Diversity gradients and range expansions

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

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Abstract

1. **1.** When species undergo poleward range expansions in response to anthropogenic change, they
2. likely encounter less diverse communities in new locations. If low diversity communities provide
3. weak biotic interactions, such as reduced competition for resources or predation, range-
4. expanding species may experience 'high niche opportunities.'
5. **2.** Here, we uncover if oak gall wasp communities experience a latitudinal diversity gradient
6. (LDG) and weaker interactions at the poles that might create high niche opportunities for a
7. range-expanding community member.
8. **3.** We performed systematic surveys of oak gall wasps on a dominant oak, *Quercus garryana*,
9. throughout most of its range, from northern California to Vancouver Island, British Columbia.
10. On 540 trees at 18 sites, we identified 23 species in three guilds (leaf detachable, leaf integral,
11. and stem galls). We performed regressions between oak gall wasp diversity, latitude, and other
12. abiotic and habitat factors to reveal if cynipid communities follow an LDG. To uncover patterns
13. in local interactions, we performed partial correlations on oak gall wasps co-occurring on trees
14. within regions. Finally, we performed regressions between abundances of co-occurring gall
15. wasps on trees to reveal potential interactions.
16. **4.** *Q. garryana*-gall wasp communities followed an LDG, with lower diversity at higher
17. latitudes, particularly with a loss of detachable leaf gall species. Detachable leaf gall wasps,
18. including the range-expanding species, co-occurred most on trees and had weak interactions in
19. the northern region. Abundances of the range-expander and detachable and integral leaf galls co-
20. occurring on trees were negatively related, suggesting antagonistic interactions. Overall, we
21. found that LDGs create communities with weaker antagonistic interactions at the poles that
22. might facilitate ecological release in a range-expanding community member.
23. **5.** Here, we uncover how regional and local scale patterns and processes create high niche
24. opportunities for a range-expanding community member. This research provides insight into how
25. biogeographical patterns in communities and species interactions influence the outcome of range
26. expansions. Given the ubiquity of LDGs, these outcomes might be expected in other
27. phytophagous insect communities.
28.
29. **Keywords:** species diversity, latitudinal diversity gradient (LDG), range expansion, niche
30. opportunity, ecological release, biotic interactions, Cynipidae.
31.
32. **Introduction**

33   Anthropogenic change is causing species to shift their ranges, including to higher
34   latitudes and elevations (Parmesan and Yohe 2003). Species experience range shifts at different
35   rates due to variation in thermal tolerances and dispersal capabilities (Parmesan and Yohe 2003,
36   Hellmann et al. 2012). As a result, range-expanding species may leave interacting species behind
37   and form novel interactions as they infiltrate new species pools (Gilman et al. 2010, Hellmann et
38   al. 2012). Depending on the net effects of lost or gained antagonistic and facilitative interactions,
39   range-expanding species may experience 'high niche opportunities' (*sensu* Shea and Chesson
40   2002) resulting from increased resource availability or reduced predation that results in higher
41   performance in new locations 'ecological release' or low niche opportunities or 'biotic
42   resistance' leading to lower performance (Shea and Chesson 2002, Gilman et al. 2010).
43   One of the most ubiquitous patterns in nature is that species diversity declines towards
44   the poles or higher elevations (Latitudinal Diversity Gradient, LDG) (Gaston 2000, Willig et al.
45   2003, Hillebrand 2004, Fitt and Lancaster 2017, Zvereva and Kozlov 2021). This pattern has
46   been observed across many taxa, including phytophagous insects and parasitoids (Cuevas-Reyes
47   et al. 2003, Willig et al. 2003, Kerr et al. 2016, Galiana et al. 2019). LDGs are often linked to
48   latitudinal gradients in biotic interactions, with weaker interactions towards the poles (Pennings
49   et al. 2009; Schemske et al. 2009, Zvereva and Kozlov 2021, except see Moles et al. 2011). Low-
50   diversity communities are predicted to have high niche opportunities if there are weak
51   interactions among competitors or with predators (Shea and Chesson 2002, Willing et al. 2003,
52   Schemske et al. 2009, Gilman et al. 2010). As a result, poleward communities may provide weak
53   biotic resistance, making high latitude communities susceptible to colonization by range-
54   expanding species and invaders (Gilman et al. 2010, Wallingford et al. 2020). Understanding if
55   LDGs provide high niche opportunities is important to uncover and predict potential outcomes of
56   range expansions.
57   While LDGs result from regional-scale processes, uncovering whether gradients provide
58   high niche opportunities requires linking regional and local scale patterns and processes (Shea
59   and Chesson 2002, Fitt and Lancaster 2017, Wallingford et al. 2020). Patterns in species
60   diversity occur through a series of 'filtering' processes. Across a geographic range, regional
61   species pools are determined by large scale processes, including gradients in abiotic conditions
62   and dispersal after historic geographical events (Gaston 2000, Willig et al. 2003, Bello et al.
63   2013, Deák et al. 2018). These factors limit species distributions generating variation in regional
64   species pools across latitude. Local species pools are determined by a combination of processes,
65   including dispersal from regional pools, suitability of abiotic conditions, and biotic interactions
66   (Chase 2011, Cornell and Harrison 2014). Response to high niche opportunities depends on
67   release from biotic interactions at local scales (Shea and Chesson 2002, Bello et al. 2013).
68   Phytophagous insects do not often compete directly, but more commonly interact
69   indirectly mediated by direct interactions with host plants or enemies (Veen et al. 2006, Kaplan
70   and Denno 2007, Prior and Hellmann 2010, Holt and Bonsall 2017). Lower phytophagous insect
71   diversity at the poles may create high niche opportunities on host plants by relaxing plant-
72   mediated competition, leading to susceptible host plants with more available resources or low
73   defenses (Woods et al. 2012, Wieski and Pennings 2014). Release from 'apparent competition'
74   (competition via shared enemies) at the poles could result from lower abundances of host or
75   enemy diversity, or if enemies fail to effectively switch to attacking novel hosts (Shea and
76   Chesson 2002, Menendez et al. 2008). There is evidence for patterns of weaker biotic
77   interactions between phytophagous insects and host plants at the poles, with studies finding
78   lower host plant damage or defenses or higher foliar nutrients (Pennings et al. 2009, Wieski and

79 Pennings 2014). Previous studies of range-expanding phytophagous insects have also found
80 evidence for weaker apparent competition, resulting from lower host and enemy diversity, and
81 from enemies failing to effectively attack novel hosts (Schönrogge et al. 2000, Menendez et al.
82 2008, Prior and Hellmann 2013).
83   Here we leverage a poleward range expansion of a phytophagous oak gall wasp,
84 *Neuroterus saltatorius* (Hymenoptera: Cynipidae) (cynipid) that occurs a dominant oak in
85 western North America, *Quercus garryana*. *Q. garryana* hosts a community of cynipid wasps
86 that co-occur with *N. saltatorius* that are attacked by a community of parasitoid wasps (Smith
87 1995, Prior and Hellmann 2013). The native range of *N. saltatorius* on *Q. garryana* spans from
88 California to Puget Sound, Washington (Russo 2006, Prior and Hulcr 2017). This species
89 recently expanded its range poleward to Vancouver Island, BC and now occurs at the most
90 northern locations of *Q. garryana* (Duncan 1997, Prior and Hellmann 2013). In its expanded
91 range, it occurs at higher abundances on a higher proportion of trees compared to its native range
92 (Prior and Hellmann 2013).
93   The objective of this study is to test whether the *Q. garryana*-cynipid community follows
94 an LDG, and if lower diversity at the poles provides weak interactions for the range-expanding
95 species. To this end, we measure cynipid diversity throughout the range of *Q. garryana* to
96 uncover if diversity follows an LDG, and if other factors contribute to patterns in regional
97 diversity. Next, we examine how regional species pools influence local patterns of cynipids that
98 co-occur and putatively interact on individual host plants. Finally, we uncover if co-occurring
99 cynipids interact with *N. saltatorius* as evidence that release from local antagonistic interactions
100 contribute to ecological release. We predict that *Q. garryana*-cynipid communities follow an
101 LDG and that regional species pools create variation in local niche opportunities, with higher
102 niche opportunities at the poles via reduced interactions on host plants.
103
104 **Methods and Materials**
105 *Study system and sites*
106   *Quercus garryana* var. *garryana* Douglas ex. Hook (Fagaceae), Garry/Oregon white oak,
107 ranges from central California to southwestern BC. *Q. garryana* occurs in semi-arid woodlands
108 or savannas and is often the predominant overstory vegetation (Stein 1990). *Q. garryana* is the
109 only oak species from central Oregon to BC but overlaps with several oak species in the southern
110 portion of its range (Stein 1990). Oak ecosystems occur in rain shadows of coastal mountains,
111 and their distribution becomes patchier (surrounded by *Pseudotsuga menziesii* forests) with
112 increasing latitude, due to decreased suitable abiotic conditions (Stein 1990, Vellend et al. 2008).
113   Cynipid wasps are a specialized group of phytophagous insects that deposit their eggs in
114 living plant tissue of Fagaceae (beech and oaks), eliciting the formation of a gall structure that
115 houses larvae while it feeds on plant tissue (Stone et al. 2002, Hayward and Stone 2005).
116 Cynipids often have two generations; a gamic (sexual) generation and an agamic (asexual)
117 generation that form distinct galls. Cynipid galls vary significantly in morphology among species
118 and among generations and occur on various plant tissues (Stone et al. 2002, Hayward and Stone
119 2005, Russo 2006). There are ~700 described oak cynipid species in North America, with
120 western oak ecosystems being a hotspot of diversity (Weld 1957, Burks 1979, Russo 2006).
121 Cynipid wasps are attacked by a suite of parasitoids wasps, largely in the Superfamily
122 Chalcidoidea, many of which are polyphagous within cynipids, but generally specialized on
123 cynipids (Hayward and Stone 2005, Bailey et al. 2009, Askew et al. 2013, Forbes et al. 2016).

124   *Neuroterus saltatorius* (Edwards), the jumping gall wasp, is one of several cynipid wasps
125 on *Q. garryana* in western North America (Russo 2006, Prior and Hulcr 2017). *N. saltatorius*'s
126 native range on *Q. garryana* occurs from northern California to Puget Sound, Washington; and
127 recently expanded its range to the northernmost extent of *Q. garryana* in BC (Duncan 1997).
128 This species is absent in historical records (Evans 1985), and its first appearance and spread in
129 BC was tracked by the Canadian Forest Service starting in 1983 around the city of Victoria
130 (Duncan 1997), and Prior and Hellmann (2013) noted that it occurred at the northern most intact
131 *Q. garryana* site in BC on Hornby Island by 2007.
132   *N. saltatorius* forms small galls (1-2 mm), with clustered integral leaf galls produced by
133 the gamic spring generation and detachable leaf galls formed by the summer agamic generation
134 (Smith 1995). The detachable agamic galls drop from the leaves in mid-late summer where the
135 galls remain in the leaf litter for the winter until the following spring (Smith 1995). The agamic
136 generation occurs at high abundance on *Q. garryana* in its expanded range, with more infested
137 trees. There are infested trees in the native range, but they are usually isolated (Prior and
138 Hellmann 2013). High abundance causes foliar scorching with putative effects on oaks and
139 documented effects on native oak insects (Duncan 1997, MacDougall 2010, Prior and Hellmann
140 2010).
141   We selected *Q. garryana* study sites based on oak dominance, patch size, and
142 accessibility. We predetermined six regions based on distribution and logistics, with three sites in
143 each region. Sites in regions were separated on average 44.67 km, with closest sites being 3 km
144 from one another. All oak patches were >1.5ha (Fig. 1; Appendix S1:Table S1). Sites were
145 managed by various landowners and varied in management practices. None of the sites had
146 visible signs of recent burning, and we avoided choosing sites with known history of recent
147 burns.

148 *Sampling cynipid communities*
149   We employed a systematic, uniform-effort sampling regime to produce comparable
150 abundance and community composition data across sites. We visited each site three times
151 (sampling periods) to capture temporal changes in cynipid communities that coincided with the
152 development time on trees of the agamic generation of *N. saltatorius* (Smith 1995). We focused
153 on the agamic generation as it is the more abundant and damaging generation (Duncan 1997,
154 Prior and Hellmann 2010). We started sampling sites when *N. saltatorius* agamic galls started to
155 develop, with the first period beginning on May 21, 2019 in the southernmost region (R1) and
156 continued in order of increasing latitude. Sampling of the northern regions (R4-R6) began on
157 June 5th, 2019 (Appendix S1:Table S1). We sampled one site per day, and regions were sampled
158 in the same order throughout the season, with an average of 20 days between site visits.
159   During each visit, we haphazardly sampled 10 trees without replacement, for a total of 30
160 trees per site. Trees were at least 10 m apart from previously sampled trees, had enough
161 reachable limbs to sample (up to 8 feet, standing on a 6-foot ladder), and contained at least one
162 cynipid when searching during the first 5 minutes of sampling. We standardized effort by
163 sampling 10 branches, where we exhaustively searched for galls on 10 leaf clusters per branch
164 and on stems on approximately 1 m. Galls occur on other structures, such as buds; however, the
165 leaves were already flushed out by our first sampling date, and it is possible that cryptic species
166 of gall wasps were not recorded. We did not search in the higher canopy of the trees; previous
167 studies found no variability in cynipid richness between the different stratifications of the canopy
168 (Eliason and Potter 2001).

169   Gall morphotypes were identified via gall morphology (Weld 1957, Russo 2006). Some
170 gall species were difficult to identify via their gall structure alone without destroying the galls,
171 and in one case we lumped species: *Disholcaspis mamillana* and *D. simulata*. (Fig. 1, Appendix
172 S1:Table S2). Total gall abundance for each cynipid morphotype was recorded for each tree. We
173 put galls into three gall-type guilds: integral leaf galls, detachable leaf galls, and non-leaf galls
174 (that included mostly stem galls, but also petiole and acorn galls; *hereafter* 'stem galls') (Russo
175 2006). *N. saltatorius* agamic generation is a detachable leaf gall (Russo 2006).
176 *Measuring abiotic and habitat variables*
177   On the first survey day at each site, we hung an iButton temperature logger (1-Wire,
178 Thermochron) on one tree to collect temperature hourly. Loggers were kept up until the final
179 sampling date. For each survey tree, we measured soil temperature and moisture at the base of
180 the tree. We measured tree height (m) and diameter at breast height (DBH) and created a
181 composite 'tree size' metric (Appendix S1:Supplementary Methods). For each site, we collected
182 BioClim variables with a spatial resolution of ~340 km^2 from WorldClim 1970-2000 data:
183 temperature and precipitation (annual mean, max., min., and seasonality) (Fick 2017) and created
184 separate composite temperature and precipitation variables using Principal component analysis
185 (PCA) (Appendix S1: Supplementary Methods; Fig.S1). We chose these variables as they
186 contribute to patterns in insect species distributions (Gonçalves-Souza et al. 2014, Moreira et al.
187 2015). We also measured survey area, oak patch size, and determined broad habitat and land use
188 categories surrounding survey areas using aerial images (Appendix S1:Supplementary Methods).
189 *Determinants of regional patterns in cynipid diversity*
190   To assess if predetermined regions reflected turnover in regional diversity, we partitioned
191 cynipid richness at several spatial scales (within (α) and among (β) regions, sites, trees) by
192 performing additive partitioning using the program PARTITION (Veech and Crist, 2009). We
193 found significant turnover in ß-richness among regions but not among sites in regions (Appendix
194 S1:Table S4; Fig.S3). Thus, we defined the regional species pools in pre-determined regions and
195 pooled trees among three study sites in our local scale analysis (see below, 90 trees per region).
196   We calculated cynipid morphotype richness for each survey period at each site. We
197 created rarefaction curves that justified our use of raw richness for subsequent analyses
198 (Appendix S1:Fig. S4). To describe cynipid community composition, we performed a canonical
199 analysis (CA) that is a suitable ordination approach to assess species composition over gradients
200 (Legendre 2008) (vegan package in R, Oksanen et al. 2013). We used a matrix of cynipid
201 morphotypes abundances observed during surveys at sites and used CA1 and CA2 as metrics of
202 community composition for models (see below). We also created a site level CA biplot (Fig. 2).
203   To determine if patterns in cynipid richness, composition, and abundance follow an LDG
204 and if abiotic and habitat factors contribute to diversity patterns, we ran linear (LMM) or
205 generalized linear mixed effect models (GLMM) with multiple predictor variables as fixed
206 effects (Appendix S1:Table S3), and survey date (Julian date) and region as random effects.
207 Since our main objective includes evaluating the LDG, we included latitude in all models. Sites
208 also varied in elevation which we also included. We included other abiotic and habitat variables
209 that may contribute to patterns in cynipid diversity, some that correlate with latitude, including
210 climate factors (PC_{temp}, PC_{precip}, soil moisture) and habitat factors (oak patch size, $PC_{habitat\ types}$)
211 (Appendix S1:Fig.S1, Table S3). First, we ran mixed effect models with single predictor
212 variables and calculated conservative Akaike information criterion (AICc) scores for each model.
213 We then built models by creating multi-factor models using a forward stepwise approach starting
214 with variables with the lowest AICc scores, and then building to add in all variables. We

5

215 compared and retained models with a ΔAICc < 2 (Hill et al. 2017). (see Appendix S1:
216 Supplementary methods for details).

217 *Local patterns in cynipid interactions*

218 To assess potential competitive interactions and variation in niche opportunities among
219 regions, we determined cynipid morphotype associations on trees, as sedentary phytophagous
220 insects most strongly interact on individual host plants (Kaplan and Denno 2007). Given that
221 diversity is relatively homogenous among sites within regions (Appendix S1:Fig. S3, Table S4),
222 we pooled sites, using 90 trees per region. We used ggcorrplot to perform partial correlation
223 analyses in R using presence/absence data of gall morphotypes on trees (Kassambara 2019).
224 Correlations were categorized as weak (R = 0.25-0.49), moderate (R = 0.50-0.74.5), or strong
225 associations (R = 0.75-1.0). Correlation values less than 0.25 were categorized as no association.
226 For correlations between morphotypes > 0.25, we performed Spearman's Rank Order
227 Correlation tests to determine if correlations were significant between morphotype pairs in each
228 region. igraph in R was used to create association networks (Csardi 2020). We performed
229 canonical correspondence analysis (CCA) with presence/absence data with several predictor
230 variables to uncover if site variables influenced tree community composition (Appendix S1:Fig.
231 S7).

232 Finally, to assess if associations on trees reflect putative interactions (with the focal
233 species), we performed LMs between the abundance of other cynipid morphotypes and the
234 abundance of *N. saltatorius* using trees where they co-occur. We performed separate analyses for
235 each gall-type guild (detachable, integral, stem) as we predict overlapping gall types might more
236 strongly interact. We scaled cynipid abundances by dividing the number of galls on trees for
237 each group (*N. saltatorius*, detachable, integral, and stem) by the total number of galls at a site to
238 make comparisons among sites with different abundances. We included other gall abundance,
239 region, and the interaction as fixed effects. We performed arcsine square root transformations on
240 relative gall abundances. Significant negative relationships provide evidence of antagonistic
241 interactions between other cynipids and *N. saltatorius*.

242 **Results**

243 *Determinants of patterns of regional morphotype pools*

244 We identified 23 morphotypes (12 detachable leaf, 9 stem, and 2 integral leaf). Cynipid
245 morphotype community composition varied among regions (Fig. 2). Variation in CA1 is
246 influenced by detachable leaf gall and stem gall types that dominate in R1-3 and are lacking in
247 the expanded range, which is dominated by integral leaf gall types (R5-6) (Appendix S1: Table
248 S5). Detachable cynipids have negative loadings along PC1 (*Trichoteras tubifaciens* = -0.97,
249 *Andricus stellaris* = -0.92, *A. kingi* = -0.85), as do stem cynipids (*A. chrysolepidicola* = -0.30, *A.*
250 *coortus* = -0.27, *A. quercuscalifornicus* = -0.27) while integral leaf gall formers (*N.*
251 *washingtonensis* = 0.26, *A. opertus* = 0.40) have positive loadings. *N. saltatorius* has a positive
252 loading along CA1 (0.66), reflecting its high abundance in the expanded range. Two other
253 detachable cynipids were found in the expanded range - *Besbicus mirabilis* is common and *A.*
254 *kingi* found at one site. CA2 variation is influenced by rare species ("pink bowtie" = -0.65 and
255 *Disholcaspis canescens* = 0.93).

256 Latitude was retained in all the final models (Fig. 3 A-D, Table 1; Appendix:Table S8).
257 Cynipid richness followed the predicted negative relationship with increasing latitude (F = 72.66,
258 P < 0.0001; Fig. 2A). CA1 increased with latitude (F = 126.27, P < 0.0001, Fig. 3B), revealing
259 latitudinal changes in community composition. Gall abundance excluding *N. saltatorius* was
260 negatively related to latitude (F = 6.47, P = 0.065, Fig. 2C). However, *N. saltatorius* abundance

261 and total gall abundance had a positive relationship with latitude (*N. saltatorius* abundance: $F =$
262 19.48, $P < 0.0001$, Fig. 2D; total gall abundance: $F = 3.89$, $P = 0.054$, Fig. S5) (Table 1). The
263 highest abundances of *N. saltatorius* were in R5 with approximately 20,000 more galls compared
264 to other regions (Appendix S1:Fig. S6). $PC1_{temp}$ was retained in several final models (Table 1)
265 and has a strong positive correlation with latitude ($R = 0.92$) such that higher latitude sites had
266 lower maximum and minimum temperatures and shorter seasonality (Appendix S1:Table S3).
267 Elevation was negatively related to latitude ($R = -0.71$) and had a negative relationship with
268 richness (Table 1). Total oak area and $PC2_{habitat}$ have a negative relationship with richness with
269 oak area negatively related to latitude ($R = -0.78$) and $PC2_{habitat}$ positively related ($R = 0.77$)
270 (Appendix S1:Table S3).
271 *Patterns in local morphotype interactions*
272 The number of significant cynipid morphotype associations varied among regions (Fig.
273 4). Most significant associations occurred between the diverse detachable leaf cynipids
274 (including *N. saltatorius*), while stem and integral cynipids had fewer significant associations.
275 Across regions, stem cynipids had 8, integral leaf 5, and detachable leaf 58 significant
276 associations. There was a decrease in significant associations with increasing latitude. *N.*
277 *saltatorius* associates with 4 species directly and 3 indirectly in R1, 4 directly and 4 indirectly in
278 R2, 1 directly, and 0 indirectly in R3, and 2 directly and 2 directly in R4, but had no significant
279 associations in R5 and R6. All direct associations of *N. saltatorius* are with detachable leaf
280 cynipids in the native range (Fig. 2). Local cynipid patterns were influenced by multiple factors,
281 mainly Julian date and soil moisture in R1-R4 but not for R5-R6 (Appendix S1:Fig. S7, Table
282 S9).
283 *N. saltatorius* gall abundance had a significant negative relationship with detachable leaf
284 gall abundance ($F = 4.19$, $P = 0.04$; Fig. 5a) along with integral leaf gall abundance ($F = 15.92$,
285 $P < 0.01$; Fig. 5b). *N. saltatorius* abundance had no relationship with stem gall abundance ($F =$
286 0.58, $P = 0.446$; Fig. 5c). For leaf and integral gall abundance there was also a significant effect
287 of region (leaf: $P < 0.0001$, integral: $P < 0.0001$); but no significant interactions between region
288 and gall type abundance for any of the gall types (leaf: $P = 0.112$, integral: $P = 0.604$).
289
290 **Discussion**
291 As predicted, cynipid diversity followed an LDG, with fewer morphotypes at higher
292 latitude sites. Community composition changed with a loss of detachable leaf and stem gall types
293 at high latitudes. These regional diversity patterns are correlated with gradients in abiotic factors,
294 such as variation in temperature extremes, and habitat factors, such as oak patch size, that
295 correlate with latitude. At local scales (on trees) *N. saltatorius* interacted the most with other
296 detachable leaf cynipids that were largely absent in the expanded range, where only 2 (out of 12)
297 morphotypes were present. On trees where other detachable leaf cynipids and *N. saltatorius* co-
298 occurred, their abundances were negatively related, suggesting antagonistic interactions. Our
299 results indicate that LDGs of oak cynipid communities provide high niche opportunities in
300 northern oak populations, resulting from weak local antagonistic interactions.
301 Phytophagous insect communities, including cynipids, that occupy post-glacial
302 landscapes in the northern hemisphere established through migration after glaciers retreated, with
303 source refuges often coming from lower latitudes (Hayward and Stone 2005, Mutun 2016, Stone
304 et al. 2017). *Q. garryana* maintained a large portion of its current range during the last glacial
305 maximum (LGM) (Fraser glaciation period, 15 kyr BP), including northern populations in
306 Oregon and Washington (Booth et al. 2003). The only portion of the current range of *Q.*

307   *garryana* that was glaciated during the LGM was the Puget Sound region, San Juan Islands, WA
308   and Vancouver Island BC (Brubaker 1991, Brown and Hebda 2002). *Q. garryana has* reduced
309   genetic diversity in northern edges and on islands, suggesting founder effects as it expanded its
310   range after ice sheets receded (Marsico et al. 2009). As *Q. garryana* experienced bottlenecks
311   when expanding, so may have their associated insect communities. In other regions, there are
312   latitudinal trends in cynipid communities with expansion from refuges occurring post-glaciation
313   (Hayward and Stone 2005, Mutun 2016), with greater community (and genetic) diversity in the
314   core, reducing towards the poles (Stone et al. 2017). The process of cynipid dispersal over long
315   distances is not fully understood as they are weak fliers and dispersal limited, but wind is a
316   possible mechanism, along with accidental transport to neighboring ranges or over long distances
317   (Gilioli et al. 2013).
318   Post-glaciation dispersal lags and limitations likely partially determine current cynipid
319   distributions. In this case, lower diversity in northern latitudes is confounded with an island
320   effect; however, we see lower diversity and changes in composition in R3 and R4, compared to
321   R1 and R2 suggesting a latitudinal gradient on the mainland. Host plants and ecosystems are
322   often patchier at range edges, which is the case for *Q. garryana*-ecosystems both on the
323   mainland in Washington and the Island (Fuchs 2001, Loughnan and Williams 2019). Dispersal
324   limitation across unsuitable non-oak habitat (forests) or other barriers, such as topographical or
325   water barriers could contribute to LDGs (Gaston 2000, Willig et al. 2003, Kerr et al. 2016).
326   Patch size correlated negatively with latitude and cynipid richness, where conditions are cooler
327   with higher precipitation - more conducive to *P. menziesii* forests. In addition to limited dispersal
328   to more isolated patches, small patches could contribute to reduced patterns in richness, as larger
329   patches often harbor higher species richness (Steffan-Dewenter and Schiele 2008). Patches are
330   also fractured due to land use change, especially in BC as most suitable habitat is encroached by
331   urban and suburban development (Fuchs 2001, Loughnan and Williams 2019). However, we did
332   not find patterns in habitat and land use borders (other than the percent of oak border)
333   contributed to patterns in richness and abundance.
334   The other regional factor that correlated with latitude and explained patterns in cynipid
335   richness was $PC1_{temp}$, representing temperature extremes and seasonality. Studies have shown
336   that gall formers are more common in dry and warm environments (Gonçalves-alvim and
337   Fernandes 2001), which represent the conditions of southern populations of *Q. garryana*.
338   Minimum temperatures decrease with increasing latitude and elevation, and studies have
339   proposed that climatic factors may limit phytophagous insects' distribution and diversity at high
340   latitudes and elevations (Willig et al. 2003, Wieski and Pennings 2014, Fitt and Lancaster 2017,
341   Zvereva and Kozlov 2021). Since $PC1_{temp}$ correlated highly with latitude, we do not know the
342   extent to which temperature contributes to patterns in diversity.
343   We found high abundances of *N. saltatorius* at northern latitudes, in the expanded range,
344   with no other factors contributing to this pattern. Thus, landscape and abiotic factors that limit
345   cynipid richness and abundance at high latitudes, do not seem to apply to the range-expanding
346   species. Thus, patterns in *N. saltatorius* abundances may be driven by other factors, such as
347   release from biotic interactions (Prior and Hellmann 2013, Fitt and Lancaster 2017).
348   *N. saltatorius* underwent a poleward range expansion, but it is unclear whether this is
349   linked to climate change or an introduction. Regardless, poleward range expansions occur via
350   various types of anthropogenic change, where interacting species are not expected to move in
351   concert (Gilman et al. 2010, Wallingford et al. 2020). One difference between populations
352   undergoing climate-driven versus other types of range expansions is that in the former case,

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353 expanding populations may come from populations at the edge of their thermal tolerances. To
354 this end, populations moving into the expanded range be small and limited by abiotic conditions.
355 Alternatively, if edge (source) populations are locally adapted to edge conditions, their
356 populations might be larger and less limited by expanded range (new edge) conditions
357 (Hellmann et al. 2008, Pelini et al. 2009). The high abundance of *N. saltatorius* in its expanded
358 range suggests that abiotic conditions in the expanded region are not limiting.
359   Cynipids are patchily distributed within oak populations, with some trees lacking galls
360 while others have moderate or high abundances (Egan and Ott 2007, Prior and Hellmann 2010).
361 We found that detachable leaf cynipids had the strongest associations on trees, including with
362 our focal species, while other gall types largely lack strong associations. Since only two
363 detachable leaf cynipids occur in R5 and R6, *N. saltatorius* does not have strong associations on
364 trees in its expanded range. Several factors could contribute to gall associations (or similar
365 preferences) for individual trees. Julian date contributed to variation in association among trees
366 (R1-4), which is expected given our sampling over time. Soil moisture and temperature (that
367 likely correlate with host plant phenology) explained trends, suggesting that microhabitat
368 differences influence gall associations. There are factors that were beyond the scope of this study
369 to measure that likely contributes to cynipid associations, such as host plant genetic variation and
370 variation in defenses.
371   Sedentary insects interact on their host plants (Veen et al. 2006, Kaplan and Denno 2007,
372 Prior and Hellmann 2013, Holt and Bonsall 2017). Our predictions that weak associations might
373 lead to high niche opportunities assumes that weak associations on trees release *N. saltatorius*
374 from antagonistic interactions. However, cynipids may coexist on trees while not
375 antagonistically interacting. The negative relationship between *N. saltatorius* abundance on trees
376 and the abundance of detachable and integral gall wasps, but not with stem gall wasps, suggests
377 antagonistic interactions. Future studies might manipulate competitor presence of abundance to
378 examine how this affects *N. saltatorius* survival and measure the proportion of shared enemies
379 between gall morphotypes.
380   That *N. saltatorius* mostly associates with detachable leaf cynipids on trees, but
381 negatively interacts when co-occurring, suggests that release from smaller regional pools that
382 lack the detachable gall group might contribute to ecological release. Cynipids can compete
383 indirectly via altering resources by acting as nutrient sinks or sequester carbon, or they could
384 interact through induced or constitutive defenses (Cuevas-Reyes et al. 2003, Prior and Hellmann
385 2010). Mechanisms of host defenses against cynipids are not well understood. Chemical defenses
386 against chewing herbivores in oaks (tannins, lignin) is suspected to not be a main defense against
387 galling insects (Barbosa and Fernandes 2014). A hypersensitive response, in which tissue
388 surrounding galls necrose or whole leaves drop, has been described as a defense against gall
389 formers (Barbosa and Fernandes 2014). If induced, this response could impede other individuals
390 from establishing, but little is known about mechanisms of this defense mechanism against
391 galling insects. While we found negative correlations in abundances between species suggesting
392 antagonistic interactions, species could also compete over 'evolutionary time' such that lower
393 diversity at the poles might have created relaxed selection for defensive responses particularly
394 against detachable leaf galls in northern populations (Woods et al. 2012, Moreira et al. 2015).
395   Insects also compete through shared enemies, i.e., apparent competition. We expect
396 stronger apparent competition for insect hosts that have similar morphological and phenological
397 traits (Bailey et al. 2009, Schönrogge et al. 2012, Holt and Bonsall 2017). *N. saltatorius* not only
398 shares the locality at which it forms its galls with other leaf detachable gall wasps, but it also

399   shares similar morphological and phenological traits (Prior, unpublished data). For example,
400   detachable leaf galls overlapped more in time with *N. saltatorius*, and many of these galls are
401   small, single chambered galls lacking gall defenses such as hard woody exteriors and large
402   interstitial space. Galls with similar shapes and phenology are more likely to share parasitoids
403   (Bailey et al. 2009). *B. mirabilis*, the predominant detachable leaf gall on the Island, does not
404   share many parasitoids with *N. saltatorius* (Prior, unpublished data), and it morphologically
405   different (25X larger). It is important to note that the spatial scale for apparent competition might
406   be greater than species co-occurring on trees, since parasitoids are not sessile (Holt and Bonsall
407   2017). However, surveyed trees were spread throughout sites, and we assume co-occurring
408   species are most likely to experience apparent competition.
409   Leveraging anthropogenic range expansions, is a powerful approach to uncover the
410   community dynamics of range expansions. This research provides valuable insight into how
411   biogeographical patterns in communities and species interactions can influence the outcome of
412   range expansions. By studying cynipid communities across the entire range of *Q. garryana*, we
413   uncovered that diversity of cynipid communities across their range creates high niche
414   opportunities (or weak biotic interactions) that might contribute to ecological release.
415   Uncovering how regional and local scale patterns and processes combine to contribute to niche
416   opportunities is important for uncovering the role of biotic interactions in range expansions.
417   Given the ubiquity of LDGs, these outcomes might be common in other phytophagous insect
418   communities.
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435   **Author contributions:** KMP, DGJ, THQP developed ideas, DGJ, JK, KMP implemented field
436   protocols, DGJ analyzed data with input from KMP, JMR performed habitat analysis, DGJ,
437   KMP, JK wrote manuscript with input from all authors.
438

439   **Data and code available: https://doi.org/10.6084/m9.figshare.18737834.v1**
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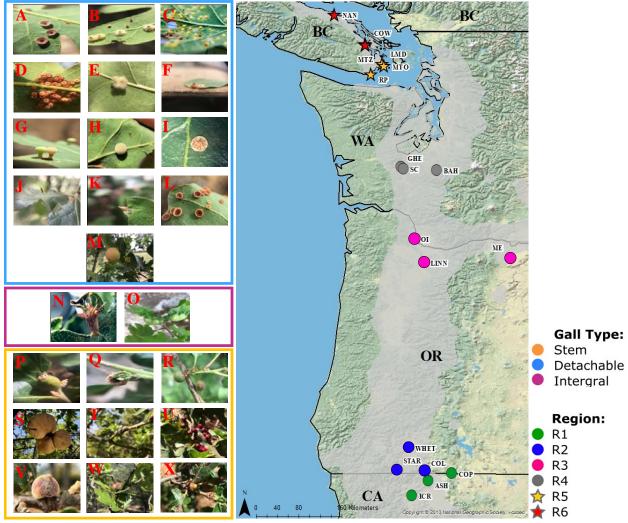611   gradient revealed by meta□analysis. Ecology Letters, 24(11), 2506-2520.

Table and Figure captions

Table 1: Slopes for best fit models after Akaike information criterion (AICc) comparisons of the final model sets. Within parentheses are confidence intervals for slopes. Bolded slopes are significant. See AICc output in Appendix 1:Tables S6-8.

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 colored 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 colors, circles represent sites in the native range, stars expanded range (see Table S1 for site acronyms).

Figure 2: Canonical Analysis (CA) 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 Fig. 1, colored gall acronyms represent gall type guild (blue = detachable leaf, purple = integral leaf, orange = stem) (Tables S1, S2).

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 colored coded (Fig. 1). Solid black line represents predicted regression lines and 95% C.I (green dashed lines) for fixed effects (latitude) only for clarity (Table 1).

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 correlation strength (weak (0.25-0.49), moderate (0.5-0.74), and strong (0.75-1.0)). Solid lines indicate a significant correlation while dashed lines are non-significant (Spearman test). Morphotypes colored by gall type category (blue = detachable, purple = integral, orange = stem), morphotype abbreviations found in Table S2.

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. Colors represent regions (Fig. 1).
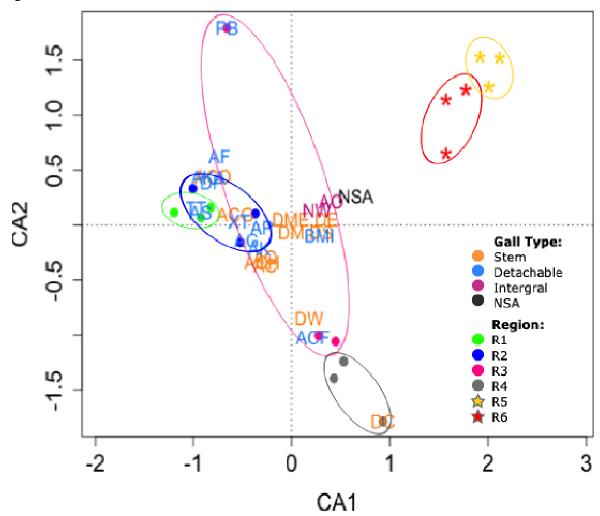
656 Table 1

Predictor variables	Cynipid morphotype richness	Cynipid community Composition (CA1)	Total gall abundance	Gall abundance excluding *N. saltatorius*	*N. saltatorius* abundance
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)**				

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Figure 1

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