



Cryptic elevational zonation in trapdoor spiders (Araneae, Antrodiaetidae, *Aliatypus janus* complex) from the California southern Sierra Nevada

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ABSTRACT

The relative roles of ecological niche conservatism versus niche divergence in promoting montane speciation remains an important topic in biogeography. Here, our aim was to test whether lineage diversification in a species complex of trapdoor spiders corresponds with riverine barriers or with an ecological gradient associated with elevational tiering. *Aliatypus janus* was sampled from throughout its range, with emphasis on populations in the southern Sierra Nevada Mountains of California. We collected multi-locus genetic data to generate a species tree for *A. janus* and its close relatives. Coalescent based hypothesis tests were conducted to determine if genetic breaks within *A. janus* conform to riverine barriers. Ecological niche models (ENM) under current and Last Glacial Maximum (LGM) conditions were generated and hypothesis tests of niche conservatism and divergence were performed. Coalescent analyses reveal deeply divergent genetic lineages within *A. janus*, likely corresponding to cryptic species. Two primary lineages meet along an elevational gradient on the western slopes of the southern Sierra Nevada Mountains. ENMs under both current and LGM conditions indicate that these groups occupy largely non-overlapping niches. ENM hypothesis testing rejected niche identity between the two groups, and supported a sharp ecological gradient occurring where the groups meet. However, the niche similarity test indicated that the two groups may not inhabit different background niches. The Sierra Nevada Mountains provide a natural laboratory for simultaneously testing ecological niche divergence and conservatism and their role in speciation across a diverse range of taxa. *Aliatypus janus* represents a species complex with cryptic lineages that may have diverged due to parapatric speciation along an ecological gradient, or been maintained by the evolution of ecological niche differences following allopatric speciation.

1. Introduction

Mountainous regions are hotspots for population divergence, speciation, and high species richness (e.g., Moritz et al., 2000; Garrick, 2011; Fjeldsø et al., 2012). Although many mechanisms of montane divergence are possible, two contrasting models predominate in both the theoretical and empirical literature (Hua and Wiens, 2013). One model invokes niche conservatism, where taxa adapted to mountainous habitats are unable to exist in lowland habitats. These low elevation habitats thus represent dispersal barriers, which combined with montane ecological niche conservatism across time and space, promotes divergence and speciation (Moritz et al., 2000; Wiens, 2004). Under an alternative niche divergence model, elevational gradients implicit with montane habitats give rise to differences in abiotic and biotic selective pressures, with disruptive selection along these selective gradients

driving *in situ* parapatric or ecological speciation (Endler, 1977; Doebeli and Dieckmann, 2003). Many empirical studies have contrasted these different mechanisms either in a single lineage (Patton and Smith, 1992; Hall, 2005; Schmitz et al., 2008; Guarnizo et al., 2009; Kozak and Wiens, 2010; Leaché et al., 2010; McCormack et al., 2010; Fuchs et al., 2011), or for multiple taxa living in different geographic regions (Kozak and Wiens, 2007; Hua and Wiens, 2010; Cadena et al., 2012).

The California Sierra Nevada (SN) mountain range includes the highest elevations (to 4421 m), and is one of the longest geographically contiguous ranges in the continental United States. Uplift has resulted in very steep elevational gradients on the eastern edge of the range, with more gentle grades on western slopes (see Moritz et al., 2008; Leaché et al., 2010). The largest rivers in the region flow from eastern high elevations to the western Central Valley; southern SN examples include the San Joaquin, Kings, and Kaweah Rivers, all with deeply

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incised canyons. For low elevation taxa, higher elevations that separate drainage basins might represent barriers, while for high elevation taxa the canyons themselves potentially represent repeated north – south barriers. Many modern (explicitly phylogenetic) biogeographic studies have been conducted in the SN, and lineage divergence associated with riverine barriers has been found in several taxa, particularly in the southern SN (Matocq, 2002; Kuchta and Tan, 2006; Rovito, 2010; Schoville and Roderick, 2010; Schoville et al., 2012). Leaché et al. (2010) explicitly tested a niche divergence model in southern SN *Sceloporus* lizards, and found support for both riverine barriers and elevational selection.

The spider genus *Aliatypus* includes fourteen described species (Coyle, 1974; Hedin and Carlson, 2011; Satler et al., 2013), twelve of which are restricted to California. *Aliatypus* are stocky, medium-sized (6–20 mm) subterranean spiders that cover silk-lined burrows with a wafer-like trapdoor. These spiders are generally highly dispersal-limited with strong preferences for cool, moist microhabitats (e.g., north-facing ravines, shaded roadcuts), and prior genetic studies have revealed geographically localized population genetic structuring and evidence for cryptic speciation (Hedin and Carlson, 2011; Satler et al., 2011, 2013). This study focuses on *Aliatypus janus*, which is phylogenetically allied with members of the *A. californicus* group, a clade also including *A. californicus*, *A. gnomus* and *A. isolatus* (Coyle, 1974; Satler et al., 2011). While most *Aliatypus* species occupy mid-elevation upland habitats and have relatively small geographic distributions (Coyle, 1974; Coyle and Icenogle, 1994), *A. janus* has an atypically large geographic distribution – populations occur in Coast Range xeric canyons (e.g., western edge of the Central Valley), to upper montane forests near the crest of the southern SN (above 2400 m), to lower xeric habitats in eastern California and western Nevada (Fig. 1). The molecular phylogenetic research of Satler et al. (2011) revealed multiple deeply divergent genetic lineages within *A. janus*, and hinted that this taxon might represent a species complex.

The *A. janus* complex represents an intriguing system in which to study the relative roles of niche conservatism versus niche divergence. Climatic zonation speciation depends upon a balance between selection and gene flow, and might be more common in dispersal-limited taxa (Cadena et al., 2012); available data suggest that gene flow is highly restricted in *A. janus* (Satler et al., 2011). The species range spans severe elevational gradients on both sides of the SN, although specimens are sparse and challenging to collect east of the range crest. In the western foothills of the southern SN specimens are readily collected, and both low and high elevation populations occupy most of the region (Fig. 1). These paired populations are separated by multiple large rivers (see above), setting up a natural design where the contrasting roles of niche divergence and conservatism can be studied (similar to Leaché et al., 2010). As in any natural system, potentially important variables are not perfectly isolated – there are expected south to north selective differences, and some east to west dispersal barriers are possible. However, most prior regional studies emphasize selective gradients on an elevational (longitudinal) axis, and dispersal barriers on a latitudinal axis (Moritz et al., 2008; Leaché et al., 2010).

Despite the apparent selective gradient encountered by *A. janus*, finding ecologically-mediated divergence in this taxon would be surprising. Most *Aliatypus* species occupy exclusive allopatric geographic distributions, and all taxa show a general preference for similar microhabitats. Species syntopy is restricted to distant phylogenetic relatives (Coyle and Icenogle, 1994; Satler et al., 2011), consistent with a non-adaptive radiation dominated by geographic isolation and ecological niche conservatism. Also, because these spiders live underground, above-ground environmental differences across habitats might be buffered (Bond and Stockman, 2008). Although most other studies of mygalomorph trapdoor spiders support a “niche conservatism plus vicariance” model (Bond et al., 2001; Hedin et al., 2013; Hedin et al., 2015; Leavitt et al., 2015; Harvey et al., 2015), some studies have explicitly tested for ecological divergence in mygalomorphs (Bond and

Stockman, 2008; Beavis et al., 2011).

Here we reconstruct the phylogeographic history of the *A. janus* complex (plus close outgroups) using a mitochondrial COI and nuclear 28S sample of over 170 specimens from 102 geographic locations. Based on congruent recovery of multiple geographic clades for these gene regions, we gathered DNA sequences for six additional nuclear genes for a subsample of specimens, placing emphasis on paired low versus high elevation populations from the western slopes of the southern SN. Using this multigenic nuclear dataset we conduct multi-species coalescent analyses to explicitly test alternative riverine versus elevational gradient divergence hypotheses. Our results support an elevational gradient hypothesis, which is further supported by ecological niche modeling and various tests for niche overlap and similarity. Overall, this research is novel in providing evidence for cryptic, ecologically-mediated divergence in the southern SN, in a taxonomic group otherwise dominated by divergence via niche conservatism.

2. Materials and methods

2.1. Specimen and genetic sampling

We sampled all members of the *A. californicus* group (defined above), with an emphasis on *A. janus* (Fig. 1, Appendix A in supplementary materials). Both leg tissues (preserved in 100% EtOH) and voucher specimens (in 80% EtOH) are housed in the San Diego State Terrestrial Arthropod Collection. Genomic DNA was extracted from leg tissue using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) following the manufacturer's protocol. Sequence data were obtained from 1–2 individuals from most localities for mitochondrial gene cytochrome c oxidase subunit I (COI) and nuclear ribosomal 28S. PCR conditions are detailed in Appendix B in supplementary materials. Six custom nuclear genes (Table 1) were sequenced for a subsample of 46 specimens. Primers for nuclear genes were designed based on comparative *Aliatypus* transcriptomics (Appendix B).

PCR products were purified using Montage columns or filter plates (Millipore) and sequenced in both directions by the University of California, Riverside IIGB Facility or MacroGen USA using amplification primers. Sequences were edited in Sequencher (Gene Codes Corp.) or Geneious Pro 6 (Kearse et al., 2012) and aligned using MAFFT (Katoh and Standley, 2013). For 28S, Gblocks (Castresana, 2000) was run under default conditions in Mesquite v3.04 (Maddison and Maddison, 2015) to remove ambiguously aligned regions. For heterozygous nuclear sequences, SeqPHASE (Flot, 2010) and PHASE v2.1.1 (Stephens et al., 2001; Stephens and Scheet, 2005) were used to bioinformatically infer alleles.

2.2. Gene trees and species trees

Individual gene trees were reconstructed with BEAST v1.8.1 (Drummond et al., 2012). Analyses were run with a lognormal relaxed molecular clock, a birth-death incomplete sampling tree prior, and sequence models determined by jModelTest 2 (Guindon and Gascuel, 2003; Darriba et al., 2012). The COI dataset was partitioned by codon position, while the less-variable nuclear datasets were not partitioned. Analyses were run for 100,000,000 generations with data stored every 10,000 generations. Log files were visualized in Tracer v1.6 (Rambaut et al., 2014). Initial analyses run with GTR sequence models failed to reach stationarity, and thus HKY models were applied with the other model parameters as determined by jModelTest 2. Maximum clade credibility trees were produced with TreeAnnotator v2.3.1 (Bouckaert et al., 2014) using mean heights for nodes and 10% burnin. Mean K2P distances were calculated for each unphased locus in Molecular Evolutionary Genetic Analysis (MEGA) v7.0 (Kumar et al., 2016).

A species tree was generated with *BEAST v1.8.1 with the individuals from the reduced nuclear gene sample (six custom + 28S data) treated as OTUs. Analyses were run with a lognormal



Fig. 1. Geographic distribution of sampled populations. Site acronyms correspond to those in Appendix A. Colors and clade names follow phylogenetic results (e.g., Figs. 2 and 3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Genetic sampling and matrix information. Gene names are based on top BLAST hit. COI is partitioned by codon position (pos).

Gene name	<i>Ixodes scapularis</i> homolog	Matrix % complete	Aligned length	Model of evolution
39S ribosomal protein L44, putative	ISCW001813	96	786	HKY + I + G
Ribonuclease P/MRP protein subunit POP5, putative	ISCW006802	100	471	GTR + G
Tartan protein, putative	ISCW021508	83	673	GTR
Sdcccag1 protein, putative	ISCW000677	98	951	HKY + G
Sushi, von Willebrand factor type A, EGF and pentraxin domain-containing protein 1, putative	ISCW006800	87	544	K80 + G
Ribosome biogenesis protein, putative	ISCW013536	100	1035	HKY + I + G
28S ribosomal rRNA	–	–	969	GTR + I + G
COI pos 1	–	–	957	GTR + I + G
COI pos 2	–	–	–	GTR + I
COI pos 3	–	–	–	GTR + I + G

relaxed molecular clock with the rate for 39S ribosomal protein L44 gene set to 1 and all others estimated. Priors for species tree and population size were set to birth-death and piecewise linear and constant root, respectively. The lognormal prior was used for species.popMean, species.birthDeath.meanGrowthRate, and species.birthDeath.relativeDeathRate. Sequence models followed individual gene tree analyses. Analyses were run for 250,000,000 generations with data stored every 25,000 generations. Analyses were run twice and log and tree files were combined in LogCombiner v2.3.1 (Bouckaert et al., 2014) with 10% burnin. Maximum clade credibility trees were produced with TreeAnnotator.

2.3. Riverine barrier hypothesis testing

Bayes Factor Delimitation (BFD, Grummer et al., 2014) was used to distinguish between alternative elevational zonation versus riverine barriers models, focusing specifically on patterns of species tree divergence in the southern SN. Here we contrasted an “unconstrained” null hypothesis (all individuals treated as OTUs) to an alternative hypothesis in which southern SN *A. janus* individuals were assigned to lineages following major river boundaries (see Results 3.3). Analyses were conducted using the reduced nuclear dataset, with *BEAST parameter settings as above. The Marginal Likelihood Estimate (MLE) was generated based on path sampling (Lartillot and Philippe, 2006) and stepping stone (Xie et al., 2011) methods with a chain length of 100,000 generations and pathSteps set at 100. The average MLEs from repeated analyses were used to calculate BFs. BF was determined by $2 * (-\ln_{\text{HypA}} - -\ln_{\text{HypB}})$, with values greater than 10 indicating decisive support for a hypothesis (Kass and Raftery, 1995).

2.4. Ecological niche modeling

Ecological niche modeling (ENM) was performed to predict current and historical distribution limits. For prediction of current distribution limits, climate data from the years 1950–2000 for 19 bioclimatic variables at 30 arc-second resolution were obtained for tiles 11 and 12 from WorldClim v1.4 (Hijmans et al., 2005; <http://www.worldclim.org/tiles.php>). Climate data from the tiles were combined into layers and converted to a raster stack using the ‘rgdal’ (Bivand et al., 2015) and ‘raster’ (Hijmans, 2015) packages in R v3.2.3 (R Core Team, 2015). The raster stack was cropped to the relevant area (northern border of CA to the southeastern border of AZ). To predict distributions during the Last Glacial Maximum (LGM; approx. 21,000 years ago), bioclimatic variables were obtained from the Community Climate System Model 4 (CCSM4; <http://www.worldclim.org/paleo-climate>) at 2.5 arc-minutes resolution.

The software ENMTools v1.3 (Warren et al., 2010) was used to find correlations among current climate data variables. Highly correlated variables ($r > 0.9$) were removed following Jezkova et al. (2011), resulting in ten variables used in generating current and LGM ENMs (BIO1-4, 8, 9, 12, 15, 17, 18). ENMs were estimated using Maxent v3.3.3k (Phillips et al., 2006) with 25% of samples randomly selected for testing, ten replicates with subsampling, and otherwise default settings, for two well-supported groups identified in species tree analyses (Western and Eastern, see Results). The mean and standard deviation for the area under receiver operating curve (AUC) for testing and training datasets were compared to assess model quality. Individuals not sampled in the species tree analyses were assigned to the two groups based on their placement in the COI and 28S gene trees. The ENM was not estimated for the ‘Yosemite’ clade due to small sample size (three localities) and the uncertain phylogenetic placement of this group. Occurrence records were based on GPS coordinates from prior publications (Coyle, 1974; Hendrixson and Bond, 2005; Satler et al., 2011), and this study (using a hand-held GPS or from Google Earth ©).

Maxent ASCII results were converted to binary presence/absence maps through ArcGIS Desktop v10.3 (ESRI) using the 10% minimum

training logistic threshold. Regions of overlap were estimated by adding binary maps together (Western versus Eastern for current and LGM predictions; Current versus LGM for both Western and Eastern) using the Raster Calculator in the Spatial Analyst toolbox.

2.5. Ecological niche hypothesis tests

For statistical comparison of Western and Eastern group predicted ENMs, we conducted analyses of niche overlap, niche identity, niche similarity, and linear and blob range-breaking tests in ENMTools (Warren et al., 2008, 2010; Glor and Warren, 2011). Niche overlap was determined by comparing habitat suitability values for each grid cell estimated from the Maxent ENMs (Warren et al., 2008, 2010). Values for two measurements of overlap were calculated, Schoener’s *D* (Schoener, 1968) and *I* (Warren et al., 2008), which range from 0 (no overlap) to 1 (complete overlap).

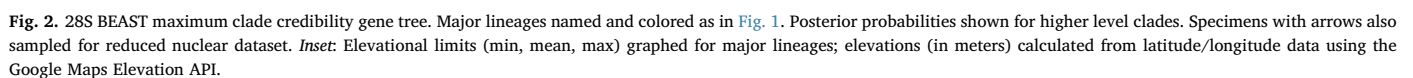
To test if Eastern and Western groups exhibit niche conservatism, we conducted the niche identity test (Warren et al., 2008, 2010). One hundred pseudoreplicates were used to generate a null distribution of niche overlap, compared to the observed overlap value using a one-tailed test. Because the niche identity test represents a very strict comparison for assessing ecological conservatism (Warren et al., 2008), we also performed the niche similarity (i.e., background) test. The test distributions for each group were generated based on minimum area polygons from occurrence points in ArcMap (ESRI), and occurrence points were tested against random points from within the distribution of the other group. Because both groups have distributions interrupted by large regions of inhospitable habitat (San Joaquin Valley for Western, Mojave and Sonoran deserts for Eastern; Fig. 1), multiple polygons were generated for each group to exclude these regions. For the Western group, polygons were generated for the Coast Range and Sierran foothill localities, and 200 random data points per occurrence point were obtained from each polygon (10,200 total random points). For the Eastern group, random data points were obtained from four polygons in proportion to the number of occurrence points used to make the polygons (200 random points/occurrence for 5200 total random points). The four polygons consisted of a minimum area polygon from occurrence points in the SN, and three polygons based on single pixel buffers surrounding Arizona sky island localities for *A. isolatus*. One hundred pseudoreplicates were used to generate null distributions of niche similarity, compared to the observed overlap value using a two-tailed test. An observed niche overlap value greater or less than the null distributions indicate niche conservation or divergence, respectively (Warren et al., 2008; McCormack et al., 2010).

We tested for an abrupt environmental gradient between Western and Eastern groups using the linear and blob range-break tests (Glor and Warren, 2011). For each test, one hundred pseudoreplicates were used to generate a null distribution. Identical partitions were removed to avoid non-independence, and the reduced null distribution was compared to the observed overlap value using a one-tailed test. Histograms for all hypothesis tests were generated using the ‘ggplot2’ v2.1.0 (Wickham, 2009) package in R.

3. Results

3.1. Data availability

The full genetic sample consisted of 171 specimens from 102 distinct geographic locations, including a sample of 129 *A. janus* specimens (Fig. 1, Appendix A). Original COI and 28S data were generated for most specimens, with some published COI and 28S data (Hendrixson and Bond, 2005; Satler et al., 2011) downloaded from GenBank. Sequence data for six custom nuclear genes was generated for 46 specimens. Unphased DNA sequences have been submitted to GenBank (Appendix A); phased matrices are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.dq28j>.



The 28S gene tree, rooted using BEAST relaxed clock model, reveals several well-supported geographic lineages (Fig. 2). In addition to a distinct *A. californicus* + *A. gnomus* lineage, multiple 28S lineages are

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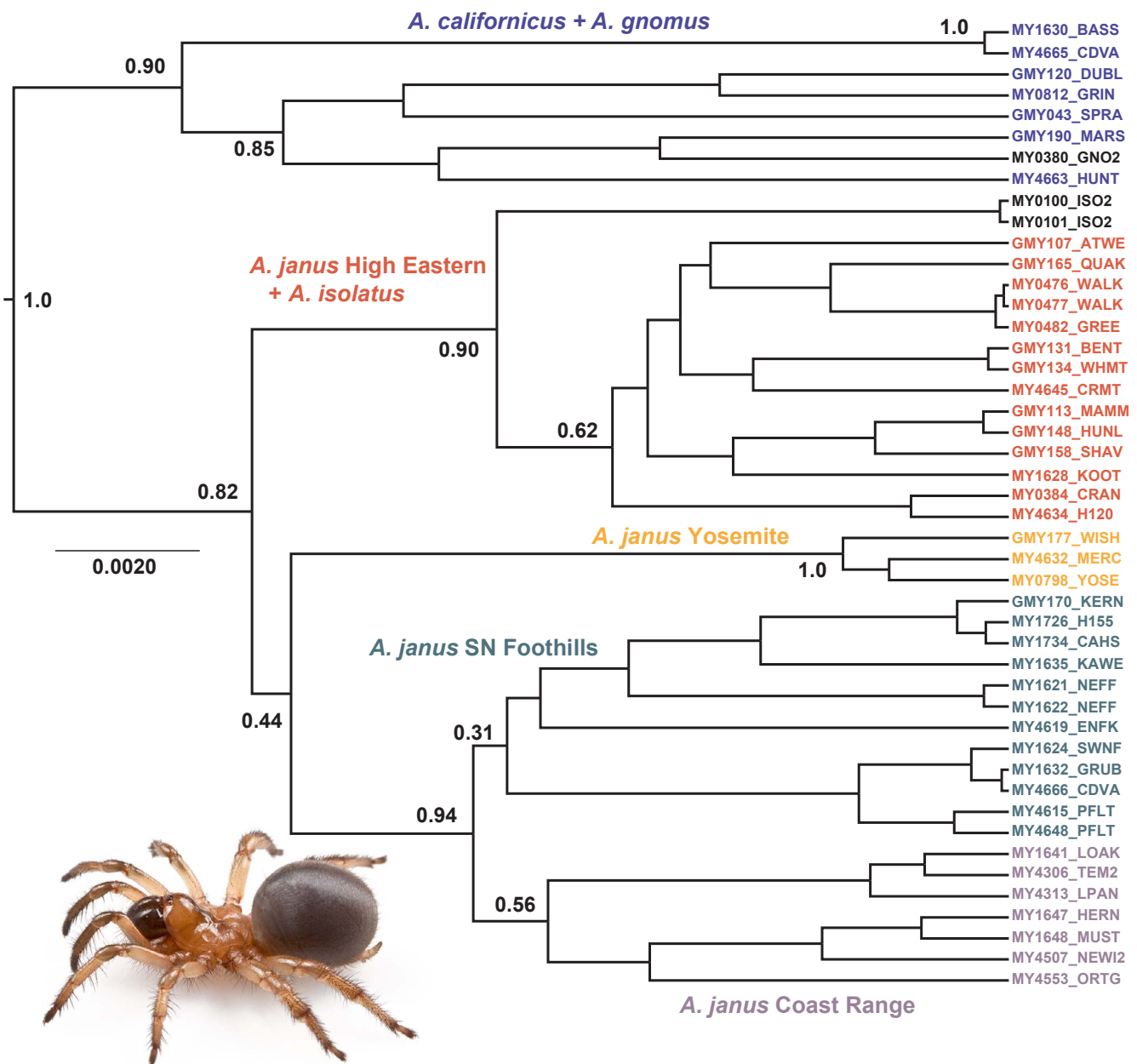


Fig. 3. All nuclear data *BEAST maximum clade credibility species tree. Major lineages named and colored as in Figs. 1 and 2. Posterior probabilities shown for higher level clades. Inset: adult female *A. janus*, San Luis Obispo County, Temblor Range.

populations (Figs. 1 and 2). For the COI tree, root placement and lineage interrelationships differ from the 28S tree, but major recovered lineages are similar (Appendix C). We discovered sympatry of divergent 28S and COI lineages at two geographic locations – we found *A. californicus* and SNF *A. janus* in sympatry in Madera County (CDVA), and HE and SNF *A. janus* in near sympatry in Kern County (GREE and H155 sites within one kilometer). This sympatry is the first ever recorded between congeners within the *A. californicus* species group (see Coyle and Icenogle, 1994; Satler et al., 2011).

A nuclear-only matrix (28S + phased data for six custom genes) was assembled for a subsample of 46 specimens. Nuclear gene characteristics are reported in Table 1, with custom nuclear gene trees found in Appendix C. The nuclear subsample spanned the phylogenetic diversity discovered in our total sample (see Fig. 2), and emphasized paired SNF versus HE *A. janus* populations sampled on the west slope of the southern SN. The nuclear only *BEAST species tree, with individuals treated as separate OTUs, recovers major lineages as found in individual COI and 28S gene trees (Fig. 3). These include *A. californicus* + *A.*

gnomus, and HE, Yosemite, SNF and CR *A. janus* lineages. The species tree includes an *A. isolatus* lineage separate from the HE *A. janus* lineage (together referred to as **Eastern group**), and monophyletic SNF and CR *A. janus* lineages (together referred to as **Western group**). Although lineages within the *A. janus* complex are strongly-supported, relationships among these lineages are relatively poorly supported. Because some ESS values did not exceed 200 in analyses that included the ribosome biogenesis gene data (the tree likelihood for this dataset failed to reach stationarity), analyses were also run without this gene. Species trees with and without this gene are topologically quite similar, with increased nodal support at certain nodes for the reduced dataset (compare Fig. 3 to Appendix C).

Mean K2P distances were calculated for all loci both within and across the major *A. janus* clades (Table 2). Intra-clade distances were similar to inter-clade distances, reflecting the deep phylogenetic breaks and high genetic variation across sampling localities within clades, as is typical for mygalomorph spiders (e.g., Bond et al., 2001; Bond and Stockman, 2008; Hedin et al., 2013; Satler et al., 2013; Leavitt et al., 2015).

Table 2
Mean K2P percent distances for each locus across and within phylogenetic groups (Y = Yosemite, E = Eastern, and W = Western). Distances were also calculated for two geographic groups in the Western group (CR = Coast Range, SNF = Sierra Nevada Foothills).

	COI	28S	39S ribosomal	Ribonuclease	Tartan	Sdcccag	Sushi	Ribosome
<i>Across</i>								
Y v E	13.1	1.7	1.5	1.1	2.0	0.6	1.4	0.9
Y v W	13.1	2.1	2.3	1.3	2.3	0.7	1.3	1.3
E v W	13.6	2.0	2.6	1.7	2.9	0.9	1.7	0.9
CR v SNF	12.8	1.9	1.8	0.6	1.9	0.8	1.6	0.9
<i>Within</i>								
Y	7.9	0.4	0.3	0.1	0.5	0.2	0.5	0.5
E	11.5	0.9	1.4	0.9	1.0	0.7	0.9	0.5
W	11.7	1.3	1.6	0.5	1.9	0.7	1.5	0.8
CR	11.3	0.8	1.0	0.6	0.8	0.5	1.3	0.7
SNF	10.2	0.8	1.6	0.4	2.3	0.7	1.3	0.6

3.3. Riverine barrier hypothesis testing

The “unconstrained” (all individuals treated as OTUs) nuclear species tree reveals a pattern of elevational tiering in the southern SN (Figs. 3 and 4). We statistically compared this to an alternative hypothesis in which southern SN *A. janus* individuals were assigned to lineages following major river boundaries (North of Merced, North of San Joaquin, North of Kings, North of Kaweah, South of

Kern; Fig. 4). For this alternative hypothesis, the phylogenetic position of specimens collected from outside of the southern SN region was left unconstrained (i.e., individuals treated as OTUs). Comparison of marginal likelihood values calculated using both path sampling and stepping stone methods reveals convincing support for the elevational tiering hypothesis (Table 3). We obtained similar results from analyses conducted with the ribosome biogenesis gene removed.

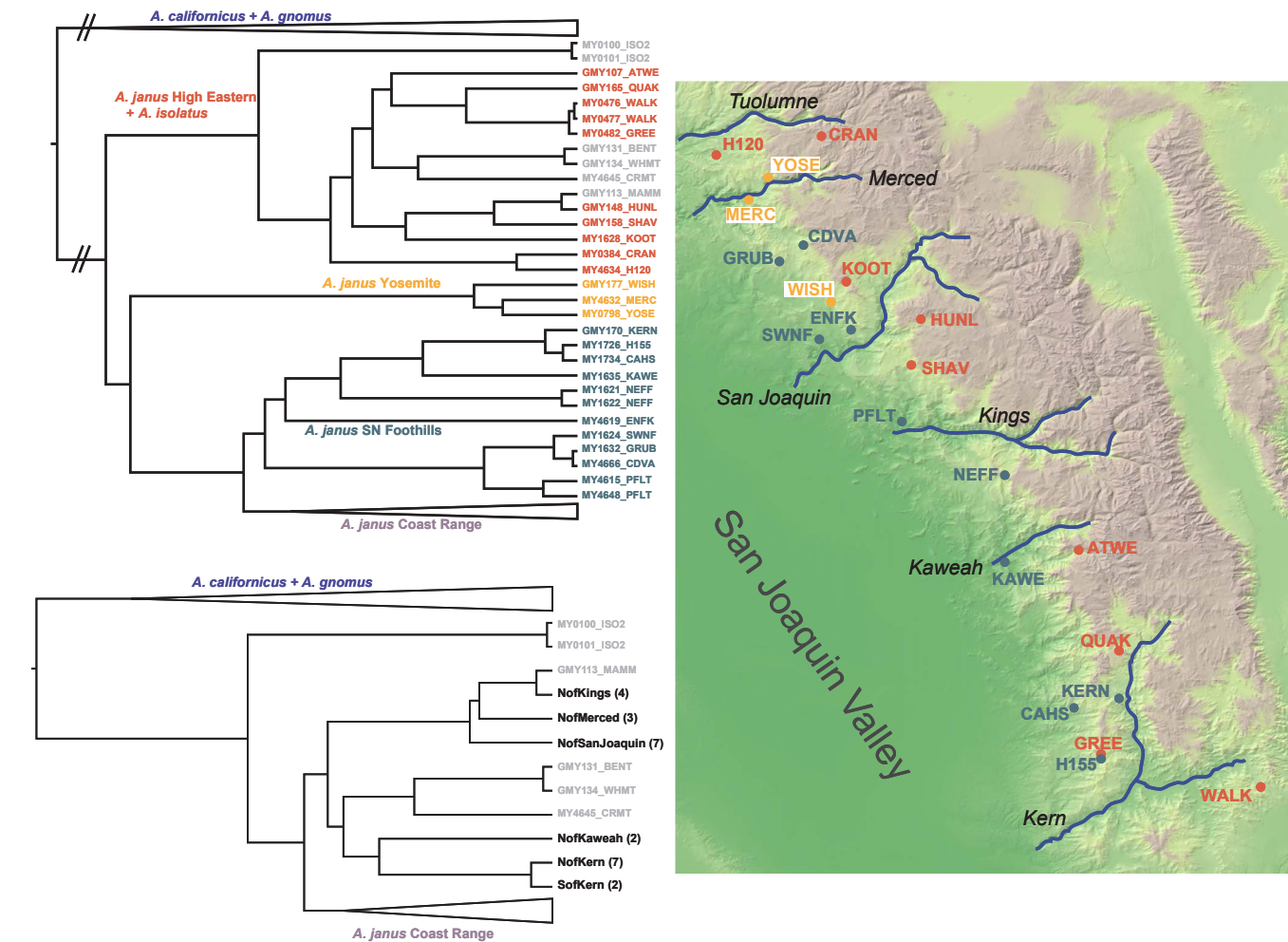


Fig. 4. Graphical portrayal of riverine barrier hypothesis test. Unconstrained (all individuals as OTUs) hypothesis (top), supporting elevational tiering (topology as in Fig. 3). Colored samples shown on inset map. Grey colored samples are phylogenetically placed in *A. isolatus* + *HE janus* clade, but not shown on map. Riverine barrier hypothesis (bottom) with individuals assigned to groups that occur between major rivers. Number after names indicate individuals assigned to that group. *Aliatypus californicus* + *A. gnomus* and *A. janus* Coast Range clades are collapsed for graphical purposes. Colors as described above.

Table 3
Results of Bayes factor delimitation (BFD) analyses comparing riverine barrier and unconstrained models. Bayes factors (BF) calculated from marginal likelihood estimates (MLE) generated using stepping-stone (SS) and path sampling (PS) methods.

ALL nuclear loci	MLE (SS)	BF	MLE (PS)	BF
Individual OTUs	−15212.93	–	−15206.55	–
River groups	−15640.01	854.16	−15625.62	838.14
<i>Ribosome biogenesis excluded</i>				
Individual OTUs	−12462.13	–	−12456.63	–
River groups	−12809.63	695.00	−12797.82	682.39

3.4. Ecological niche model predictions

Mean AUC values for training and test datasets were similar under both current and LGM conditions. Under current conditions, AUC values for training and test datasets, respectively, for the Western group were 0.989 and 0.981 (standard deviation = 0.006), and for the

Eastern group 0.962 and 0.933 (standard deviation = 0.032). Under LGM conditions, AUC values for training and test datasets, respectively, for the Western group were 0.998 and 0.998 (standard deviation = 0.001), and for the Eastern group 0.999 and 0.995 (standard deviation = 0.002). Binary ENM predictions produced minimally overlapping distributions for Western and Eastern *A. janus* groups under both current and LGM bioclimatic conditions (Fig. 5). The predicted ENM for the Western group during the LGM in the SN foothills is nearly identical to that under current conditions, and predictions in the Coast Ranges are largely similar, with expansion further southwest during the LGM (Fig. 5). For the Eastern group, the ENM predicted under LGM conditions shows greater expansion further north in the SN (Fig. 5), in particular in the high elevation regions, as well as a greater area surrounding current *A. isolatus* localities in Arizona (not shown).

3.5. Ecological niche hypothesis testing

Niche overlap estimates from ENM predictions under current conditions are moderately low ($D = 0.175$; $I = 0.368$). ENM hypothesis

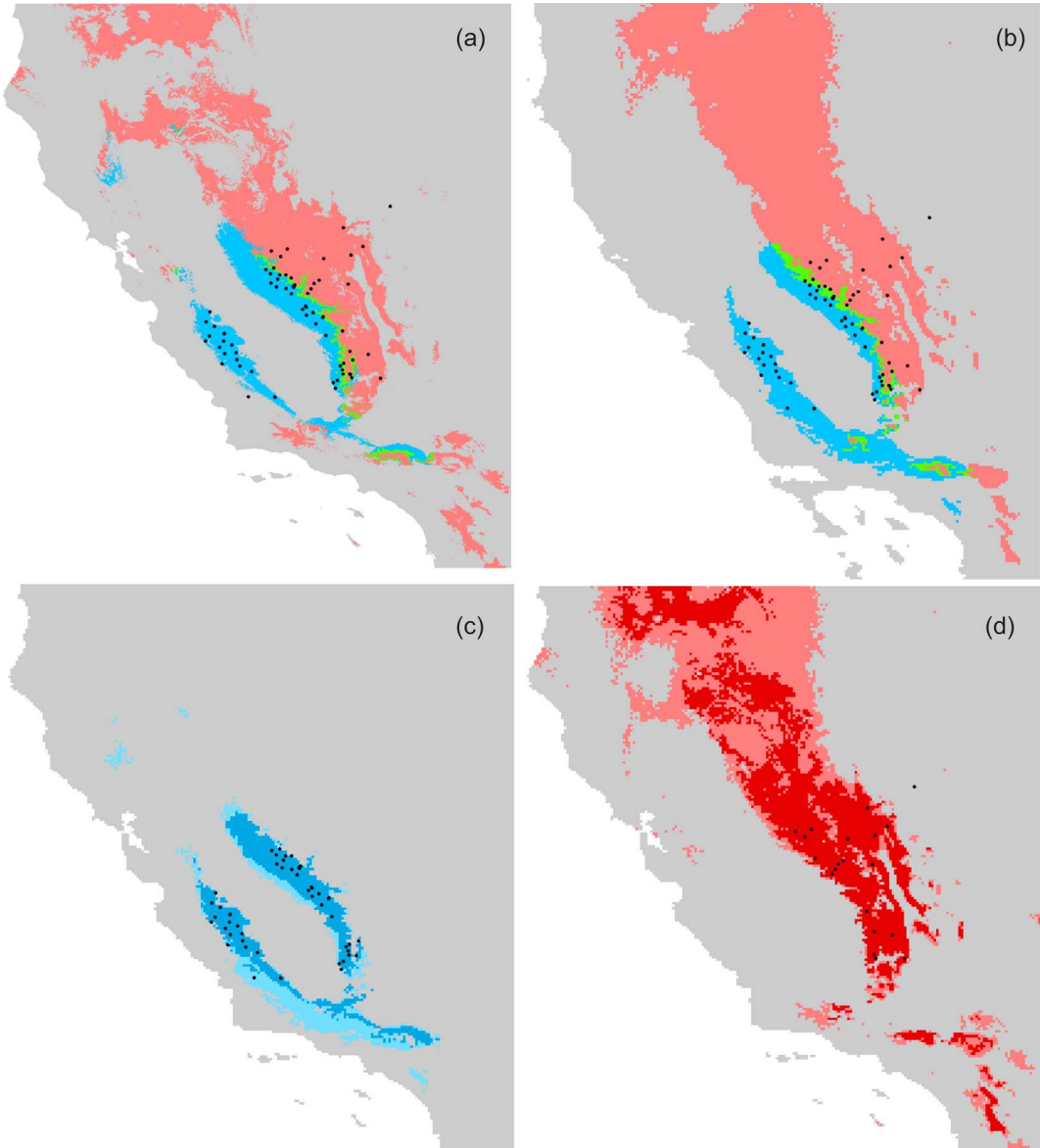


Fig. 5. ENM binary predictions, showing California *Aliatypus janus*. (a) based on current conditions for Western (blue) and Eastern (red) with overlap indicated by green; (b) based on LGM conditions, with same color scheme; (c) Western group current (dark blue) versus LGM (light blue); (d) Eastern group current (dark red) versus LGM (light red). Black dots indicate occurrence points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tests produced the same qualitative results using D and I statistics; thus, we only present results for I . The observed niche overlap estimation occurred below the null distribution for the niche identity test (Fig. 6a) rejecting niche conservatism between Western and Eastern ENMs ($p < 0.01$). For the niche similarity test (Fig. 6b), observed niche overlap fell within the null distributions for each comparison (West versus East background, $p = 0.168$; East versus West background $p = 0.426$). Removal of duplicated pseudoreplicates for linear and blob range break analyses resulted in 42 and 66 data points, respectively. Observed niche overlap occurred below the null distribution for both tests (Fig. 6c and d), thus rejecting the null of no abrupt transition ($p < 0.05$).

4. Discussion

4.1. Cryptic diversity in the *Aliatypus janus* species complex

Coalescent analyses of the multi-locus dataset revealed deep phylogenetic breaks, confirming that *A. janus* represents a species complex (Satler et al., 2011), and further supporting the SN as an evolutionary hotspot (Davis et al., 2008). Deep phylogenetic breaks consistent with species level divergences are common in named mygalomorph species and other dispersal limited arachnid species (e.g., Bond et al., 2001; Graham et al., 2015; Bryson et al., 2016; Derkarabetian et al., 2016; Hamilton et al., 2016; Opatova et al., 2016). We recovered three well-supported groups (Fig. 3; PP ≥ 0.9) in the SN: (1) a widespread clade distributed in the southern Coast Range and the western SN foothills, (2) a widespread clade distributed at high elevation in the SN (> 1300 m), montane regions in eastern CA/western NV, and montane

regions of AZ, and (3) a geographically-restricted clade with populations known only from near Yosemite and Bass Lake (Fig. 1).

Riverine barriers have played a major role in lineage diversification in a number of SN taxa (Jockusch and Wake, 2002; Kuchta and Tan, 2006; Feldman and Spicer, 2006; Polihronakis and Caterino, 2010; Rovito, 2010; Leaché et al., 2010; Schoville and Roderick, 2010; Schoville et al., 2012). Coalescent based hypothesis tests did not support major lineages of *A. janus* conforming to current river barriers (Table 2, Fig. 4), despite evidence of initial incision occurring in the late Cretaceous for some southern SN canyons (House et al., 1998; Clark et al., 2005). Riverine barriers likely contribute to genetic structuring within the Western and Eastern *A. janus* lineages, but testing this phylogeographic hypothesis will require much denser geographic sampling and more rapidly-evolving molecular datasets.

Both Western and Eastern groups include deep phylogeographic divisions (Fig. 3). For the Western group, coalescent analysis resulted in reciprocally monophyletic CR and SNF groups, albeit with low PP support. Suitable habitat was not predicted under current or LGM conditions for most of the Central Valley, which is considered a major barrier to gene flow for mesic adapted taxa (Calsbeek et al., 2003; Rissler et al., 2006). However, the Central Valley has undergone periods of suitability, allowing for so-called ‘trans-valley leaks’ in multiple arachnids and salamanders (Kuchta et al., 2009; Satler et al., 2011; Hedin et al., 2013; Leavitt et al., 2015; Reilly et al., 2015; Emata and Hedin, 2016). The trans-valley pattern we observe, with a deep phylogenetic break between CR and SNF, is not consistent with a recent west to east range expansion resulting in secondary contact with Eastern *A. janus*. Within the Eastern group, deep intraspecific divergences may reflect the complex geologic and climatic history of the

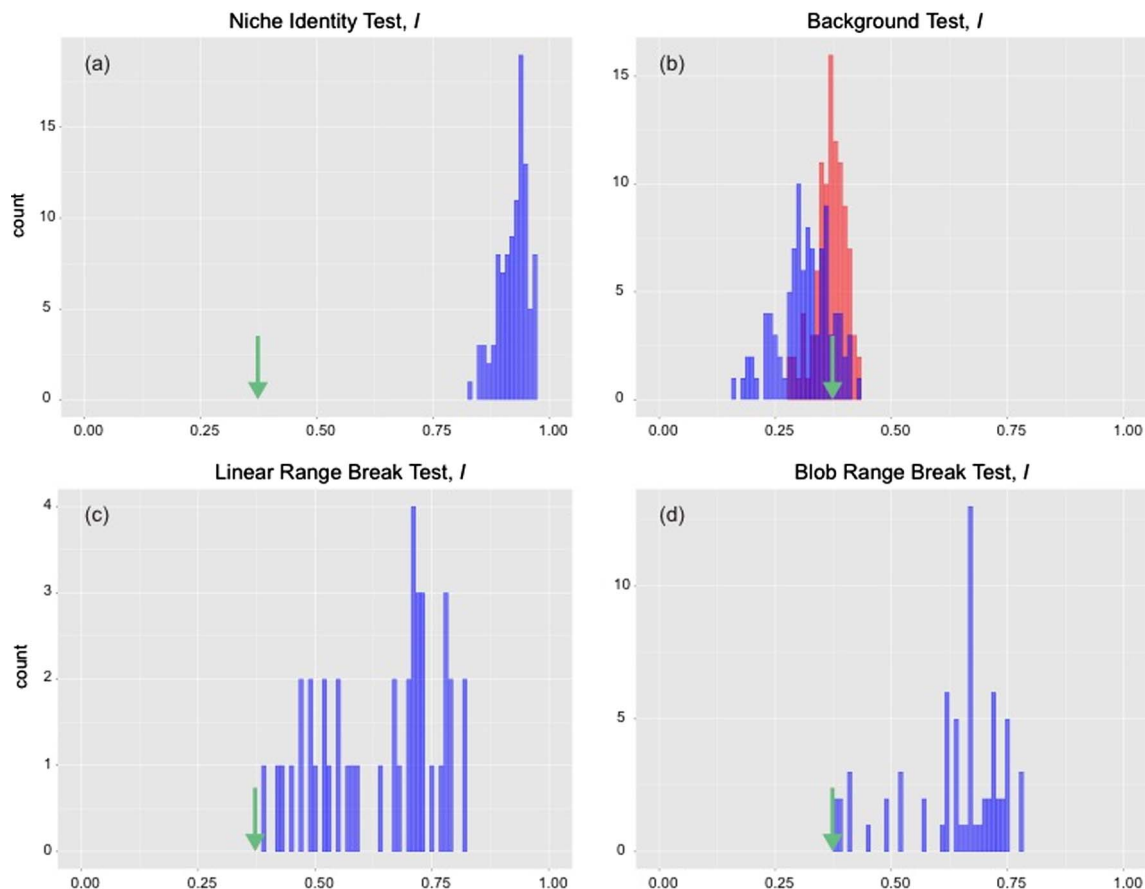


Fig. 6. Ecological niche hypothesis tests. Niche overlap values (I) from ENM predictions based on occurrence data (green arrow) and pseudoreplicates (null distributions). (a) Niche identity, (b) niche similarity, West predicting East (blue) and vice versa (red). Range break tests (c) linear and (d) blob. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

SN, which has undergone repeated glaciation events in the Pliocene and Pleistocene (reviewed in Gillespie and Zehrfuss, 2004). These glaciation events have contributed to genetic divergences observed in other high elevation SN taxa (Rovito, 2010; Schoville and Roderick, 2010; Schoville et al., 2012; Rubidge et al., 2014).

4.2. Ecological divergence associated with elevational tiering

We found evidence that ecological niche divergence may play a prominent role in the maintenance of cryptic species in the *A. janus* species complex. No obvious physical barrier to gene flow occurs between Western and Eastern *A. janus* groups, and range break tests indicate that these groups meet along an abrupt environmental gradient in the western SN. The predicted distributions of the Western and Eastern groups appear to have remained largely stable and with minimal overlap since the LGM, indicating that contact between the two groups is not a recent phenomenon.

The minimal overlap of ENMs, abrupt environmental gradient, and lack of evidence of recent secondary contact between Western and Eastern groups could be evidence of parapatric speciation. However, phylogenetic analyses did not recover multiple high elevation groups derived from low elevation groups, which would represent an expected pattern consistent with repeated parapatric speciation events (Patton and Smith, 1992; Moritz et al., 2000). The deep divergence and phylogenetic uncertainty among the three major *A. janus* lineages limits our ability to infer whether ecological divergence drove speciation, or if such divergence acts to maintain species boundaries after secondary contact following allopatric speciation.

While niche identity, in the strict sense, was rejected, Western and Eastern *A. janus* groups do not occupy more conserved (or divergent) niches than those available to each other. It is perhaps surprising that conservatism was not detected considering the divergent ecological backgrounds that the two groups occupy, and the substantial evidence for niche conservatism in mygalomorphs and other dispersal limited arachnids (Bond et al., 2001; Keith and Hedin, 2012; Bryson et al., 2016; Derkarabetian et al., 2016; but see Beavis et al., 2011). Failure to reject the null may be due to insufficient sample size or a result of ambiguity in the ranges of the two groups (Warren et al., 2008). Increased sampling, particularly for the Eastern group, could provide greater power for niche similarity analysis. An alternative explanation is that Western and Eastern *A. janus* inhabit conserved or divergent niches, but the level of resolution currently available for ENM does not account for specific and specialized microhabitats (e.g., north-facing slopes, shaded ravines, soil types; e.g., Anacker and Strauss, 2014; Massatti and Knowles, 2014; Varner and Dearing, 2014).

The relative roles of ecological niche divergence and conservatism in species formation remains an important topic in biogeographic research. Ecological niche divergence associated with the evolution of cryptic *A. janus* lineages highlights the need for further investigation into the role of elevational tiering in SN taxa. Study of short range endemic arachnids (and other invertebrates) may be particularly insightful for revealing patterns of evolutionary divergence along elevational gradients (Garrrick, 2011). These studies will take on greater importance given the potential impacts of climate change on montane restricted taxa (Rubidge et al., 2012).

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Appendices A, B, & C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2017.09.003>.

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