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Phylogeny and diversification of the gallopheasants (Aves: Galliformes): Testing roles of sexual selection and environmental niche divergence

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Abstract

The gallopheasants comprise a clade of 22 species including some of the most elaborately plumaged and highly ornamented birds in the world. They also occupy a remarkable breath of environments and habitats, ranging from lowland rainforests to high grasslands and steppes of the Tibetan plateau. Here, we provide the first well-resolved species phylogeny of this charismatic group, inferred from ultraconserved elements, nuclear introns and mitochondrial DNA sequences. Unlike previous studies which found unresolvable relationships and suggested a rapid initial burst of diversification, we identified a well-resolved phylogeny supported in both concatenated and coalescent analytical frameworks, and a steady accrual of lineages through time. Morphological trait reconstructions demonstrated strong phylogenetic signal, not only for highly ornamented males, but also in more cryptically plumaged females. Environmental niche similarly exhibited strong phylogenetic signal. Moreover, evolution of male traits, female traits and environmental niche were all significantly correlated, making it difficult to disentangle their individual roles in gallopheasant diversification.

KEYWORDS

Lophura, *Phasianus*, phylogenomics, *Syrmaticus*, ultraconserved elements

1 | INTRODUCTION

The avian family Phasianidae (pheasants, partridges and allies) exhibits several examples of sexual dimorphism where sexual selection has presumably affected evolution and diversification (Kimball & Braun, 2008; Kimball, St. Mary, & Braun, 2011; Kraaijeveld, Kraaijeveld-Smit, & Maan, 2011). Males in the family are often brightly coloured and display elaborate feathers or other ornaments that are highly modified and aid in courtship of females. Females are typically drab with little to no ornamentation. Camouflaging patterning in females is seemingly important in background matching to decrease predation (Endler, 1978; Kenward, Marcstrom, & Karlbom, 1981; Michalis, Scott-Samuel, Gibson, & Cuthill, 2017). However, Phasianidae also includes examples where the sexes are monomorphic (or largely so), relatively drab in coloration, and lacking in any ornamentation. Early classifications separated highly dimorphic, ornamented species (Phasianini) and monomorphic, unornamented taxa (Perdicini) into separate subfamilies (Johnsgard, 1986; Johnsgard & Jones, 1988). Molecular phylogenies have instead shown that ornamentation characters are plastic, and that repeated transitions between highly dimorphic and monomorphic phenotypes are common (Hosner, Tobias, Braun, & Kimball, 2017; Kimball, Braun, Zwartjes, Crowe,

& Ligon, 1999; Kimball et al., 2011; Wang, Kimball, Braun, Liang, & Zhang, 2013).

Even among their showy phasianid relatives, the degree of male ornamentation expressed in the gallopheasants or 'true pheasants', is extreme. This clade comprises the genera *Catreus*, *Crossoptilon*, *Chrysolophus*, *Lophura*, *Phasianus* and *Syrmaticus* (Kimball & Braun, 2014; Wang et al., 2013), although some authors have ascribed *Lophura* alone to gallopheasants (Delacour, 1948). Male Reeves' Pheasant (*Syrmaticus reevsei*) has the longest avian tail, exceeding two metres. Male Bulwer's Pheasants (*Lophura bulweri*) have 32 rectrices—the greatest number of any bird. Males of the two species of *Chrysolophus* (Golden Pheasant, *C. pictus*, Lady Amherst's Pheasant, *C. amherstiae*) are among the most colourfully plumaged birds. These ornaments are featured in display behaviours to attract female mates, including inflation of colourful male facial wattles, wing whirring and associated vocalizations (Delacour, 1948). Most gallopheasants are sexually dimorphic, such as the well-studied Ring-Necked Pheasant, *Phasianus colchicus* (Mateos, 1998). However, this clade also includes two monomorphic genera: *Crossoptilon* (eared pheasants) in which both sexes are ornamented (elaborate facial wattles, tails and ear tufts) and the monotypic genus *Catreus* (*Catreus wallichii*, Cheer Pheasant) in which both sexes are relatively drab and largely lack ornamentation. Both *Catreus* and *Crossoptilon* are appeared to be socially monogamous. Sister to the gallopheasants is the monomorphic genus *Perdix* (true partridges), in which both sexes feature muted plumages lacking in ornamentation.

Sexual selection has long been considered responsible for ornamentation and the principle driver of diversification in Galliformes (Andersson, 1994; Kimball et al., 2011; Petrie, Tim, & Carolyn, 1991; Sun et al., 2014). Behavioural studies of several sexually dimorphic species have documented that sexual selection is important in mate choice (Buchholz, 1997; Dakin & Montgomerie, 2009; Ligon, Kimball, & Merola-Zwartjes, 1998; Mateos, 1998). In theory, sexual selection for ornamentation can reduce the time needed for speciation, increasing net diversification relative to non-ornamented lineages (Kazancıoğlu, Near, Hanel, & Wainwright, 2009; Wagner, Harmon, & Seehausen, 2012). When evolving independently in geographic isolation, selection for ornaments and associated behaviours will differ idiosyncratically among populations. Upon secondary contact, selection for different ornaments will render these populations less likely to interbreed even if they are physiologically capable of doing so (Kraaijeveld et al., 2011; Ritchie, 2007; West-Eberhard, 1983). However, even when restricting analyses to well-studied groups such as birds, large-scale analyses examining the role of sexual selection in speciation using a variety of approaches have come to conflicting conclusions (Huang & Rabosky, 2014; Morrow, Pitcher, & Arnqvist, 2003; Seddon, Merrill, & Tobias, 2008). Both modelling and empirical studies have suggested that tradeoffs are complex and that in different parts of parameter space, sexual selection can inhibit or promote speciation (Servedio & Buerger, 2014). Furthermore, speciation may not only be influenced by the emergence of ornamentation, but also the elaboration of that ornamentation (Gomes, Sorenson, & Cardoso, 2014).

Spectacular ornaments can perhaps also successfully draw the attention of biologists away from life history traits that could instead influence their evolution. Sexual selection is likely to work in concert with ecological divergence and other factors that are subject to natural selection (Maan & Seehausen, 2011; Ritchie, 2007; Servedio & Boughman, 2017; Wagner et al., 2012). Thus, understanding factors that might promote speciation in sexually dimorphic taxa ideally requires understanding patterns of both morphological and ecological change. Within their broad range in Asia, different gallopheasant species occupy a broad variety of habitats and environments (Lyu, Päckert, Tietze, & Sun, 2015; Wang et al., 2017), from equatorial lowland rainforest to the high plains of the Tibetan plateau (>5,000 m elevation). Although not ornamented to the degree of males, female plumage varies considerably among species and is presumably under strong selection pressure. Potential also exists for natural selection on female plumage patterns for background matching while nesting (Kenward et al., 1981). When large-scale studies have explored these questions, they have often relied on simple measures of trait evolution such as presence/absence of dimorphism (Huang & Rabosky, 2014). Thus, our understanding may also benefit from focusing on fewer taxa, but with deeper examination of both morphological and environmental changes in the group.

A first step in exploring factors that influence diversification and trait evolution in the gallopheasants is a well-sampled and well-supported phylogeny. Previous molecular phylogenetic studies of gallopheasants have demonstrated rampant conflict, and relationships among and within genera have been challenging to resolve (Meiklejohn, Faircloth, Glenn, Kimball, & Braun, 2016; Randi et al., 2001; Wang et al., 2013; Zhan & Zhang, 2005). Previous studies have suggested this may be due to relatively rapid speciation among genera leading to short internodes that until recently have been problematic to resolve (Kimball & Braun, 2014). Alternatively, their radiation into nearly all non-arctic habitats in Asia could explain a burst of diversification.

In this study, our first goal was to estimate robust phylogenetic relationships among all gallopheasant species using a combination of thousands of ultraconserved element loci, nuclear introns, and mitochondrial data. With the advent of phylogenomic data collection methods, relationships among genera appear to be stabilizing (Hosner, Faircloth, Glenn, Braun, & Kimball, 2016; Meiklejohn et al., 2016). Still, relationships within the genera have received less attention; the most speciose genus (*Lophura*) has only been

examined with mitochondrial data which failed to identify relationships with strong support (Randi et al., 2001; Zhan & Zhang, 2005). Our second goal was to explore whether phenotypic trait or environmental niche evolution may have influenced diversification both among and within gallopheasant genera.

2 | MATERIALS AND METHODS

2.1 | Taxon selection

We selected a single individual to represent each of the 22 Gallopheasant species of the genera *Syrmaticus*, *Chrysolophus*, *Phasianus*, *Crossoptilon*, *Catraeus* and *Lophura* (Clements et al., 2019). Additionally, we sampled *Lophura edwardsi hatinhensis*, which has been considered a species in previous taxonomic treatments (Hennache, Mahood, Eames, & Randi, 2012), resulting in 23 ingroup samples (Appendix S1). We selected seven outgroup taxa based on Hosner, Faircloth, et al. (2016) including all three species in the genus *Perdix*, thought to be the sister group to Gallopheasants. Many sequences were downloaded from GenBank after publication across a variety of phylogenetic studies (Bao et al., 2010; Bush, 2003; Dimcheff, Drovetski, Krishnan, & Mindell, 2000; Dimcheff, Drovetski, & Mindell, 2002; Hosner, Faircloth, et al., 2016; Kimball et al., 1999; Kornegay, Kocher, Williams, & Wilson, 1993; Li, Huang, & Lei, 2015; Mindell, 1997; Persons, Hosner, Meiklejohn, Braun, & Kimball, 2016; Randi et al., 2001; Sun et al., 2014; Zhan & Zhang, 2005). For newly collected data, we extracted DNA from blood or muscle tissue using the Puregene Genomic DNA Purification Kit, following the protocol for 5–10 mg of fresh or frozen solid tissue.

2.2 | DNA sequencing

We amplified two mitochondrial genes (12s and ND2) and seven nuclear introns (CLTC, CLTCL1, EEF2, FGB5, SERPINB14, RHO and TGBF2) using gene-specific PCR conditions (Kimball et al., 2009; Wang et al., 2013). PCR products were assessed for size and intensity on a 1% agarose gel using ethidium bromide and purified for sequencing by PEG: (20% PEG: 2.5 M NaCl) precipitation protocol. Purified samples were sequenced at the Interdisciplinary Center for Biotechnology Research (University of Florida, Gainesville, FL) utilizing the same primers used for amplification. All mitochondrial cytochrome *b* (CYTB) sequences were from previous studies and sourced from GenBank. All DNA sequences were edited in Geneious 6.1.6. For nuclear introns, the sequences were trimmed to the GT and AG splice sites, ND2 was trimmed to the coding region, and 12s was trimmed to match the previous published boundaries for this gene region. The sequences were then aligned within Geneious using six iterations of MUSCLE (Edgar, 2004) and edited by eye in MacClade 4.06 (Maddison & Maddison, 2000). Hereafter, we refer to these data as the Sanger data set.

Samples representing all genera and clades found to be poorly resolved in multigene data sets by Wang et al. (2013) were selected for target-capture sequencing of ultraconserved elements by RAPiD Genomics (Gainesville, FL). Only two species of *Crossoptilon* whose placement has not been controversial in previous studies (Wang et al., 2013, 2017) lacked UCE data. Briefly, Illumina TruSeq libraries were prepared following standard manufacturer's protocol (Illumina Inc., San Diego, CA, USA), adjusted to use primers with custom index tags designed by (Faircloth & Glenn, 2012). Libraries were enriched for 5,060 UCE loci targeted with a set of 5,472 probes (Mycroarray, Ann Arbor, MI; http://www.mycroarray.com/mybaits/mybaits-UCEs.html). Paired-end sequence reads (100nt) were generated on an Illumina HiSeq 2500. UCEs for some taxa were generated by a previous study (Hosner, Faircloth, et al., 2016).

Raw reads were demultiplexed and quality controlled with Trimomatic using default settings (Bolger, Lohse, & Usadel, 2014). Following quality control, we assembled contigs from cleaned and trimmed reads with Trinity r20131110 (Grabherr et al., 2011). We extracted UCE loci from assembled contigs using the PHYLUCE pipeline (Faircloth, 2015), and aligned sequences for each locus with MAFFT 7 (Katoh & Standley, 2013). We trimmed ends of alignments when 35% of cells were missing across 20 bp sliding window. All locus alignments with greater than 75% sequence recovery were retained for data analysis. Sanger sequences generated for this study are archived in the GenBank Nucleotide database (MT524008–MT524067) and Illumina reads are archived at the GenBank Short Read Archive (PRJNA634234).

2.3 | DNA sequence characteristics

The concatenated Sanger data set included 3,193 bp of mitochondrial DNA and 4,443 bp of nuclear introns, totalling 7,636 bp. Nuclear data included a few regions that were problematic to align (e.g. *Crossoptilon* had a small microinversion [30 bp] in the FGB5 intron region); but no genomic anomalies supported divisive relationships and were therefore not an impetus for producing a well-resolved phylogeny. The UCE data set comprised 3,486 loci and totalled 1,580,739 bp (NEXUS formatted alignments are archived in Appendix S2). Of these loci, 234 contained more than 25 informative sites and were selected for downstream gene tree reconciliation with ASTAL III.

2.4 | Phylogenetic analysis

We analysed Sanger data as individual gene data sets, a mitochondrial data set (where 12S, ND2 and CYTB were concatenated), a nuclear intron data set (where the seven nuclear loci were concatenated) and a combined Sanger data set including all nuclear and mitochondrial gene regions. We analysed the UCE dataset alone and combined with the Sanger data for a total nucleotide (TN) analysis. To select a partitioning scheme for maximum likelihood analyses, we implemented partitionFinder 2.1.1 for each alignment (Lanfear, Calcott, Ho, & Guindon, 2012; Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) treating each marker (UCE locus, intron or mitochondrial region) and codon position (ND2 and CYTB) as data subsets. We treated branch lengths as linked, assumed the GTR + G model of sequence evolution, selected Akaike's information criterion corrected for small sample size (AICc), and the greedy (Sanger) or rcluster (UCE) search schemes.

For the Sanger, UCE and TN data sets, we estimated the maximum likelihood (ML) tree for each data set using RAxML 8.0.25 (Stamatakis, 2006, 2014) with 10 random additions and the GTR + Γ model. ML bootstrap analysis of each data set was also conducted using RAxML 8.0.25 with either 100 (UCE, TE) or 1,000 replicates (Sanger) and the GTR + Γ model. To estimate a phylogeny incorporating the multispecies coalescent, we implemented ASTRAL III 5.5.6 (Mirarab et al., 2014; Zhang, Rabiee, Sayyari, & Mirarab, 2018). ASTRAL III finds the tree that shares the maximum number of quartets with input trees and computes a posterior probability for each node; nodes with greater discordance among gene trees have lower posterior probabilities. We inferred nuclear intron and UCE input trees with PhyML (Guindon et al., 2010), using the best fit model as selected with the program MrAIC (Nylander, 2004) using the Akaike's information criterion corrected for small sample size (AICc). PhyML uses a broader selection of DNA sequence models than RAxML (e.g. JC69, HKY, GTR; with and without estimating invariant sites and gamma-distributed rate heterogeneity), but does not operate on partitioned alignments. We only inferred gene trees for UCE alignments that contained over 25 informative sites ($n = 234$), because uninformative gene trees may disrupt or bias gene tree reconciliation approaches (Hosner, Braun, & Kimball, 2016; Meiklejohn et al., 2016; Zhang et al., 2018). We analysed four different gene tree data sets with ASTAL III: nuclear introns, all Sanger data (mtDNA considered a single locus), the 234 most informative UCEs, and TN (mtDNA, all introns, and the 234 most informative UCEs) using ML trees for each locus (seven introns and mtDNA) as input trees. To obtain a second topology estimate consistent under the multispecies coalescent, we implemented SVDquartets (Chifman & Kubatko, 2014) on the concatenated Sanger, UCE and TN data sets with 1,000 (Sanger) or 100 bootstraps (UCE, TE), in PAUP*4a159 (Swofford, 1999).

In addition to analyses to estimate topology, we inferred an ultrametric phylogeny with BEAST 2.2.0 (Bouckaert et al., 2014). Estimating branch lengths from the TN UCE/Sanger data sets is challenging due to missing data issues (Hosner, Braun, et al., 2016), so we restricted analysis to the more widely sampled Sanger data set. Because topology of the Sanger data alone was poorly resolved, we constrained the topology to the TN tree supported by ML, ASTRAL III and SVDquartet approaches. We selected the partitioning strategy and models of sequence evolution using partitionFinder 2.2.1 (Lanfear et al., 2016), allowing models supported by BEAST 2.2.0, and treating each locus and each codon position (ND2, CYTB) as a data subset. Because the GTR model and I + Γ rate heterogeneity often result in poor convergence in BEAST, we instead selected the simpler HKY and + Γ settings, respectively. We selected a relaxed lognormal clock model, birth-death tree prior. We executed two independent runs of 50,000,000 generations, sampled every 50,000 generations, and discarded the initial 25% of trees as burnin, resulting in a posterior treeset of 1,500 from the combined runs. We examined MCMC behaviour with Tracer 1.5 (Rambaut & Drummond, 2009) and ensured that effective sample sizes of parameter estimates were greater than 200. Resulting treefiles are archived in Appendix S3.

2.5 | Morphological traits data collection

We gathered information on 93 morphological traits to assess the tempo of morphological trait evolution in gallopheasants. These included continuous measurements related to body size: tarsus length, wing chord, tail length; (Johnsgard, 1986), as well as traits describing facial skin colour, facial skin patch size, facial skin erectile features, leg colour, iris colour, presence of feather ornaments on the head (crests, ruffs, ear tufts), presence of feather ornaments related to the tail (elongated uppertail coverts, curled rectrices), and colour, structural iridescence, and patterning of plumage patches (crown, breast, belly, mantle, rump, uppertail coverts, scapulars, wing coverts/remiges, rectrices). Males and females were scored separately based on descriptions by Johnsgard (1986; Appendix S4). Male and female data sets were then each centred and transformed separately using principal components analysis for use in comparative phylogenetic analysis. Details of these calculations can be found in a supplemental R script (Appendix S5; R Core Team). In addition to scoring male and female morphological characters separately, we also compared

them within species to assess the relative degree of sexual dimorphism within each species. For continuous characters, we used the difference between males minus females; for binary traits, we scored 0 as monomorphic (identical trait values for males and females) and 1 as dimorphic (different trait values for males and females; Appendix S4).

2.6 | Ecological niche modelling

Ecological niche models were developed for each of the 23 gallopheasant taxa using the correlative niche modelling algorithm MAXENT v3.3.3k (Phillips & Dudík, 2008). Georeferenced occurrence data were downloaded from eBird (ebird.org; Sullivan et al., 2009) and augmented with records from literature (Collar et al., 2001). Duplicate records and records that were judged to be inaccurate based on known distributions of species were removed; the remaining data sets were downsampled to 2.5 arc-minutes, the spatial resolution of the environmental data (WorldClim; Hijmans et al., 2005). To diminish the likelihood of overfitting, we reduced the initial variable set (19 Bioclim layers and altitude) by removing data layers until no data layer pairs were strongly correlated ($r > .80$). The remaining data layers were further reduced by assessing variable contributions in preliminary model runs; variables which contributed less than 1% to most species' models were eliminated. The final environmental data set comprised layers summarizing altitude, annual mean temperature, mean diurnal temperature range, precipitation seasonality and precipitation of the wettest quarter. Model calibration regions for each species were designed to reflect known distributions and dispersal capabilities, as an approximation of species' ability to sample suitable and unsuitable environments (Appendix S6; Barve et al., 2011). We performed 10 bootstrapped replicates of model calculations, with a maximum of 10,000 iterations each. For each replicate, 50% of occurrence points were chosen at random for intrinsic model testing. To avoid overfitting ENMs with biologically unrealistic environmental response curves, no threshold or hinge features were permitted. Details of these calculations can be found in the supplemental bash shell script (Appendix S7).

Suitable environmental conditions for each species for subsequent comparative analyses were defined using a 95% minimum occurrence point threshold within the training region of each model. While more complex methods of thresholding have demonstrated better skill in classifying suitable and unsuitable environments (Jiménez-Valverde & Lobo, 2007; Liu, Berry, Dawson, & Pearson, 2005), our data set lacks true absence data, and therefore, a simple fixed threshold technique was preferable (Bean, Stafford, & Brashares, 2012). For each species, environmental conditions within the extent of suitable habitat were extracted, and the mean value of each environmental variable was calculated. These values were then centred, and principal components were calculated for comparative phylogenetic analysis. Details of these calculations can be found in the supplemental R script (Appendix S5).

2.7 | Comparative phylogenetic analysis

To test if gallopheasants underwent an initial burst of diversification, we estimated diversification rates across the gallopheasant phylogeny with Bayesian Analysis of Macroevolutionary Models 2.5 (BAMM; Rabosky, 2014). We used the ultrametric tree produced in BEAST, selected priors with the 'setBAMMpriors' function in BAMMtools (Rabosky, 2014) in R (lambdaInitPrior = 0.00739547211384755; lambdaShiftPrior = 11.4972261491666; muInitPrior = 0.00739547211384755), set 'expectedNumberOfShifts' to 1, and used species-specific sampling fractions. We ran the MCMC simulation for 20,000,000 generations, sampling every 10,000 generations, and discarded the first 10% of samples as burnin (Appendix S8). We identified rate shifts by posterior probabilities and by computing Bayes Factors in BAMMtools.

To visualize clustering of species and genera in multivariate space, we performed non-metric multidimensional scaling on the four trait data sets (male, female, dimorphism, and abiotic environmental niche; Appendix S9). We then conducted comparative phylogenetic analyses on the principal components of each suite of characters (23 principal components of male, female and trait dimorphism scores and five principle components of abiotic environmental niche) in a multivariate framework, as characters within these suites of characters are not likely to have evolved independently from each other (Eliason, Maia, & Shawkey, 2015; Onstein et al., 2016). First, we estimated phylogenetic signal and its statistical significance using K_{mult}, a generalization of Blomberg's K that allows estimation of phylogenetic signal of suites of correlated characters (Adams, 2014; Blomberg, Garland, & Ives, 2003). Just as with the traditional Blomberg's K statistic, the closer K_{mult} is to 1, the more variation in a character can be explained by phylogenetic relationships under a Brownian motion model of evolution; values of $K < 1$ indicate more variation than expected under Brownian motion, and thus less phylogenetic signal (Adams, 2014; Blomberg et al., 2003). As in Denton and Adams (2015), we also calculated the multivariate net evolutionary rates of each of these four characters suites (male traits, female traits, dimorphism, environment), and compared the results as a series of character suite partitions (male and female traits; dimorphism and environment) to determine

the potential significance of these differences (Denton & Adams, 2015). Finally, we compared patterns of evolution among male traits, female traits, sexual dimorphism and environmental traits to determine whether these character suites were correlated using phylogenetic generalized least squares regression (Denton & Adams, 2015). Details of these calculations can be found in the supplemental R script (Appendix S5).

3 | RESULTS

3.1 | Phylogenetic analysis

All analyses returned a gallopheasant clade sister to *Perdix* and supported all established gallopheasant genera as monophyletic (Figure 1). Using either the UCE or TN data sets, relationships were generally highly supported, with most nodes having 100% bootstrap support. Although support values using methods that incorporated the multispecies coalescent (SVDquartets and ASTRAL III) were sometimes lower, there were no topological differences when analysing the UCE and TN data using either of these methods versus RAxML.

Discordance among analyses was primarily limited to nodes with poor support in one or more analysis, and mostly between unresolved relationships in the Sanger data sets and strongly supported relationships in the UCE data sets (Figure 1). For example, mtDNA placed *L. bulweri* sister to a clade of five other *Lophura* species, but with poor support (62% of ML bootstraps). Nuclear introns instead placed *L. bulweri* sister to *L. nycthemera* and *L. leucomelanos*, but with no statistical support (<50% of ML bootstraps; Figure 1a,b). However, the UCE and TN data sets also placed *L. bulweri* sister to *L. nycthemera* and *L. leucomelanos* with moderate to strong support in all analytical frameworks (Figure 1c). We found similar patterns in the topological placements of *L. erythropthalma* within *Lophura*, *S. reevesii* and *S. soemmerringii* within *Syrmaticus*, and placement of the genera *Catreaus*, *Phasianus* and *Chrysolophus*.

Within *Lophura*, there were two strongly supported differences between mtDNA and UCE trees. In both cases, the UCE and intron topology agreed, though only the UCE data set exhibited strong support for the conflicting topology. These involved the sister to *L. ignita* and the placement of the *L. nycthemera* + *L. leucomelanus* clade (Figure 1a,c). Outside of these two examples of cyto-nuclear discordance, the data sets agree for well-supported relationships. Overall, the TN analysis was well-supported across the gallopheasant tree with multiple analytical approaches, lending confidence to the topology and justifying its use in generation of a downstream BEAST ultrametric tree (Figure 2) and its use in comparative phylogenetic analyses.

3.2 | Ecological niche models

Distributions of all species within training regions as inferred from 95% minimum training presence (Appendix S6) were largely congruent with previous understanding of phasianid ranges (Johnsgard, 1999). AUC scores for training and testing data sets for all species indicated the models fit the data better than random (Appendix S10); for each species, mean AUC_{DIFF} scores (the difference between training and testing AUC scores; Appendix S10) were very low, indicating the models were not overfit to the training data set and likely captured the fundamental environmental niche of each species reasonably well. Scatterplots of environmental niche characteristics based on modelled distributions (Appendix S11) show that the niches of closely related species are generally conserved.

3.3 | Comparative phylogenetic analyses

BAMM did not identify evidence for shifts in diversification rate across the gallopheasant phylogeny. The zero rate-shift posterior probability was 0.83. Bayes factors for all non-zero rates were < 1, indicating the posterior probabilities for all non-zero rate categories were less those of the prior probabilities.

The phylogenetic signal of all four trait suites (all 23 principal components of male and female traits scores separately, dimorphism, and all 5 principal components of abiotic environmental niche) was moderate and statistically significant ($p < .01$; environmental niche: $K_{mult} = 0.362$, female traits: $K_{mult} = 0.378$, male traits: $K_{mult} = 0.329$, dimorphism: $K_{mult} = 0.457$). Environmental niche evolved at a slower rate than male, female and combined trait character suites (environmental variables: $\sigma = 77.031$; female traits: $\sigma = 508.971$; male traits: $\sigma = 548.389$; combined male and female traits: $\sigma = 528.678$, trait dimorphism $\sigma = 488.758$); however, these differences were not significantly different ($p = .373$).

After controlling for phylogeny, male and female traits were both strongly and significantly correlated with environment (male plumage characters versus environmental variables: $r = .827$, $p = .012$; female traits versus environmental variables: $r = .853$, $p = .008$); male and female traits were also strongly and significantly correlated ($r = .936$, $p < .004$). The correlation between sexual dimorphism and environmental variables was weaker ($r = .796$, $p = .076$).

Genera were often separated in different areas of trait space for each character suite, male traits, female traits, sexual dimorphism and environment (Figure 3). For male/female traits, there was almost no overlap among genera, except that male *Catraeus* grouped with *Syrmaticus*, and that female *Phasianus* grouped with *Chrysolophus*. For sexual dimorphism, the non-dimorphic genera *Crossoptilon* and *Catraeus* logically formed a tight cluster. Otherwise

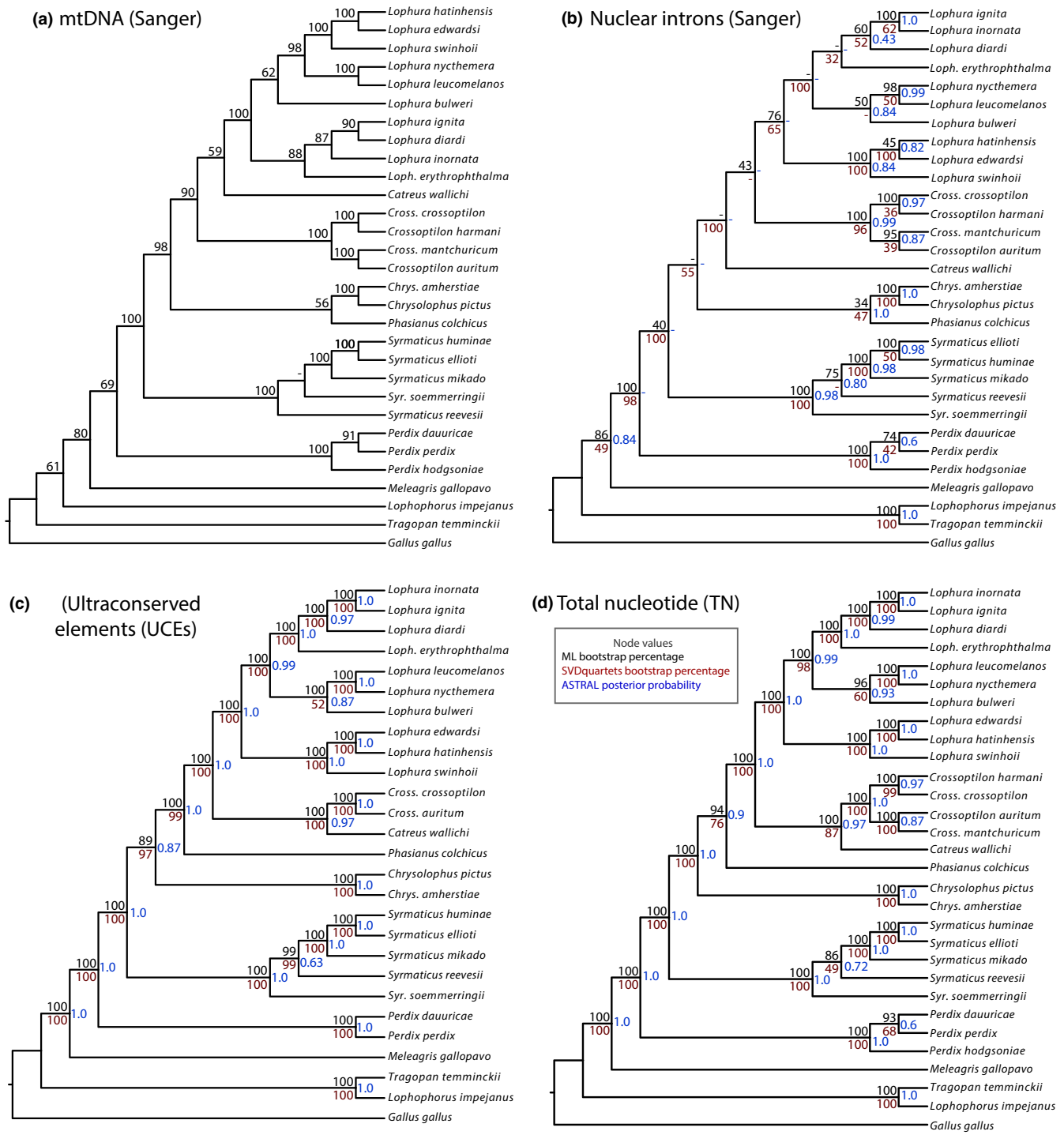

FIGURE 1 Comparison of topology and support values for gallopheasant phylogeny inferred with different data subsets and different analytical frameworks: (a) ML inference of mitochondrial DNA, (b) ML, SVDquartets and ASTRAL inference of nuclear introns, (c) ML, SVDquartets and ASTRAL inference of ultraconserved elements, and (d) ML, SVDquartets and ASTRAL inference of the combined 'Total nucleotide' (TN) data [Colour figure can be viewed at wileyonlinelibrary.com]

genera and species were spread widely across trait space, illustrating great variation in how sexual dimorphism is expressed among gallopheasants. Like male/female traits, most genera occupied different environmental niche space. As a counter example, *Lophura* and *Syrmaticus* overlapped substantially, mirroring evidence from raw species distributions.

4 | DISCUSSION

Our UCE and TN (UCE + other; Figure 1d) datasets estimated a phylogeny that was well-supported and without conflicts between concatenated and coalescent analyses. Whereas earlier molecular studies had come to conflicting conclusions, and/or estimates of relationships with low

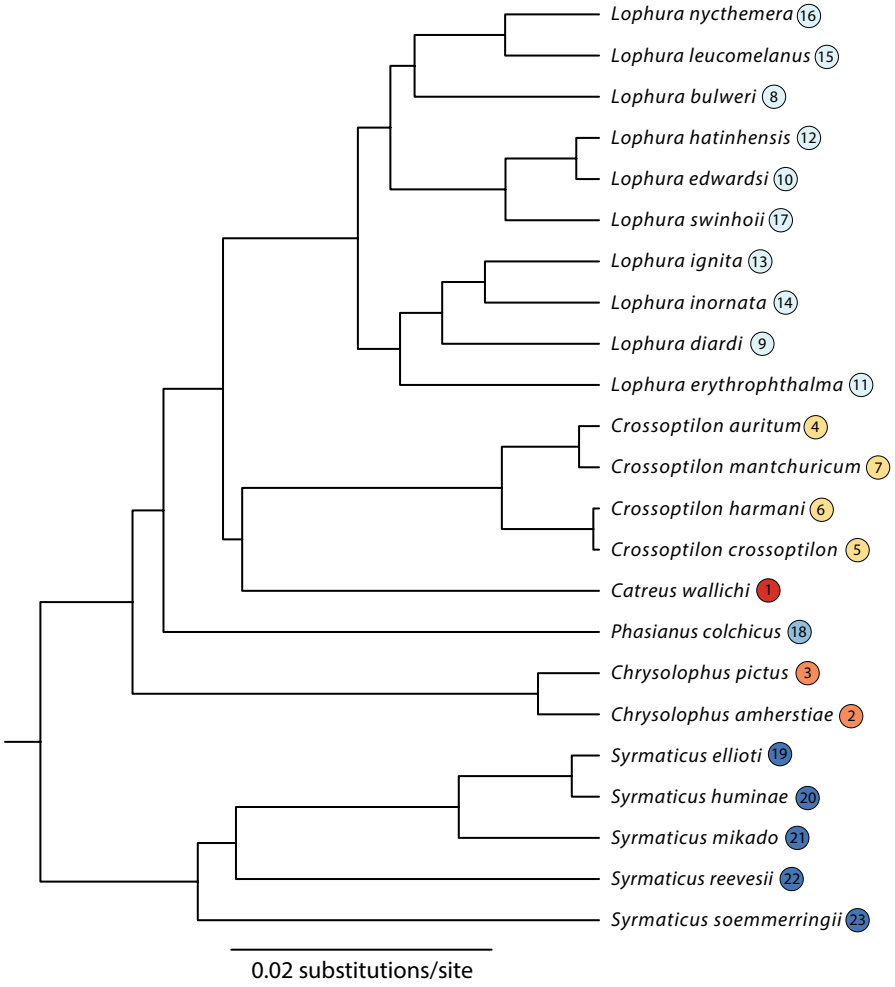

FIGURE 2 Ultrametric phylogeny of gallopheasants. Contradicting previous studies, we found no evidence for short internodes or shifts in diversification across the phylogeny. Tip numbering and colour coding for each taxon matches those in Figure 3 [Colour figure can be viewed at wileyonlinelibrary.com]

support among the gallopheasants (Meiklejohn et al., 2016; N. Wang et al., 2013), our TN and UCE-only phylogenies showed high support for relationships among genera. An earlier study on gallopheasants that also used UCEs (Meiklejohn et al., 2016) came to similar conclusions. However, in that study, which employed sparser taxon sampling, the positions of *Chrysolophus* and *Phasianus* were not well-supported—or even consistent—in all phylogenetic analyses. The more taxon-rich matrix analysed here appears to stabilize these inconsistences.

We did observe some conflict between the TN (or UCE) data set with the smaller data sets (mitochondrial and intron), though most of these involved nodes that were weakly supported using the smaller datasets. Thus, conflict among previous studies (reviewed by Wang et al., 2013) is likely due primarily to the limited numbers of characters and loci sampled. The exception to this was the cyto-nuclear discordance observed in the genus *Lophura*. Although our study only included three mitochondrial regions, relationships within *Lophura* were strongly supported. However, an analysis of complete mitochondria (Jiang, Wang, Peng, Peng, & Zou, 2014) produced a topology among the three *Lophura* species congruent with our mitochondrial topology and discordant with our TN topology. While some cases of cyto-nuclear discordance may be genuine, others can be due to inaccurate estimation of the mitochondrial tree, due to issues including poor taxon sampling or poor fit of empirical data to models of DNA sequence evolution (Tamashiro et al., 2019).

The short internodes among many genera in this group identified in previous studies (Kimball & Braun, 2014; Meiklejohn et al., 2016) hinted at rapid diversification at the base of gallopheasants. Yet, with expanded taxon and character sampling, we did not identify shifts in gallopheasant diversification rates. The discrepancy between this and previous studies may stem from a combination of factors. First, our study employed broad taxon sampling of all recognized species, rather than one or a limited selection from each genus. This may have improved estimation of branch-length patterns across the gallopheasant tree (Heath, Hedtke, & Hillis, 2008). Second, previous ideas of rapid gallopheasant diversification were based off of observations of tree shape, not formal tests for shifts in diversifications rate such as we employed in this study. Third, it remains possible that diversification shifts have occurred in gallopheasants, but we failed to detect them owing to the limited statistical power to infer them across relatively small phylogenies (Kodandaramaiah & Murali, 2018).

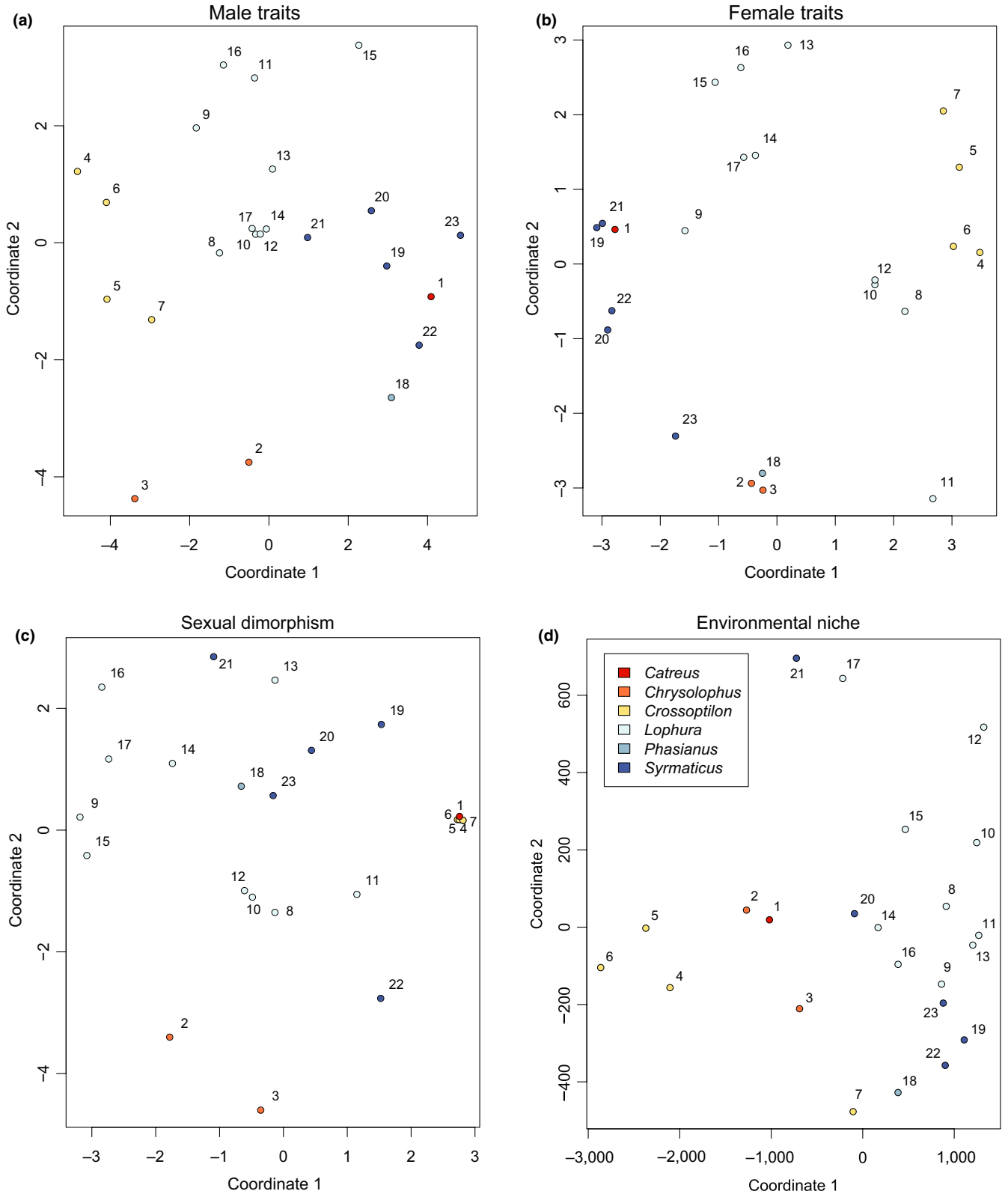

FIGURE 3 Non-metric multidimensional scaling of trait space for (a) male plumage and morphological traits (b) female plumage and morphological traits (c) sexual dimorphism, and (d) ecological niche. Although these visualizations are non-phylogenetic, genera and closely related species within genera clustered strongly. Numbers for each point correspond to a gallopheasant taxon: 1. *Catreus wallichii*, 2. *Chrysolophus amherstiae*, 3. *C. pictus*, 4. *Crossoptilon auritum*, 5. *C. crossoptilon*, 6. *C. harmani*, 7. *C. mantchuricum*, 8. *Lophura bulweri*, 9. *L. diardii*, 10. *L. edwardsi*, 11. *L. erythrophthalma*, 12. *L. edwardsi hatinhensis*, 13. *L. ignita*, 14. *L. inornata*, 15. *L. leucomelanos*, 16. *L. nycthemera*, 17. *L. swinhoii*, 18. *P. colchicus*, 19. *Syrmaticus ellioti*, 20. *S. huminae*, 21. *S. mikado*, 22. *S. reevessi*, 23. *S. soemmerringii* [Colour figure can be viewed at wileyonlinelibrary.com]

If gallopheasant diversification was indeed sparked by initiation of strong sexual selection, then the gain of sexual dimorphism observed here should accompany accelerated diversification. The negative result achieved here suggests a more nuanced role of sexual selection in relation to diversification rates in gallopheasants. Without formal evidence for diversification rate shifts in gallopheasants, the question of which factors have influenced gallopheasant trait evolution remains. The extreme sexual dimorphism and ornamentation common among pheasants logically suggest that sexual selection has been important in generating these novel ornamental traits. Yet, the rates of evolution and phylogenetic signal we observed among male traits, female traits, sexual dimorphism and environment were all similar, suggesting other factors were similarly influential. Additionally, the high degree of correlation among these trait suites prevents identifying whether evolution was due primarily to one of these trait suites, with others changing in response, or whether all of these trait suites evolved collectively (Maan & Seehausen, 2011; Ritchie, 2007; Servedio & Boughman, 2017; Wagner et al., 2012).

If sexual selection was an overwhelming force in gallopheasant trait evolution, to the exclusion of other factors, change in male traits would be expected to be show the greatest degree of divergence, whereas changes in female traits would be expected to be limited. While this pattern did hold in two of four genera with multiple species (*Chrysolophus* and *Syrmaticus*), it was not universal. For *Crossoptilon*, in which both sexes are very similar and share the same ornaments (ear tufts, plumed tail), the correlated changes in males and females were expected. Surprisingly, in *Lophura* it appears that there has been more change in female morphology than male morphology. This may suggest that sexual selection is less important in this group than in the others, and/or that there has been strong natural selection driving differences in female morphology, perhaps for background matching (Endler, 1978; Kenward et al., 1981; Michalis et al., 2017). Interestingly, the mating system of at least some species of *Lophura* may involve cooperative breeding (Zeng, Rotenberry, Zuk, Pratt, & Zhang, 2016). This unusual mating system may have either reduced the role of sexual selection within at least some *Lophura* species, and could have altered selection on female traits as well.

Although our results fail to identify sexual selection as a unique factor driving gallopheasant diversification, the results do not exclude a role for sexual selection in gallopheasant evolution. First, the history of male trait evolution does show some differences among genera, and there are some obvious differences in overall appearance when looking at the different genera. Second, differences in traits may have been greater at the time genera diverged than may be currently apparent, consistent with our observation that traits appear to be evolving slightly more rapidly than niche. What we can state based on our results is that, even if sexual selection was a factor in divergence among genera, female traits and environmental divergence were also similarly influential. This adds to the growing body of literature suggesting that multiple factors work in concert (Maan & Seehausen, 2011; Ritchie, 2007; Servedio & Boughman, 2017), and that focusing on sexual selection alone as a driver of diversification may lead to erroneously narrow conclusions. For example, adaptive radiation in African rift lake cichlids is linked to sexual selection, but only when appropriate environmental conditions are met (Wagner et al., 2012).

Our conclusion that environmental niche divergence is influential in gallopheasant diversification extends ideas gleaned from two of the more temperate genera, *Chrysolophus* and *Crossoptilon* (Lyu et al., 2015; Wang et al., 2017), to the broader gallopheasant clade. Between the two *Chrysolophus* species, Lyu et al. (2015) found that niche overlap was less than would be expected by chance, suggesting niche divergence has occurred. Similarly, Wang et al. (2017) suggests that there is niche divergence between two species of *Crossoptilon* (*C. mantchuricum* and *C. auritum*) though not between the very recently separated *C. crossoptilon* and *C. harmani*.

We extend these observations to *Syrmaticus* and *Lophura*. At first glance, close relatives and sister taxa *S. ellioti* and *S. huminae* appear allopatrically distributed across similar montane broadleaf and coniferous forest environments in mainland Asia. However, geographical projections of the niche models suggest that despite superficial similarity, potentially suitable environmental for *S. ellioti* and *S. huminae* has diverged substantially and has little overlap (Appendix S6). Across *Syrmaticus*, overlaps of potentially suitable environmental are more prevalent in distantly related taxa: projected niche of Japanese endemic *S. soemmerringii* broadly overlaps *S. reevesii* (eastern China) and *S. mikado* (montane Taiwan). However, geographical projections of environmental niche are not necessarily reciprocal—suitable environments for *S. reevesii* do not overlap *S. soemmerringii* or *S. mikado*. Similar idiosyncratic examples are found throughout *Lophura*. Sister taxa *L. ignita* and *L. inornata* are each distributed across Sundaland, but occupy non-overlapping ecological niches, with *L. ignata* occupying lowland forests and *L. inornata* restricted to montane forests of Sumatra, suggestive of niche partioning. However, these patterns are not universal—potentially suitable environments for sister taxa *L. leucomelanos* and *L. nycthemera* broadly overlap one another. The two species regularly hybridize across a narrow zone (Dong, Heckel, Liang, & Zhang, 2013). These examples each illustrate the broader macroevolutionary pattern of the phylogenetic analysis that environmental niche evolution is dynamic across gallopheasants.

Our careful examination of factors that have affected diversification and trait evolution among gallopheasants

suggests that although this clade is characterized by species where males are highly ornamented and where sexual selection is known to be important in at least one well-studied species (Mateos, 1998)—and likely in others, environmental niche and female traits showed correlated macroevolutionary patterns that suggest a more complex suite of factors involved in diversification and trait evolution of this group.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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