were managed by various landowners and varied in management practices. None of the sites had visible signs of recent burning, and we avoided choosing sites with known history of recent burns.

2.2 | Sampling cynipid communities

We used a systematic, uniform-effort sampling regime to produce comparable abundance and community composition data across sites. Sites were visited three times (sampling periods) to capture temporal changes in cynipid communities that coincided with the development time on trees of the agamic generation of *N. saltatorius* (Smith, 1995). The focus was on the agamic generation as it is the more abundant and damaging generation (Duncan, 1997; Prior & Hellmann, 2010). Sampling started when *N. saltatorius* agamic galls started to develop, with the first period beginning on 21 May 2019, in the southernmost region (R1) and continued in order of increasing latitude. Sampling of the northern regions (R4–R6) began on 5 June 2019 (Table S1). Sites were sampled in a single day, and regions were sampled in the same order throughout the season, with an average of 20 days between site visits.

During each visit, we haphazardly sampled 10 trees without replacement, for a total of 30 trees per site. Trees were at least 10 m apart from previously sampled trees, had enough reachable limbs to sample (up to 8 feet, standing on a 6-foot ladder), and contained at least one cynipid when searching during the first 5 min of sampling. We standardized effort by sampling 10 branches, where we exhaustively searched for galls on 10 leaf clusters per branch and along branches for approximately 1 m. Galls occur on other structures, such as buds; however, the leaves were already flushed out by our first sampling date, and it is possible that species of gall wasps were not recorded. We did not search in the higher canopy of the trees; previous studies found no variability in cynipid richness between the different stratifications of the canopy (Eliason & Potter, 2001).

Gall morphotypes were identified via gall morphology (Russo, 2006; Weld, 1957). Some gall species were difficult to identify via their gall structure alone without destroying the galls, and in one case we lumped species: *Disholcaspis mamillana* and *D. simulata* (Figure 1, Table S2). Total gall abundance for each cynipid morphotype was recorded for each tree. We put galls into three gall-type guilds: integral leaf galls (galls continuous with leaf material; Figure 1n–o), detachable leaf galls (galls not integrated into leaf material that are often detachable; Figure 1a–m), and non-leaf galls (that included mostly stem galls, but also petiole and acorn galls; *hereafter* 'stem galls', Figure 1p–x) (Russo, 2006).

2.3 | Measuring abiotic and habitat variables

To uncover if abiotic and habitat variables correlate with latitude, and gall wasp diversity and abundance, we measured abiotic and

habitat factors at sites. On the first survey day at each site, we hung an iButton temperature logger (1-Wire, Thermochron) on one tree to collect temperature hourly. Loggers were kept up until the final sampling date. For each survey tree, we measured soil temperature and moisture at the base of the tree. We measured tree height (m) and diameter at breast height (DBH) and created a composite 'tree size' metric (Appendix S1). For each site, we collected 'BioClim' variables that are climatic variables available at a spatial resolution of ~340 km^2 from WorldClim 1970–2000 data (Fick & Hijmans, 2017). We collected temperature and precipitation (annual mean, max., min., and seasonality) variables and created separate composite temperature and precipitation variables using principal component analysis (Figure S1). We chose these variables as they contribute to patterns in insect species distributions (Gonçalves-Souza et al., 2014; Moreira et al., 2015). We also measured survey area, oak patch size, and determined broad habitat and land-use categories surrounding survey areas using aerial images (Appendix S1).

2.4 | Determinants of regional patterns in cynipid diversity

To assess if predetermined regions reflected turnover in regional diversity, we partitioned cynipid richness at several spatial scales (within (ɑ) and among (ß) regions, sites and trees) by perform-ing additive partitioning using the program PARTITION (Veech & Crist, 2009). We found significant turnover in ß-richness among re-gions but not among sites within regions (Table S4; Figure S3). Thus, we defined the regional species pools in predetermined regions and pooled trees among three study sites in our local scale analysis (see below, 90 trees per region).

We calculated cynipid morphotype richness for each survey period at each site. We created rarefaction curves that justified our use of raw richness for subsequent analyses (Figure S4). To describe cynipid community composition, we performed a canonical analysis (CA) that is a suitable ordination approach to assess species composition over gradients (Legendre, 2008) (package in , Oksanen et al., 2013). We used a matrix of cynipid morphotypes abundances observed during surveys at sites and used CA1 and CA2 as metrics of community composition for models (see below). We also created a site level CA biplot (Figure 2).

To determine if patterns in cynipid richness follows an LDG, along with if composition and abundance changes with latitude, we ran separate linear model (LM) or GLMs between richness, CA, and abundance (with and without *N. saltatorius* and latitude (Figure 3; Table 1). Next, to examine if biotic and habitat factors correlated or contributed to patterns in diversity, we ran with multiple predictor variables as fixed effects (Table S3), along with survey date (Julian date) and region as random effects. Since our main objective includes evaluating the LDG, we included latitude in all models. Sites also varied in elevation which we also included. We included other abiotic and habitat variables (predictor variables)

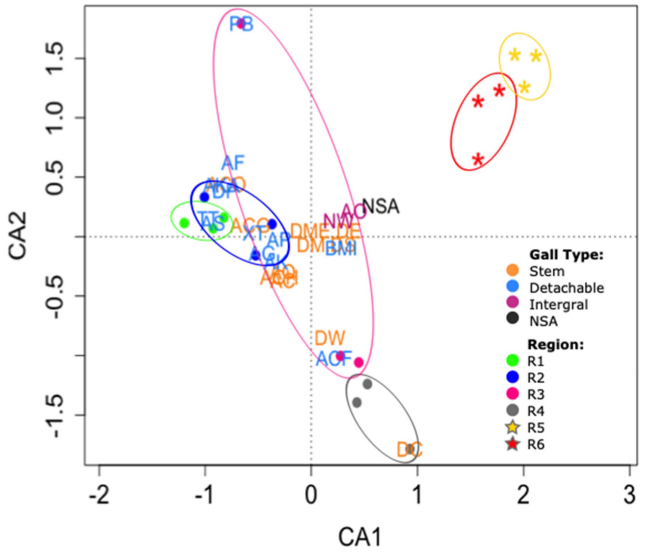

FIGURE 2 Canonical analysis biplot of cynipid morphotype composition at sites across regions. Circles denote sites in the native range and stars in the expanded range. Ellipses encompass sites within regions. Gall morphotype and site abbreviations Figure 1, coloured gall acronyms represent gall type guild (blue = detachable leaf, purple = integral leaf, orange = stem) (Tables S1 and S2).

that may contribute to patterns in cynipid diversity, some that correlate with latitude, including climate factors (PC_{temp}, PC_{precip}, soil moisture) and habitat factors (oak patch size, $PC_{habitat\ types}$) (Figure S1; Table S3). First, we ran mixed effect models with single predictor variables and calculated conservative Akaike information criterion (AICc) scores for each model. We then built models by creating multi-factor models using a forward stepwise approach starting with variables with the lowest AICc scores, and then building to add in all variables. We compared and retained models with an AICc < 2 (Hill et al., 2017) (see Appendix S1 for details).

2.5 | Local patterns in cynipid interactions

To assess potential competitive interactions and variation in niche opportunities among regions, first to determine the potential for cynipid morphotype interactions on trees, we assessed which cynipid morphotypes co-occurred on trees, as sedentary phytophagous insects most strongly interact on individual host plants (Kaplan & Denno, 2007). Given that diversity is relatively homogenous among sites within regions (Figure S3; Table S4), we pooled sites, using 90 trees per region. We used ggcorrplot to perform partial correlation analyses in R using presence/absence data of gall morphotypes on trees (Kassambara, 2019). Positive correlations were categorized as weak (R = 0.25–0.49), moderate (R = 0.50–0.74.5), or strong associations (R = 0.75–1.0). Correlation values less than 0.25 were categorized as no association. For correlations between morphotypes >0.25, we performed Spearman's Rank Order Correlation tests to determine if

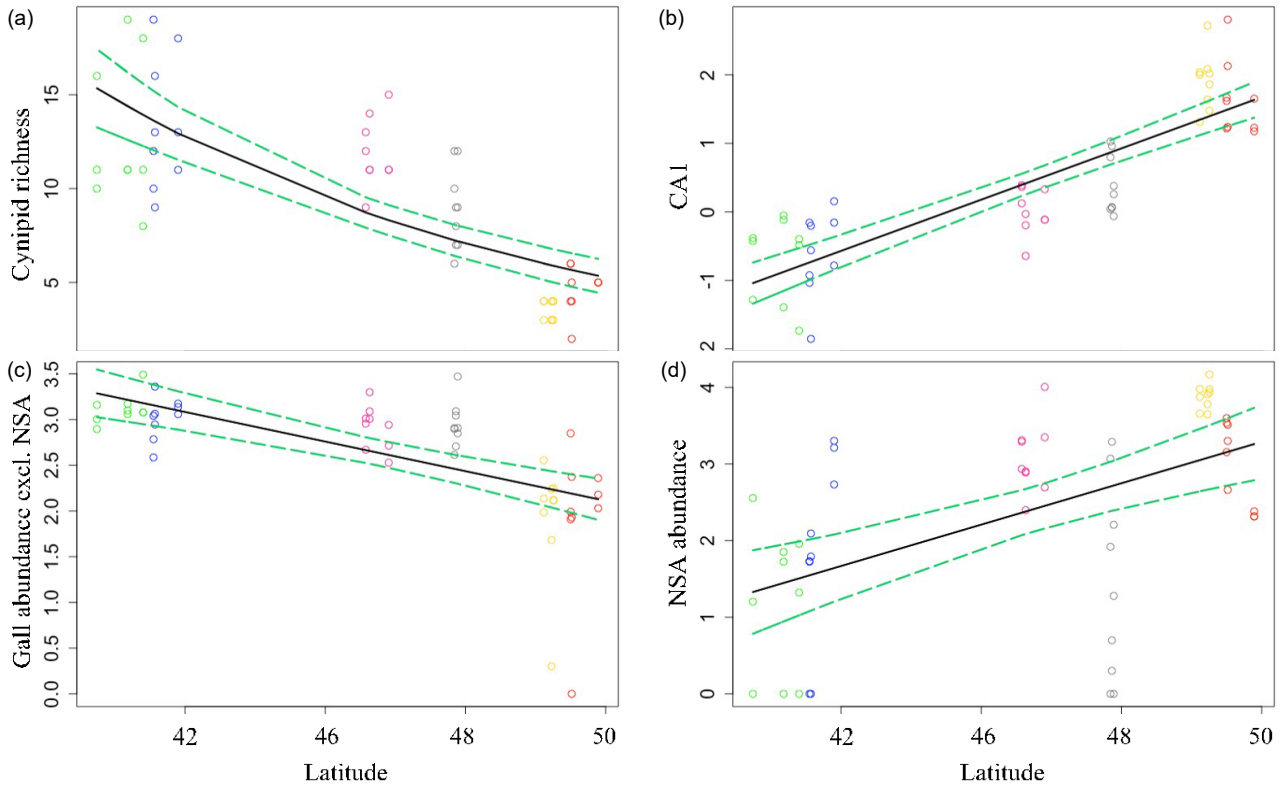

FIGURE 3 Regressions between (a) cynipid morphotype richness, (b) cynipid morphotype composition (CA1), (c) gall abundance excluding *N. saltatorius* (log-transformed), and (d) *N. saltatorius* abundance (log-transformed) and latitude (log-transformed) for each survey date/site. Regions are coloured coded (Figure 1). Solid black line represents predicted regression lines and 95% C.I. (green dashed lines) for fixed effects (latitude) only for clarity (Table 1).

TABLE 1 Slopes ± (C.I.) for single-factor regressions with latitude (Figure 3), and for best fit models after Akaike information criterion (AICc) comparisons of the final model sets for multi-factor models. Within parentheses are confidence intervals for slopes. Bolded slopes are significant. See AICc output in Tables S6–S8.

Predictor variables	Cynipid morphotype richness	Cynipid community composition (CA1)	Total gall abundance	Gall abundance excluding *N. saltatorius*	*N. Saltatorius* abundance
Single-factor models					
Latitude	**−5.88 (±1.30)**	**14.96 (±0.71)**	**1.77 (± 0.84)**	**−6.48 (±1.13)**	**10.80 (±2.37)**
Multi-factor models					
Latitude	**−5.58 (± 2.00)**	**14.55 (± 2.78)**	**−6.46 (±1.74)**	−5.79 (±2.28)	−1.99 (± 5.75)
Elevation	**−0.64 (± 0.18)**				
$PC1_{temp.}$	**−0.27 (± 0.11)**		**0.36 (± 0.07)**		**0.55 (± 0.23)**
$PC2_{habitat}$	−0.19 (±0.13)				
Oak habitat area	**−0.0003 (± 0.18)**				

correlations were significant between morphotype pairs in each region. Igraph in R was used to create association networks (Csardi, 2020). We performed canonical correspondence analysis (CCA) with presence/absence data with several predictor variables to uncover if site variables influenced gall morphotype composition (Figure S7).

Next, to assess if cynipid morphotypes co-occurring on trees reflect putative negative or positive interactions (with the focal species), we performed LMs between the abundance of the defined gall guilds and the abundance of *N. saltatorius* using trees where they co-occur. We performed separate analyses for each gall-type guild (detachable, integral, stem) as we predict overlapping gall types might more strongly interact. We scaled cynipid abundances by dividing the number of galls on trees for each group (*N. saltatorius*, detachable, integral, and stem) by the total number of galls at a site to make comparisons among sites with different abundances. We included other gall abundance, region, and the interaction as fixed effects. We performed arcsine square root transformations on relative gall abundances. Significant negative relationships provide potential

evidence of antagonistic interactions between other cynipids and *N. saltatorius*.

2.6 | Field study permits and approvals

We did not need approval from an animal's ethic committee to conduct this research. Shipment permit: USDA: P526P-17-03013. Collection and landowner permits: WA State Collection Permit (WA Dept. of Fish & Wildlife (PRIOR 21-085); BLM (CANO6-F-2019.00000003); USDA Forest Service (2720); The Nature Conservancy (verbal, Molly Morison); Southern Oregon Land Conservancy (verbal, Stan Dean); Sauvie Island Wildlife Area (verbal, Mark A. Nebeker); OR Parks & Rec. (037-19); Tualatin Hills Parks & Rec. District (2021-03); West Linn White Oak Savanna (verbal, Roberta Schwarz); Weyerhaeuser Company (V21-1100); OR State Parks (#188); WA Dept. Fish & Wildlife (1162020); Capital Regional District Parkes (37/17); Saanich Parks (R9799); Nature Conservancy Canada (verbal, Ginny Hudson); Canadian National Defence (0103A-7603-1(BExec NMU AA/RDIMS 938864)); BC Parks (109824)).

3 | RESULTS

3.1 | Determinants of patterns of regional morphotype pools

We identified 23 cynipid gall morphotypes in three guilds: 12 detachable leaf morphotypes, 9 stem, and 2 integral leaf. We performed a CA using the whole gall morphotype community while highlighting changes in community composition and guilds. Morphotype community composition varied among regions (Figure 2). Variation in CA1 is influenced by detachable leaf gall and stem gall types that dominate in R1-3 and are lacking in the expanded range, which is dominated by integral leaf gall types (R5-6) (Table S5). Detachable leaf gall types have negative loadings along CA1 (*Trichoteras tubifaciens* = −0.97, *Andricus stellaris* = −0.92, *A. kingi* = −0.85), as do stem gall types (*A. chrysolepidicola* = −0.30, *A. coortus* = −0.27, *A. quercus-californicus* = −0.27) while integral leaf gall types (*N. washingtonensis* = 0.26, *A. opertus* = 0.40) have positive loadings. *N. saltatorius* has a positive loading along CA1 (0.66), reflecting its high abundance in the expanded range. Two other detachable cynipids were found in the expanded range—*Besbicus mirabilis* is common and *A. kingi* found at one site. CA2 variation is influenced by rare species ('pink bow-tie' = −0.65 and *Disholcaspis canescens* = 0.93).

In single models with latitude only, cynipid richness followed the predicted negative relationship with increasing latitude (*ResDev* = 53.964, $p < 0.0001$; Figure 3a). CA1 increased with latitude ($F = 131.84$, $p < 0.0001$, Figure 3b), revealing latitudinal changes in community composition. Gall abundance excluding *N. saltatorius* was negatively related to latitude ($F = 32.69$, $p < 0.0001$, Figure 2c). However, *N. saltatorius* abundance and total gall abundance had a positive relationship with latitude (*N. saltatorius* abundance: $F = 20.82$, $p < 0.0001$, Figure 2d; total gall abundance: $F = 4.45$, $p = 0.04$, Figure S5) (Table 1). The highest abundances of *N. saltatorius* were in the expanded range R5 with approximately 20,000 more galls compared with other regions (Figure S6).

In the models with multiple predictor variables, latitude was retained in all final models (Table 1; Table S8). $PC1_{temp}$ was retained in several final models (Table 1) and has a strong positive correlation with latitude ($R = 0.92$) such that higher latitude sites had lower maximum and minimum temperatures and shorter seasonality (Table S3). Elevation was negatively related to latitude ($R = -0.71$) and had a negative relationship with richness (Table 1). Total oak area and $PC2_{habitat}$ have a negative relationship with richness with oak area negatively related to latitude ($R = -0.78$) and $PC2_{habitat}$ positively related ($R = 0.77$) (Table S3).

3.2 | Patterns in local morphotype interactions

For local interactions, we analysed the whole community, but highlight interactions within guilds. The number of positive significant cynipid gall morphotype co-occurrences on trees varied among regions (Figure 4). Most significant positive associations occurred between the diverse detachable leaf cynipids (including *N. saltatorius*), while stem and integral cynipids had fewer significant positive associations. Across regions, stem cynipids had 8, integral leaf 5, and detachable leaf 58 significant positive associations. There was a decrease in significant associations with increasing latitude. *N. saltatorius* associates with four species directly and three indirectly in R1, four directly and four indirectly in R2, one directly, and one indirectly in R3, and two directly and two directly in R4, but had no significant associations in R5 and R6. All direct associations of *N. saltatorius* are with detachable leaf cynipids in the native range (Figure 4). Local gall wasp composition patterns (from the CCA) were influenced by multiple factors, mainly Julian date, and soil moisture in R1–R4 but not for R5–R6 (Figure S7; Table S9).

N. saltatorius gall abundance had a significant negative relationship with detachable leaf gall abundance ($F = 4.19$, $p = 0.04$; Figure 5a) along with integral leaf gall abundance ($F = 15.92$, $p < 0.01$; Figure 5b). *N. saltatorius* abundance had no relationship with stem gall abundance ($F = 0.58$, $p = 0.446$; Figure 5c). For leaf and integral gall abundance there was also a significant effect of region (leaf: $p < 0.0001$, integral: $p < 0.0001$); but no significant interactions between region and gall type abundance for any of the gall types (leaf: $p = 0.112$, integral: $p = 0.604$).

4 | DISCUSSION

Our objective was to uncover if patterns in LDGs create weak local interactions and high niche opportunities at higher latitudes, potentially contributing to increased performance of a poleward range-expanding species. As predicted, cynipid diversity followed an LDG,

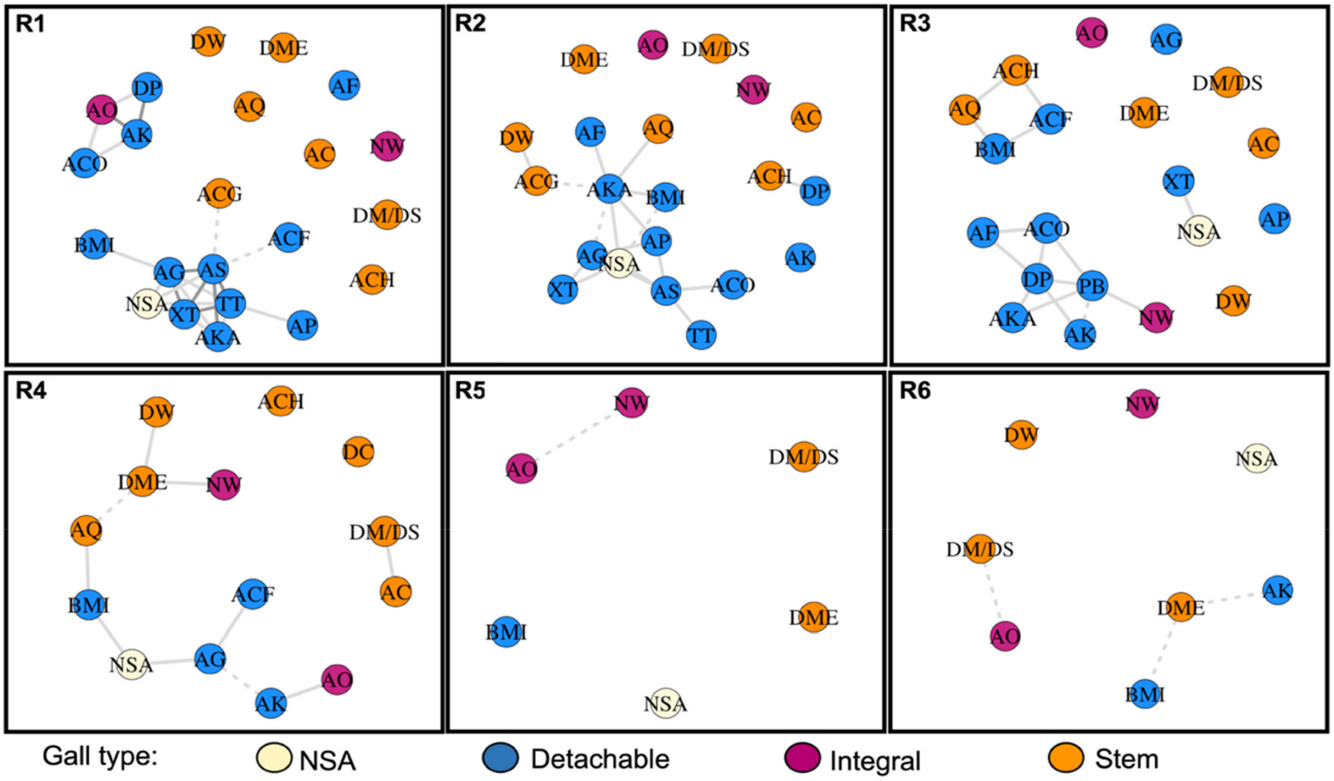

FIGURE 4 Partial correlation analysis using presence absence data of cynipid morphotypes on trees. Networks display interactions between morphotypes on trees ($n = 90$) in a region. Shades of lines represent positive correlation strength (weak (0.25–0.49), moderate (0.5–0.74), and strong (0.75–1.0)). Solid lines indicate a significant correlation, whereas dashed lines are non-significant (spearman test). Morphotypes coloured by gall-type category (blue = detachable, purple = integral, orange = stem), morphotype abbreviations found in Table S2.

with fewer morphotypes at higher latitude sites. Community composition changed with a loss of detachable leaf and stem gall types at high latitudes. These regional diversity patterns are correlated with gradients in abiotic factors, such as variation in temperature extremes, and habitat factors, such as oak patch size, that correlate with latitude. At local scales (on trees) *N. saltatorius* co-occurred the most with other detachable leaf gall wasps that were largely absent in the expanded range, where only 2 (out of 12) morphotypes were present. On trees where other detachable leaf gall wasps and *N. saltatorius* co-occurred, their abundances were negatively related, suggesting antagonistic interactions. Our results indicate that LDGs of oak cynipid communities provide high niche opportunities in northern oak populations, resulting from weak local antagonistic interactions. Given the ubiquity of LDGs, regional patterns should be considered as a mechanism influencing outcomes of altered biotic interactions under poleward range expansions.

Phytophagous insect communities, including cynipids, that occupy post-glacial landscapes in the northern hemisphere established through migration after glaciers retreated, with populations often coming from source refuges at lower latitudes (Hayward & Stone, 2005; Mutun, 2016; Stone et al., 2017). *Q. garryana* maintained a large portion of its current range during the last glacial maximum (Fraser glaciation period, 15 kyr BP), including northern populations in Oregon and Washington (Booth et al., 2003). The only portion of the current range of *Q. garryana* that was glaciated during the last glacial maximum was the Puget Sound region, San Juan Islands, WA and Vancouver Island BC (Brown & Hebda, 2002; Brubaker, 1991). *Q. garryana has* reduced genetic diversity in northern edges and on islands, suggesting founder effects as it expanded its range after ice sheets receded (Marsico et al., 2009). As *Q. garryana* experienced bottlenecks when expanding, so may have their associated insect communities. In other regions, there are latitudinal trends in cynipid communities with expansion from refuges occurring post-glaciation (Hayward & Stone, 2005; Mutun, 2016), with greater community (and genetic) diversity in the core, reducing towards the poles (Stone et al., 2017). The process of cynipid dispersal over long distances is not fully understood as they are weak fliers and dispersal limited, but wind is a possible mechanism, along with accidental transport (e.g., via vehicles) to neighbouring ranges or over long distances by humans (Gilioli et al., 2013).

Post-glaciation dispersal lags and limitations likely partially determine current cynipid distributions. In this system, lower diversity in northern latitudes is confounded with an island effect; however, we see lower diversity and changes in composition in R3 and R4, compared with R1 and R2 suggesting a latitudinal gradient on the mainland. Host plants and ecosystems are often patchier at range edges, which is the case for *Q. garryana*-ecosystems both on the mainland in Washington and the Island (Fuchs, 2001; Loughnan

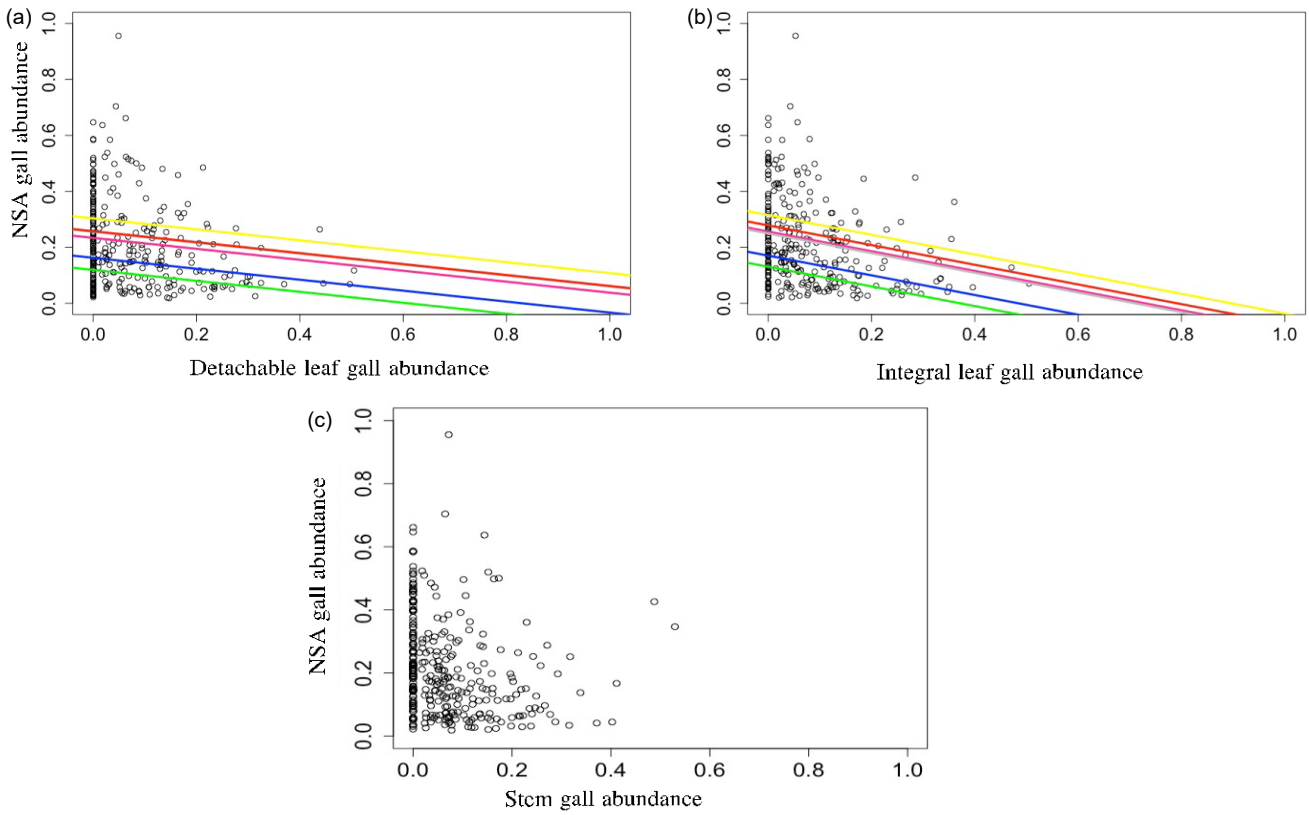

FIGURE 5 Regressions between relative abundance of (a) other detachable leaf cynipids, (b) integral leaf cynipids, and (c) stem cynipids and *N. saltatorius* abundance. Symbols represent trees where *N. saltatorius* and gall types co-occur. Gall abundances are transformed (arcsine sqrt). Regression lines (LM) are shown for significant relationships. Colours represent regions (Figure 1).

& Williams, 2019). Dispersal limitation across unsuitable non-oak habitat (forests) or other barriers, such as topographical or water barriers could contribute to LDGs (Gaston, 2000; Kerr et al., 1998; Willig et al., 2003). Patch size correlated negatively with cynipid richness as well as latitude, where conditions are cooler with higher precipitation—more conducive to *P. menziesii* forests. In addition to limited dispersal to more isolated patches, small patches could contribute to reduced patterns in richness, as larger patches often harbour higher species richness (Steffan-Dewenter & Schiele, 2008). Patches are also fractured due to land-use change, especially in BC as most suitable habitat is encroached by urban and suburban development (Fuchs, 2001, Loughnan & Williams, 2019). However, we did not find patterns in habitat and land-use borders (other than the percent of oak border) contributed to patterns in richness and abundance.

The other regional factor that correlated with latitude and explained patterns in cynipid richness was $PC1_{temp}$, representing temperature extremes and seasonality. Studies have shown that gall formers are more common in dry and warm environments (Gonçalves-Alvim & Fernandes, 2001), which represent the conditions of southern populations of *Q. garryana*. Minimum temperatures decrease with increasing latitude, and studies have proposed that climatic factors may limit phytophagous insects' distribution and diversity at high latitudes (Fitt & Lancaster, 2017; Więski & Pennings, 2014; Willig et al., 2003; Zvereva & Kozlov, 2021). Because $PC1_{temp}$ correlated highly with latitude, we do not know the extent to which temperature contributes to patterns in diversity.

Elevation and latitude are negatively correlated (Table S3) in that sites in northern CA and southern OR were generally at higher elevation than sites in the north. While elevation relates to patterns in richness, but we cannot tease apart its influence from latitude because they are correlated. If there were an elevational gradient in diversity, we would predict lower richness at higher elevations; however, we found the opposite with higher richness at higher elevation sites. As a result, we largely think the relationship between diversity and elevation is driven by latitude.

We found high abundances of *N. saltatorius* at northern latitudes, in the expanded range, with no other factors contributing to this pattern. Thus, landscape and abiotic factors that limit cynipid richness and abundance at high latitudes, do not seem to apply to the range-expanding species. Patterns in *N. saltatorius* abundances may be driven by other factors, such as release from biotic interactions (Fitt & Lancaster, 2017; Prior & Hellmann, 2013, Prior et al., 2022).

N. saltatorius underwent a poleward range expansion, but it is unclear whether this is linked to climate change or an introduction. Regardless, for poleward range expansions that occur via various types of anthropogenic change, interacting species are not expected to move in concert (Gilman et al., 2010; Wallingford et al., 2020). One difference between populations undergoing climate-driven versus other types of anthropogenic range expansions is that in the

former case, expanding populations are more likely to come from populations at the edge of their thermal tolerances. To this end, populations moving into the expanded range may be small and limited by abiotic conditions. Alternatively, some edge (source) populations are locally adapted to edge conditions and their populations might be larger and less limited by expanded range (new edge) conditions (Hellmann et al., 2008; Pelini et al., 2009). The high abundance of *N. saltatorius* in its expanded range suggests that abiotic conditions in the expanded region are not limiting *N. saltatorius*'s abundance.

Cynipids are patchily distributed within oak populations, with some trees lacking galls whereas others have moderate or high abundances of galls (Egan & Ott, 2007, Prior & Hellmann, 2010). Less is known about patchiness of multiple, co-occurring gall wasp species. We found that detachable leaf cynipids had the strongest co-occurrences or associations on trees, including with our focal species, whereas other gall types largely lack strong associations. Since only two detachable leaf cynipids occur in R5 and R6, *N. saltatorius* does not associate with other species on trees in its expanded range. Several factors could contribute to gall co-occurrences on individual trees. In our CCA, we found that Julian date contributed to variation in association among trees (R1–R4), which is expected given our sampling over time. Soil moisture and temperature (that likely correlate with host plant phenology) explained trends, suggesting that microhabitat differences influence gall associations. There are several other factors, including variation in host plant genetics or defences, that were beyond the scope of this study to measure that likely contributes to patterns of cynipid patchiness and associations on trees.

Sedentary insects interact on their host plants (Frank van Veen et al., 2006; Holt & Bonsall, 2017; Kaplan & Denno, 2007; Prior & Hellmann, 2013). Our predictions that weak associations might lead to high niche opportunities assumes that weak associations on trees release *N. saltatorius* from antagonistic interactions. However, cynipids may coexist on trees while not antagonistically interacting. The negative relationship between *N. saltatorius* abundance on trees and the abundance of detachable and integral gall wasps, but not with stem gall wasps, suggests antagonistic interactions. However, as we also mentioned above, there are alternative hypotheses that could explain this variation, including variation in host plant traits, such as phenology, nutritional quality, or chemical defences that could influence patterns in abundance. Future studies might evaluate traits or manipulate competitor presence or abundance to examine how other gall former species affects *N. saltatorius* performance.

That *N. saltatorius* is mostly associated with detachable leaf cynipids on trees, but negatively interacts when co-occurring, suggests that release from smaller regional pools that lack the detachable gall group might contribute to ecological release. Cynipids can compete indirectly via altering resources by acting as nutrient sinks or sequester carbon, or they could interact through induced or constitutive defences (Cuevas-Reyes et al., 2003; Prior & Hellmann, 2010). Mechanisms of host defences against cynipids are not well understood. Chemical defences against chewing herbivores in oaks (tannins, lignin) is suspected to not be a main defence against galling insects (Barbosa & Fernandes, 2014). A hypersensitive response, in which tissue surrounding galls necrose or whole leaves drop, has been described as a defence against gall formers (Barbosa & Fernandes, 2014). If induced, this response could impede other individuals from establishing, but little is known about mechanisms of this defence against galling insects. While we found negative correlations in abundances between species suggesting antagonistic interactions, species could also compete over 'evolutionary time' such that lower diversity at the poles might have created relaxed selection for defensive responses particularly against detachable leaf galls in northern populations (Moreira et al., 2015; Woods et al., 2012).

Insects also compete through shared enemies, that is, apparent competition. We expect stronger apparent competition for insect hosts that have similar morphological and phenological traits (Bailey et al., 2009; Holt & Bonsall, 2017; Schönrogge et al., 2012; Prior et al., 2022; Zhang et al., 2022). *N. saltatorius* not only shares the locality at which it forms its galls with other leaf detachable gall wasps, but it also generally shares similar morphological and phenological traits with many of these co-occurring species (Prior et al., 2022). For example, detachable leaf galls overlapped more in time with *N. saltatorius*, and many of these galls are small, single chambered galls lacking gall defences such as hard woody exteriors and large interstitial space. Galls with similar shapes and phenology are more likely to share parasitoids and enemies (Bailey et al., 2009). However, *B. mirabilis*, the dominant native detachable leaf gall on the Island, does not share many parasitoids with *N. saltatorius* (Prior et al., 2022), and it is one of few morphologically different (25× larger) detachable leaf gall formers. It is important to note that the spatial scale for apparent competition might be greater than species co-occurring on trees since parasitoids are not sessile (Holt & Bonsall, 2017). However, surveyed trees were spread throughout sites, and we assume co-occurring species are most likely to experience apparent competition.

Leveraging anthropogenic range expansions, is a powerful approach to uncover the community dynamics of range expansions. This research provides valuable insight into how biogeographical patterns in communities and species interactions can influence the outcome of range expansions. By studying cynipid communities across a majority of the range of *Q. garryana*, we uncovered that diversity of cynipid communities across their range creates high niche opportunities (or weak biotic interactions) that might contribute to ecological release.

Our study highlights that biogeographical patterns in LDGs should be incorporated into predictions about how species interactions will be altered under poleward range expansions. This is especially important given the ubiquity of LDGs, but few studies have evaluated out comes of anthropogenic range expansions in the context of biogeographical patterns in diversity (Wallingford et al., 2020). Future studies in other systems should take similar approaches to uncover how regional and local scale patterns and processes combine to contribute to niche opportunities that influence the outcomes of range expansions. Here, we provide a robust example of this mechanism of altered biotic interactions and range expansions and a framework for testing this biogeographical mechanism

of altered biotic interactions under anthropogenic range expansions in other systems.

AUTHOR CONTRIBUTIONS

Kirsten M. Prior, Dylan G. Jones, and Thomas H. Q. Powell developed ideas; Dylan G. Jones, Julia Kobelt, Kirsten M. Prior implemented field protocols; Dylan G. Jones analysed data with input from Kirsten M. Prior; Jenna M. Ross performed habitat analysis; Dylan G. Jones, Kirsten M. Prior, Julia Kobelt wrote manuscript with input from all authors. All authors gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code available via Figshare https://doi.org/10.6084/m9.figshare.18737834.v1 (Jones & Prior, 2022).

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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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