Biogeographical variation in arthropod communities on coyote bush, *Baccharis pilularis*

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Abstract. 1. A classic pattern in biogeography is the decline in species richness from lower to higher latitudes. Communities, however, can also vary with other geographical patterns, such as the abiotic gradients that occur from coastal to interior habitats.

2. In this study, we surveyed arthropod communities and herbivore pressure on populations of a dominant shrub, *Baccharis pilularis*, across a 2000 km latitudinal transect to determine whether coastal versus interior location mediates arthropod responses to latitude.

3. We found that arthropod species richness and abundance declined with increasing latitude. We also found significant coastal-interior shifts in community composition and trophic structure. Specifically, predator and scavenger richness were two and three fold greater at coastal sites compared to interior sites, and were three- and six-fold more abundant on the coast than in the interior. Herbivore pressure displayed a similar pattern, with greater abundance at lower latitudes and at coastal sites.

4. Our results corroborate the general macroecological pattern that diversity declines with increasing latitude, and that coastal versus interior location can also shape community assemblages. We did not, however, find any interaction between latitude and location suggesting the effect of latitude on arthropod communities remains consistent inland compared to more constant coastal conditions.

Key words. Arthropods, coastal-interior gradients, herbivore, latitudinal gradient, predator, trophic structure.

Introduction

The latitudinal gradient in species diversity within communities is perhaps the most well-established biogeographical pattern, with species richness declining towards the poles (Fischer, 1960; Pianka, 1966; Gaston, 2000; O'Brien *et al.*, 2000; Willig *et al.*, 2003; Hillebrand, 2004;

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Qian & Ricklefs, 2008; Salazar & Marquis, 2012). With some exception, this pattern holds for the majority of plants and animals of terrestrial and marine ecosystems worldwide, and for arthropods in particular (O'Brien *et al.*, 2000; Hillebrand, 2004; Qian & Ricklefs, 2008). For example, the richness of butterflies across 514 locations in North America shows a two-fold increased from southern Canada to Mexico (Kocher & Williams, 2000). Abiotic factors, such as climate, geographic constraints, and biogeographic history have been proposed as driving factors for latitudinal gradients within communities (Wallace, 1878; Dobzhansky, 1950; MacArthur, 1972; Rapoport, 1982; Whittaker *et al.*, 2001; Hawkins *et al.*, 2003;

Hillebrand, 2004). As ectotherms, arthropods are thought to be highly sensitive to climate (Speight *et al.*, 1999; Progar & Schowalter, 2002). For example, temperature and precipitation combined explain 80% of the variation in ant species richness in mountains of Nevada – USA (Sanders *et al.*, 2003). Other studies, however, show that the latitudinal patterns persist even when accounting for sample area, climate, topographic heterogeneity, and differences between continents (Qian & Ricklefs, 2000), suggesting that biotic interactions are also important drivers of arthropod diversity across different latitudes (Schemske *et al.*, 2009).

One particular biotic interaction that can vary with latitude is the interaction between insect herbivores and their host–plants (Coley & Barone, 1996; Price *et al.*, 1998; Pennings *et al.*, 2009; Schemske *et al.*, 2009). Plant–insect interactions can be shaped by latitude in at least two ways. First, the diversity of insect herbivores can vary with distance from the poles, with declining herbivore diversity moving away from the equator (Lewinsohn *et al.*, 2005; Novotny *et al.*, 2006; Pennings *et al.*, 2009). Second, the pressure of herbivores (e.g. rates of herbivory or the density of specific herbivores) might also change with latitude and is thought to lessen towards the poles (Coley & Barone, 1996; Price *et al.*, 1998; Andrew & Hughes, 2004; Pennings *et al.*, 2009). Yet, the evidence for whether the herbivore pressure on host–plants decreases with species richness and latitude remains mixed (Andrew *et al.*, 2012). For example, Coley and Barone (1996) found that herbivore damage to plants averages 7% per year in the temperate zone, and 11% in the tropics. In addition, Fagundes and Fernandes (2011) found that richness of gall-forming insects on *Baccharis dracunculifolia* was positively correlated with latitude, while a recent meta-analysis by Moles *et al.* (2011) showed no support to the widespread view that herbivory declines with increasing latitude. Similarly, we should expect differences in other trophic groups (i.e. predators and scavengers, Pianka, 1966). The pattern may derive from a positive correlation of adjacent trophic groups, where higher diversity at basal levels results in higher diversity on the next higher trophic level (Hillebrand, 2004). What is clear is that the role of latitude in shaping trophic interactions in arthropod communities associated with host–plant deserves further exploration in additional study systems before general conclusions can be drawn.

In addition to latitude, there can be substantial variation in communities with other geographical patterns, such as the gradients that occur from coastal to interior (continental) habitats. For example, on the west coast of North America, there is a temperature and precipitation gradient when moving from the mild and fairly uniform conditions along the Pacific Ocean to more extreme and variable conditions inland (Rotenberry, 1978; Ohmann & Spies, 1998). Indeed, Progar and Schowalter (2002), found significant changes in canopy arthropod assemblages associated with a precipitation gradient in old-growth forest of Washington and Oregon. Similarly, Bairstow *et al.*

(2010) found that herbivore species richness varied with climate and plant traits in a coastal – inland gradient in eastern Australia. What is less clear is whether coastal-interior gradients interact with latitude to shape patterns of arthropod diversity or herbivore pressure. The goal of this study was to compare the influence of latitudinal and coastal-interior gradients on arthropod communities associated with *Baccharis pilularis* (coyote bush) along a ~2000 km latitudinal gradient in the western United States. Specifically, we ask whether arthropod species richness, abundance, and composition vary with latitude? Do specific trophic groups respond differentially to latitude? And do milder Pacific coastal conditions dampen arthropod responses to latitude compared to interior sites?

Methods

Baccharis pilularis De Candolle (Asteraceae, 'coyote brush') is a dominant shrub that ranges from northern Baja California to Tillamook County, Oregon - USA. While this species contains an architectural polymorphism, with a prostrate form that tends to be restricted to the coast and a more widespread erect that occurs both on the coast and in interior populations (Munz & Keck, 1973), we focused on only the erect form for this study. *B. pilularis* is also host to a diverse arthropod community (Crutsinger *et al.*, 2014), including two conspicuous stem (*Gnorimoschema baccharisella*) and leaf (*Rhopalomyia californica*) galling species (Rudgers & Whitney, 2006).

Arthropod community sampling

In 2010, we sampled the arthropods on three individuals of *B. pilularis* at 42 sites spanning from San Diego, California to Manzanita, Oregon – USA (~2000 km, Fig. 1; Table S1). Twenty-three sites were located within 300 m of the Pacific Ocean, and 19 sites were located at least 6 kilometres (range: 6–60 km) inland from the coast. Sites were selected haphazardly with the stipulation that they represented relatively undisturbed patches containing at least three individuals of *B. pilularis*. We sampled all sites within a period of 4 weeks in July to minimise phenological differences in the arthropod community and *B. pilularis* shrubs among sites. Sites were sampled beginning in the centre of the range working southward and then northward (Fig. 1).

At each site, we vacuum-sampled the entire crown of each of the three *B. pilularis* using a modified leaf blower/vacuum (Craftsman 25 cc 2-cycle) with a fine insect net attached. We also visually surveyed each plant for sedentary arthropods including leaf and stem galls. Vacuum samples were transferred to plastic storage bags and stored on ice in a cooler. In the laboratory, we sorted arthropods and identified them to species or morphospecies (Oliver & Beattie, 1993), and assigned them to a trophic level based on the feeding morphology and the literature.
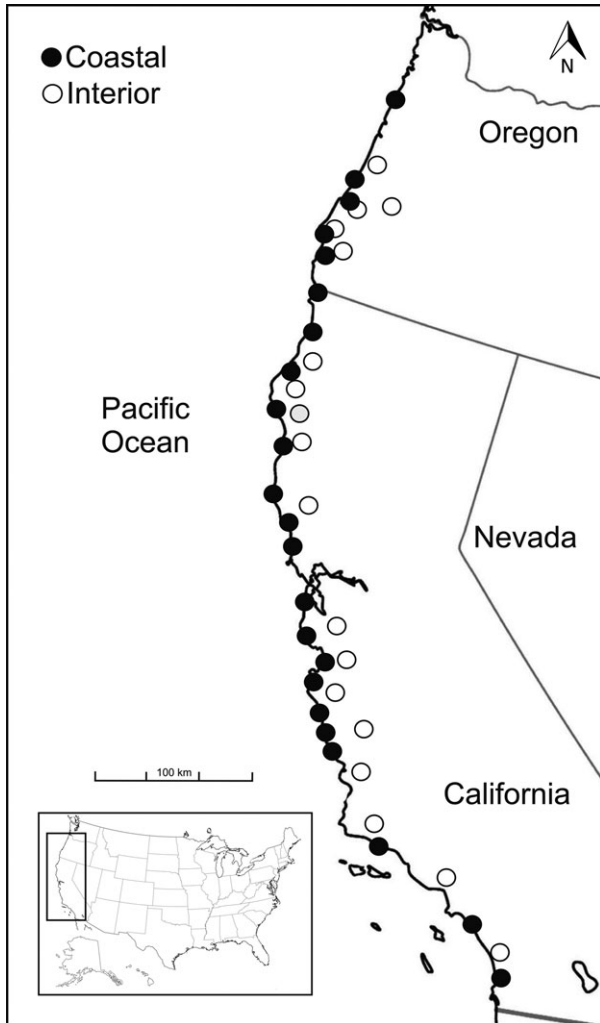
Fig. 1. Geographic distribution of the 42 *Baccharis pilularis* populations surveyed across the western United States. The sites covered a region that represents a 13° variation in latitude along a 2000 km transect, from south California to Northern Oregon.

Here, we focus on the responses of the three most abundant trophic levels (i.e. herbivores, predators, and scavengers). In total, we collected 4609 individuals of 411 species of which 75% were herbivores, 19% predators, and 6% scavengers. To control for differences in number of individuals among sites we calculated individual-based rarefaction in PRIMER V.6 (Clarke & Gorley, 2006), using the sample with the fewest numbers of individuals for the whole community or the different trophic levels.

Plant traits

We also examined a suite of *B. pilularis* traits that could vary across latitude and coastal-interior gradients and potentially account for variation in the arthropod community composition and abundance. At each site, we

measured the height (cm), basal stem diameter (mm), and the length of three leaves (mm) for each of the three shrubs. We collected several full-sized green leaves to estimate specific leaf area (SLA). Leaves were scanned with a LI-3000C Portable area meter (LI-COR Inc., Lincoln, NE, USA), oven-dried for 48 hours, and weighed. Next, we estimated leaf nutrient content by grinding over-dried leaf material to a fine powder in a ball mill (8000D Mixer/Mill, SPEX; SamplePrep, Metuchen, NJ, USA) and analysing total carbon (C) and nitrogen (N) content using a ECS 4010 elemental combustion system (Costech Analytical Technologies Inc., Valencia, CA, USA) at the University of British Columbia with Atropine (4.84% N and 70.56% C) as a reference standard. We did not examine *B. pilularis* secondary defense chemistry as part of this study.

Statistical analyses

To examine how the arthropod community varied with geography, we used separate Analysis of CoVariance (AN-COVAS) to assess effects of coastal versus interior gradients on total richness, rarefied richness, and abundance with latitude as a covariate. Latitude was treated as a fixed continuous factor and coastal-inland locations were treated as a fixed categorical factor. This was done for the entire community, as well as for each trophic group. We log-transformed each variable to meet normality assumptions. To test for the effects on predator and herbivore rarefied richness, scavenger richness, abundance, and rarefied richness we used generalised linear models (GLM) with a Poisson distribution and log-link function. We also used spline correlogram procedures computed with the 'ncf' package in R (BjØrnstad & Falck, 2001) to test for spatial autocorrelation among sites. This analysis describes the correlation between a community structure metric (e.g. species richness) at pairs of locations as a function of the geographical distance. Confidence intervals for the estimated functions were calculated using 1000 bootstrap iterations (BjØrnstad & Falck, 2001). Spatial correlograms were calculated for each community metric. We then examined shifts in community trophic structure by comparing the predator-to-herbivore richness and abundance ratios along the latitudinal gradient and across coastal to interior sites using separate ANCOVAS on logit-transformed data.

To determine how arthropod community composition varied along the latitudinal gradient and in coastal vs. interior sites, we used Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) using the Bray–Curtis dissimilarity matrix on log-transformed abundance data in PRIMER V.6. We also examined whether arthropod community turnover between paired coastal and interior sites varied with latitude. This was done by estimating both β-diversity and community similarity between pairs of coastal and inland sites. For β-diversity, local (α) diversity was estimated as the richness per site

Table 1. Results of ANCOVAS and generalised linear models (indicated with 'GLM') examining the effects of latitude and location (coastal vs. interior sites) on arthropod community structure.

Response variable	Source	d.f.	F/χ^2	P	Std beta
Arthropod richness	Model	3, 39	3.97	**0.0154**	
	Latitude		−2.74	**0.0095**	−0.40
	Location		2.09	**0.0433**	0.30
	Latitude × Location		0.22	0.8278	0.03
Arthropod abundance	Model	3, 39	3.59	**0.0229**	
	Latitude		−2.57	**0.0145**	−0.38
	Location		1.88	0.0681	0.27
	Latitude × Location		−0.49	0.6255	−0.07
Rarefied richness (GLM)	Model	3, 38	3.28	0.3505	
	Latitude		2.90	0.0885	
	Location		0.31	0.5781	
	Latitude × Location		0.30	0.5833	
Herbivore richness	Model	3, 39	3.50	**0.0252**	
	Latitude		−3.05	**0.0043**	−0.45
	Location		−0.94	0.3539	−0.13
	Latitude × Location		−0.17	0.8676	−0.02
Herbivore rarefied richness (GLM)	Model	3, 38	0.82	0.4901	
	Latitude		−1.47	0.1500	
	Location		−0.55	0.5869	
	Latitude × Location		0.27	0.7879	
Predator richness	Model	3, 39	3.00	**0.0430**	
	Latitude		−0.41	0.6826	−0.06
	Location		2.84	**0.0073**	0.42
	Latitude × Location		0.91	0.3987	0.14
Predator abundance	Model	3, 39	3.24	**0.0332**	
	Latitude		−0.38	0.7051	−0.06
	Location		2.94	**0.0057**	0.43
	Latitude × Location		1.01	0.3175	0.15
Predator rarefied richness (GLM)	Model	3, 38	4.44	0.2174	
	Latitude		2.83	0.0924	
	Location		1.48	0.2231	
	Latitude × Location		0.68	0.4079	
Predator:herbivore richness	Model	3, 36	3.10	**0.040**	
	Latitude		0.78	0.4416	0.12
	Location		2.91	**0.0064**	0. 45
	Latitude × Location		0.55	0.5867	0.08
Predator:herbivore abundance	Model	3, 34	3.84	**0.0190**	
	Latitude		1.90	0.0668	0.29
	Location		2.47	**0.0190**	0.38
	Latitude × Location		1.21	0.2337	0.19
Scavenger richness (GLM)	Model	3, 36	19.57	**0.0002**	
	Latitude		0.06	0.8081	
	Location		16.09	**< 0.0001**	
	Latitude × Location		1.46	0.2269	
Scavenger abundance (GLM)	Model	3, 36	121.83	**< 0.0001**	
	Latitude		0.40	0.5253	
	Location		109.26	**< 0.0001**	
	Latitude x Location		1.70	0.1917	
Scavenger rarefied richness (GLM)	Model	3, 38	11.57	**0.0090**	
	Latitude		0.86	0.3536	
	Location		9.06	**0.0026**	
	Latitude × Location		0.38	0.5368	

Significant *P*-values are in bold.

(pooling the species from all three shrubs within a site), while regional (γ) diversity was measured as the pooled richness from paired sites, one coastal site and the nearest inland site ($n = 19$ pairs total). β-diversity (turnover between sites) across the transect was measured as $1 - \alpha/\gamma$ (Kraft *et al.*, 2011).

We used separate ANCOVAS to assess effects of coastal versus interior gradients and latitude on plant traits. We

log-transformed leaf length and SLA to meet normality assumption. To examine which plant traits (height, stem diameter, leaf length, SLA, C:N) accounted for variation in arthropod community composition we used distance-based multivariate regression in PRIMER V.6 (DistLM, McArdle & Anderson, 2001).

Finally, to test whether herbivore pressure, measured as the density of leaf and stem galls per shrub varied with the coastal and interior latitudinal gradients, we used GLM with a Poisson distribution and log-link function. All statistical analyses were conducted using JMP Pro 10

statistical software with alpha set *a priori* as $\alpha < 0.05$ (SAS Institute, Pacific Grove, CA, USA, 2001).

Results

Across the ~2000 km transect, total arthropod richness and abundance declined with increasing latitude, with a 1.3-fold and 2.2-fold difference between the lowest and highest latitude sites (Table 1; Fig. 2). Similarly, herbivore richness declined 1.6-fold with latitude. There were no
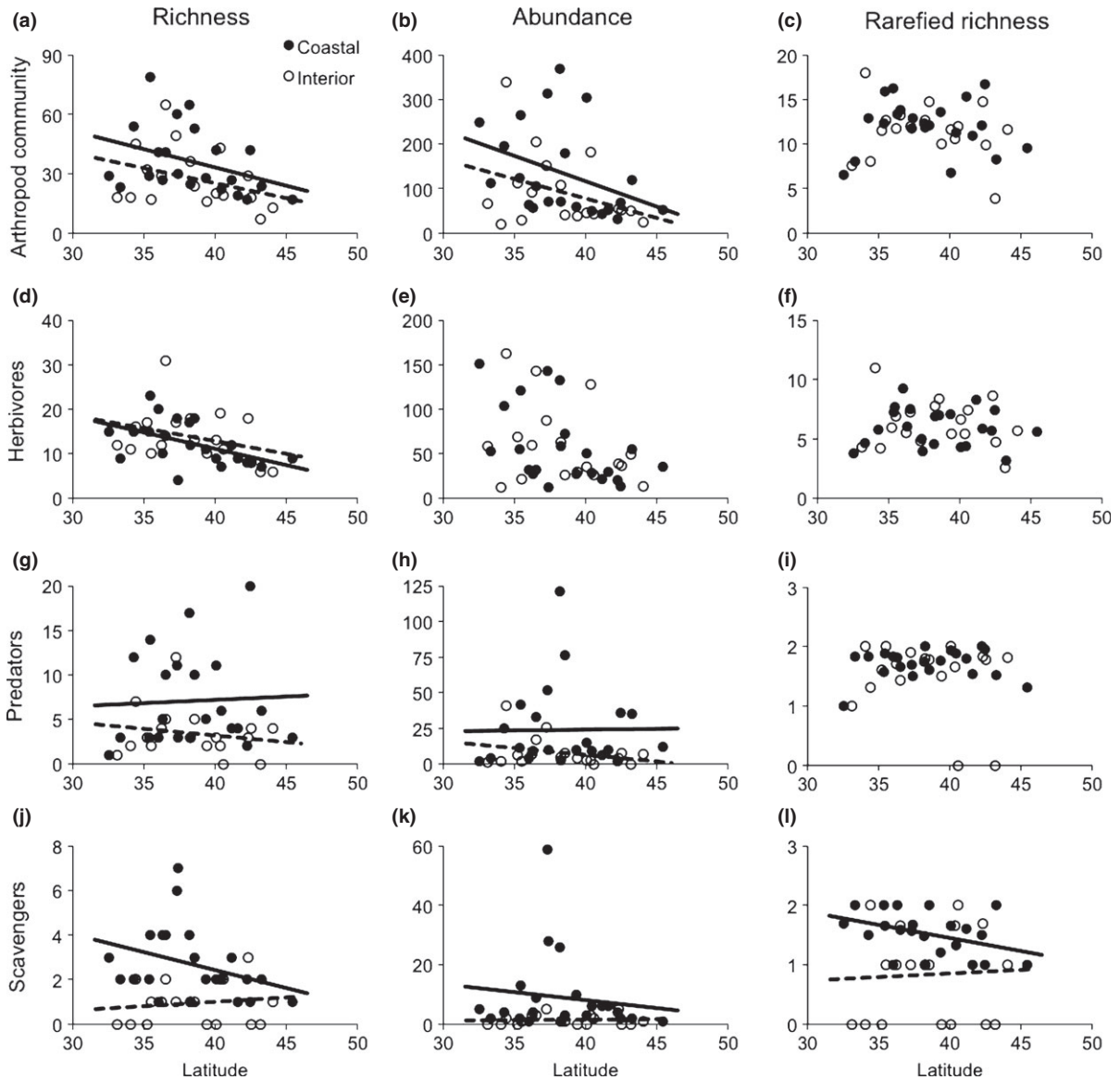
Fig. 2. Relationship between the arthropod richness (a), arthropod abundance (b), and arthropod rarefied richness (c), associated with *Baccharis pilularis* on coastal and interior sites across a latitudinal gradient. (d), (e), and (f), show results for herbivores, (g), (h), and (i) for predators, and (j), (k), and (l), for scavengers. Solid line shows significant relationship between response variable and latitude for coastal sites, and dashed line for interior sites.
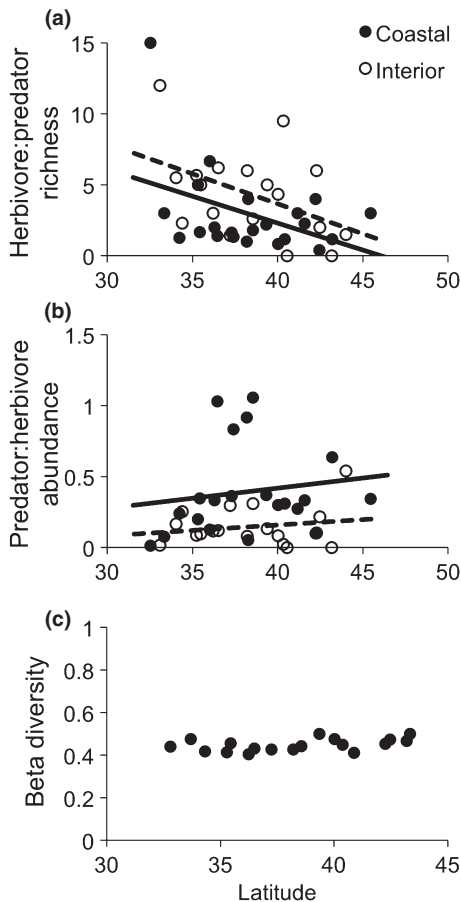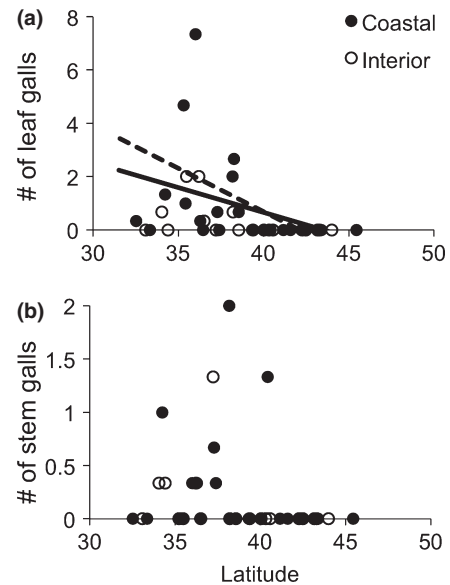
Fig. 3. Relationship of predator:herbivore richness (a), predator: herbivore abundance (b), and beta diversity (c) of arthropods associated with *Baccharis pilularis* across a latitudinal gradient in coastal and interior sites. Solid line shows significant relationship between response variable and latitude for coastal sites, and dashed line for interior sites.

Fig. 4. Relationship between the number of *Gnorimoschema baccharisella* stem galls (a) and *Rhopalomyia californica* leaf galls (b) associated with *Baccharis pilularis,* and latitude in coastal and interior sites. Solid line shows significant relationship between response variable and latitude for coastal sites, and dashed line for interior sites.

differences in total rarefied richness or herbivore abundance and rarefied richness along the latitudinal gradient. Nor did predator or scavenger richness, abundance, and rarefied richness vary with latitude (Table 1; Fig. 2). When we looked at the overall community, we found that total arthropod community composition shifted with latitude (PERMANOVA, pseudo $F = 3.73$, $P = 0.0001$). We did not, however, observe any variation in trophic structure, measured as predator-to-herbivore richness and abundance ratios with latitude (Table 1; Fig. 3).

When we explored patterns of herbivore pressure, measured as the abundance of *Gnorimoschema* stem galls and *Rhopalomyia* leaf galls on shrubs, we found that the number of leaf galls decreased by 3-fold with latitude ($\chi^2 = 21.32$, d.f. = 3, 37, $P < 0.0001$, Fig. 4) or an average of three galls per plant in southern sites compared to no galls in northern sites. Loleta, California was the most northern site in which leaf galls were observed. There was no difference in *Gnorimoschema* stem gall abundance with latitude.

In addition to the influence of latitude on community structure, we also observed that arthropod diversity and composition varied across the coastal-interior gradient. Arthropod richness was 1.3-fold greater in coastal compared to interior sites (Fig. 2). While there were no differences in total arthropod abundance and rarefied richness or herbivore richness, abundance, and rarefied richness, we found that predator richness and abundance was 2- and 3-fold higher, respectively, at coastal sites compared to interior sites (Fig. 2; Table 1). Within scavengers, there was also 3-fold and 6-fold greater richness and abundance, respectively, at coastal sites (Fig. 2; Table 1). Rarefied predator richness did not vary between coastal and interior sites, while rarified scavenger richness was 2.8-fold higher on the coast (Fig. 2; Table 1). Interestingly, the predator-prey richness and abundance ratios also varied by 2-fold between coastal and interior sites with coastal sites being more predator dominated (Table 1; Fig. 3). In addition to differences in the numbers of species and individuals, we found that arthropod community composition varied between coastal and interior sites, indicating a shift in the identities of species with distance from the Pacific Ocean (PERMANOVA, pseudo $F = 2.71$, $P = 0.0001$). Although there were differences in community composition between coastal and interior sites, the magnitude of these differences did not change with latitude. When we compared turnover between paired coast and interior localities across latitude, β-diversity did not vary ($P = 0.330$, Fig. 3).

Table 2. Results of generalised linear models examining the effects of latitude and location (coastal vs. interior sites) on gall abundance.

Response variable	Source	d.f.	X^2	P
No. leaf galls	Model	3, 37	21.32	**< 0.0001**
	Latitude		11.63	**0.0006**
	Location		4.06	**0.0439**
	Latitude × Location		0.15	0.6951
No. stem galls	Model	3, 38	7.50	0.4111
	Latitude		4.04	0.1761
	Location		0.34	0.2353
	Latitude × Location		0.02	0.5318

Significant *P*-values are in bold.

Herbivore pressure also changed between coastal-interior locations. Leaf gall abundance was higher on the coast, with 3-fold more *Rhopalomyia* rosette galls compared to interior sites ($\chi^2 = 4.06$, d.f. = 3, 37, $P = 0.0439$). The abundance of *Gnorimoschema* stem galls did not differ between locations (Table 2; Fig. 4). We found no significant interactions between latitude and location (coastal vs. interior) for any of the arthropod community variables, suggesting that the influence of latitude is similar on the coast as it was in interior habitats (Tables 1 and 2).

Furthermore, the spatial correlograms (Figure S1) carried out on the arthropod community showed low and non-significant spatial autocorrelation values for each of the community metrics (abundance, richness, and rarefied richness).

When we explored potential *B. pilularis* traits that might account for arthropod patterns, we found a variety of plant traits that changed with latitude and location. For example, leaf length increased by 1.4-fold with increasing latitude ($F = 7.96$, d.f. = 3, 41, $P < 0.0001$; Table 3; Fig. 5), while the C:N content in leaves declined by 0.9-fold ($F = -2.57$, d.f. = 3, 41, $P = 0.0144$). In contrast, plant height and SLA were ~1.2-fold greater in inland sites than coastal sites ($F = -2.40$, d.f. = 3, 41, $P = 0.0214$ and $F = -3.40$, d.f. = 3, 41, $P = 0.0016$ respectively). Plant height showed a significant interaction between latitude and location, increasing with latitude in coastal sites, but declining with latitude in interior habitats ($F = 2.69$, d.f. = 3, 41, $P = 0.0106$, Fig. 5). *Baccharis pilularis* plant height and leaf length best explained shifts in community composition, but accounted for only 10.3% of arthropod composition variation across all sites (Dist-LM pseudo $F = 1.42$, $P = 0.0462$, and pseudo $F = 2.35$, $P = 0.0001$, respectively).

Discussion

Our results indicate that arthropod diversity associated with *B. pilularis* displays the classic latitudinal pattern of

Table 3. Results of ANCOVAS examining the effects of location (coastal vs. interior sites) and latitude on plant traits.

Response variable	Source	d.f.	F	P	Std beta
Plant height (m)	Model	3, 41	4.34	0.0100	
	Latitude		−0.09	0.9320	−0.01
	Location		−2.40	0.0214	−0.34
	Latitude × Location		2.69	0.0106	0.37
Stem diameter (mm)	Model	3, 41	1.11	0.3583	
	Latitude		1.54	0.1329	0.24
	Location		0.97	0.3402	0.15
	Latitude × Location		0.03	0.9763	0.01
Leaf length (mm)	Model	3, 41	22.36	**< 0.0001**	
	Latitude		7.96	**< 0.0001**	0.78
	Location		−1.86	0.0708	−0.18
	Latitude × Location		−0.43	0.6731	−0.04
SLA	Model	3, 41	5.54	**0.0030**	
	Latitude		1.19	0.2430	0.16
	Location		−3.40	**0.0016**	−0.46
	Latitude × Location		1.77	0.0850	0.24
C:N	Model	3, 41	3.08	**0.0390**	
	Latitude		−2.57	**0.0144**	−0.37
	Location		−1.61	0.1158	−0.23
	Latitude × Location		0.58	0.5656	0.08

Significant *P*-values are in bold.

decreasing richness with increasing latitude, as well as coastal-interior shifts in community composition and trophic structure. In particular, predators and scavengers were more diverse and abundant in coastal than interior habitats. Except for plant height, we found no interaction between latitude and coastal-interior sites. These findings suggest that latitudinal patterns in arthropods were not mediated by coastal-interior differences but were independently affected by both geographic gradients.

Our latitudinal results were consistent with other studies of arthropod diversity associated with single plant species. For example, Andrew and Hughes (2004) found that phytophagous beetle species richness associated with *Acacia falcata* declined with latitude in southeastern Australia. Similarly, Novotny *et al.* (2006) found more species of insect herbivores in tropical forests of Papua New Guinea compared to temperate forests of Central Europe. Our results, however, also showed community shifts between coastal and interior sites, particularly for predators and scavengers. It was surprisingly difficult to find other studies that compared arthropod communities between coastal-interior areas. There are, however, a substantial number of studies looking at temperature and precipitation, two key factors that vary with distance from the coast, and which support that arthropods respond strongly to abiotic conditions (Speight *et al.*, 1999; Progar & Schowalter, 2002; Sanders *et al.*, 2003).
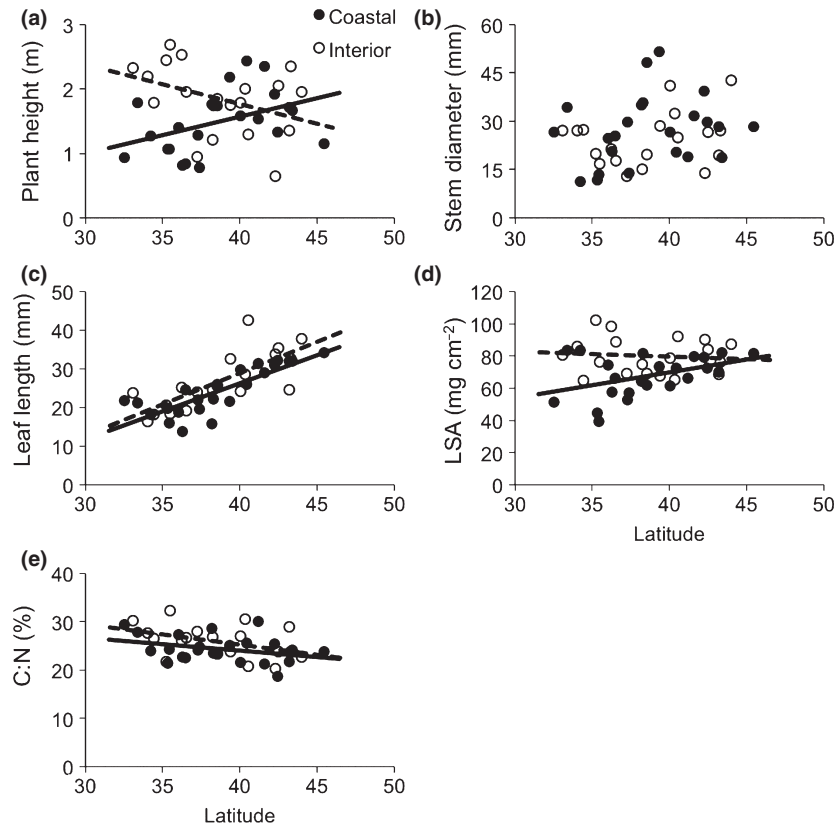
Fig. 5. Relationship between *Baccharis pilularis* traits; plant height (a), basal stem diameter (b), leaf length (c), SLA (d), and C:N (e) with latitude in coastal and interior sites. Solid line shows significant relationship between response variable and latitude for coastal sites, and dashed line for interior sites.

Differences in scavengers and predator richness and abundance between coastal and interior localities resulted in a different trophic structure of communities, with 0.5 predator species per herbivore species on the coast compared to 0.25 in interior sites. Similarly, there were 0.4 predator individuals per herbivore in coastal sites compared to only 0.15 predators per herbivore in interior sites. Prior studies have focused on the influence of latitude rather than coastal-interior gradients, and found higher proportion of predators with decreasing latitude (Pianka, 1966) and greater predation rates at low latitude (Schemske *et al.*, 2009). While we did not specifically examine predation rates in our study, the potential for increased predation associated with *Baccharis* shrubs in coastal sites deserves further attention.

Interestingly, only scavenger rarefied richness matched observed richness patterns, while total arthropod, herbivore, and predator rarefied richness did not show any significant relationship with latitude, location, or their interaction. This result suggest that both latitudinal and coastal-interior patterns may be driven primarily by the differences in the abundance of the individuals sampled along the transect. Certainly, we found higher numbers of total arthropods, herbivores, and predators in more

southern locations along the latitudinal gradient. Though we did not measure host–plant density at all our sites, there tended to be large patches of *B. pilularis* at these localities (MNBG personal observation), which would reinforce the 'More Individuals Hypothesis' (Srivastava & Lawton, 1998), which states that more individuals, and thus species, are supported at more productive sites.

Species turnover (β-diversity) was higher between coastal and interior habitats, with an average of 45% turnover in community composition. The magnitude of this turnover, however, remained constant across the latitudinal gradient despite changes in biotic (plant traits) and abiotic conditions. This result was surprising given that previous studies reported a pattern of increasing β-diversity with decreasing latitude (Harrison *et al.*, 1992; Stevens & Willig, 2002; Qian & Ricklefs, 2007). Nevertheless, a recent study by Kraft *et al.* (2011) demonstrated that this pattern can be driven by differences in the regional species pool, which, after correcting for, results in a consistent β-diversity across latitudinal gradients.

We found that herbivore pressure, measured as the gall density per shrub, was higher in lower latitudes. Other studies have tested for latitudinal variation in herbivore pressure within individual plant species or plant

communities. For example, Fagundes and Fernandes (2011) reported that species richness of gall-forming insects on *B. dracunculifolia* was positively correlated with latitude. In contrast, Pennings *et al.* (2009) found that gall-making herbivores in salt marshes (*Iva frutescens*) were 10 times more abundant at low-latitude sites than at high-latitude sites. Yet, another study by Crutsinger *et al.* (2013) showed that gall abundances associated with goldenrod (*Solidago altissima*) peaked at mid-latitudes. Such mixed results suggest that the effects of latitude on herbivore pressure may be species specific and likely depend on the factors governing susceptibility of a particular host–plant species or the range of a particular herbivore.

We examined several plant traits that were related to the productivity and nutrient content of *B. pilularis* that might account for differences in arthropod communities. Leaves were smaller and less nutritious in southern compared to northern latitudes. Shrubs were also shorter, but only on the coast. Shrubs in interior sites were taller and height declined with increasing latitude. One hypothesis is that height differences might be influenced by a combination of moisture for coastal shrubs and temperature for interior shrubs. Precipitation increases on the Pacific coast as we move northward (Dettinger *et al.*, 1998), resulting in an increase in the size of coastal shrubs, while temperatures inland become colder during the winter season and hotter during summer season, which limits the growing season of interior plants (Whittaker, 1960).

Numerous studies have examined how plant traits vary with latitude (see Reich & Oleksyn, 2004; other global datasets). In general, tropical plants tend to have tougher leaves of lower nutritional quality with a higher concentration of condensed tannins than do temperate plants (Coley & Aide, 1991). Although plant traits varied with both latitude and between coastal-inland sites, these traits accounted for a relatively small proportion of variation in arthropod community composition. We acknowledge that other plant traits, such as secondary defenses, or biotic interactions, such as pathogens, that we did not measure in this study, may account for the remaining variation in the diversity and composition of arthropods in this system. In addition, abiotic factors have strong effects on arthropods (Speight *et al.*, 1999; Progar & Schowalter, 2002), and were likely the pre-dominant force structuring arthropod communities associated with *B. pilularis* across latitude and coastal and interior sites.

Conclusions

Taken together, our results suggest that different geographic gradients, including latitude and coastal-interior gradients, are key factors shaping arthropod communities associated with hostplants. We found support for the classic latitudinal pattern of decreasing richness with increasing latitude, but did not find that mild coastal conditions dampen the effects of latitude on arthropods compared to the more variable conditions of inland sites. We also observed significant differences in the diversity, composition, and trophic structure of arthropod communities between coastal and interior sites that were independent of latitude. Given the lack of broad scale geographic comparisons, we encourage more studies to examine the relative effects of multiple geographic gradients for other plant–insect study systems.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12086:

Table S1. Study sites, location, and GPS coordinates

Figure S1. The spatial covariance functions estimated from latitudinal data from arthropods associated to *Baccharis pilularis*. The upper and lower dashed lines represent the 95% bootstrap confidence intervals. (A) Total richness, (B) Total abundance, (C) Total rarefied richness, (D) Herbivore richness, (E) Herbivore abundance, (F) Herbivore rarefied richness, (G) Predator richness, (H) Predator abundance, (I) Predator rarefied richness, (J) Scavenger richness, (K) Scavenger abundance, and (L) Scavenger rarefied richness.

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