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Spatial patterns of genetic diversity in eight bear (Ursidae) species

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Abstract: Many of the 8 extant bear species have large ranges, yet range-wide studies of genetic diversity are often impractical because of logistic challenges or focus on local questions. However, understanding the levels of diversity among populations of a species can be useful for conservation and management. Bear researchers were at the forefront of using microsatellites to study the demographics and diversity of populations, such that 3 species have complete sampling and 3 others are represented across their range breadth. Yet there has not been a synthesis of these data within or among species because of difficulties comparing microsatellites. We extracted microsatellite summary statistics from 104 papers that sampled 284 populations of any species within Ursidae, then yardstick-transformed the data for direct comparison. Studies had a median of 2 geographic sites, 30 individuals sampled per site, and 12 loci genotyped. We identified 193 loci genotyped in bears and argue this is a limitation within and among species comparisons. *Tremarctos ornatus* had the lowest average range-wide genetic diversity ($A_r = 2.5$; $H_e = 0.43$), although ascertainment bias may affect the results, whereas *Ursus arctos* had the highest diversity ($A_r = 6.4$; $H_e = 0.69$). We argue that at the spatial scale of a species' range, variation due to phylogeography and anthropogenically influenced diversity will overwhelm accuracy issues between studies and reveal broad spatial patterns. Further, by comparing allelic richness to heterozygosity across the range of a species, managers may identify populations in need of genetic management. We end by summarizing what is known about within-species lineages and genetic diversity and identify priority areas for future studies.

Key words: bears, conservation genetics, microsatellite, population genetics, short tandem repeat, simple sequence repeat, spatial genetic diversity, SSR, STR, Ursidae

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Genetic variation is an important feature of populations, particularly because it is the raw material upon which neutral and adaptive processes act. Populations are the units of evolutionary change and extirpation, so they frequently are concordant with management units. Managers use a variety of metrics related to both habitat (e.g., size, patchiness, quality) and intrinsic population characteristics (e.g., age structure, density, mortality rate) to promote species persistence with other land use goals. Genetic diversity may also inform management (Johnson et al. 2010), particularly by identifying populations at risk of extirpation as a result of loss of genetic diversity, inbreeding, and the fixation of deleterious alleles (Blomqvist et al. 2010). Studies have shown that genetic diversity has decreased across taxa and geography since the Industrial Revolution (Leigh et al. 2019), and that habitat fragmentation is one cause of this decline (DiBattista 2008). Both contemporary processes at the population level and older lineage-specific histories will influence diversity; thus, comparison among populations can be useful to assess whether a population has absolute and relative diversity levels lower than those observed across the range.

Bear researchers were early adopters of microsatellites (Paetkau et al. 1995, Taberlet et al. 1997) for the study of population structure, gene flow, genetic diversity, and evolutionary relationships. Moreover, the bear management community has widely adopted the use of genetic mark–recapture of noninvasively collected hair samples to estimate census size, density, and sex ratio in managed populations (Mowat and Strobeck 2000, Garshelis and Noyce 2006, Gardner et al. 2009, Sawaya et al. 2012). The result is that the evolution and management communities have produced an extensive literature on population genetic diversity, although we acknowledge this work is skewed toward *Ursus americanus* and *U. arctos*. By combining genetic diversity estimates with their spatial coordinates, we can infer additional information about how a population fits into the landscape, and broader

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phylogeographic patterns, such as the higher diversity in areas that were former glacial refugia (Hewitt 2000) or regions of admixture (Petit et al. 2003).

Microsatellite data are not readily comparable between studies; however, recent work has begun to synthesize this large literature (Lawrence et al. 2019). The factors that preclude comparison between microsatellite studies include allele calling differences between researchers, use of different loci, use of different primers for the same locus, variation due to sequencing platform, variation due to florescent labels, and variation due to multiplexing (Moran et al. 2006, de Valk et al. 2009, Ellis et al. 2011, Lawrence et al. 2019). Moreover, variation in sample size and the number of microsatellite loci genotyped affect accuracy and precision of the population estimate. We acknowledge that comparability of microsatellite studies has real biases, yet we also see the value of placing individual studies within their broader spatial context. Specifically, geographic patterns of spatial diversity are associated with lineage divergence, locations of glacial refugia, areas of secondary contact, and directionality of range expansions. Yet these historical evolutionary processes may be obscured by more recent events, including habitat loss, habitat fragmentation, or declining census size due to persecution or harvest (DiBattista 2008). For example, a spatial analysis of genetic diversity in *U. americanus* identified that areas of the range that were glacial refugia had lower allelic richness (A_r) and expected heterozygosity (H_e) than sites colonized after glacial retreat, suggesting that contemporary, and not older, processes strongly influenced diversity (Puckett 2015).

Use of data from across research studies enables both range-wide within-species, and among-species, comparisons of diversity. For many researchers, range-wide or multispecies sampling is too logistically difficult, expensive, or unnecessary for their research question. The comparison of microsatellite studies has been advanced by groups applying novel methods to the data prior to analysis, including using linear modeling to estimate diversity at multiple scales of biological organization (Pinsky and Palumbi 2014, Lawrence et al. 2019), and resampling diversity compared with a reference population (e.g., yardstick transformation) such that populations are one-to-one comparable (Skrbinšek et al. 2012). The latter technique sets the average genetic diversity of a reference population to 100%, then scales other populations for comparison (e.g., 60% of the diversity of the reference), based on number of shared loci and sample size.

We investigated spatial genetic variation among populations and species of bears. Our objectives were to (1) compare microsatellite loci usage within and across species to identify common and rare markers in bear research, and (2) estimate range-wide patterns of spatial genetic diversity for each species. Incidentally, our work highlights which species and geographic regions have seen little population genetic study. Thus, our results can inform future research on bears by identifying high-priority study areas and a set of markers to increase comparability across studies.

Study area

We studied all 8 species of Ursidae across their range where relevant literature was available.

Methods

Literature search

We searched for research papers and theses or dissertations that estimated genetic diversity in each of the 8 bear species using both Web of Science and Google Scholar as of 31 May 2019. We used keyword searches with both bear common or scientific names and "microsatellite*." For sloth and sun bears, we ran searches with both genera names, *Melursus* and *Helarctos* respectively, and *Ursus*. We scanned each paper to identify whether microsatellite summary statistics were included, and that the paper estimated values from ≥1 populations. We excluded papers that genotyped microsatellites yet reported no genetic data (e.g., genetic mark–recapture studies). We excluded microsatellite loci on the X or Y chromosomes. We acknowledge the loci developed by Shen et al. (2005, 2007) and Meredith et al. (2009), but excluded these studies because they reported their summary statics collapsed across geographic areas. We excluded one study that appeared to report diversity estimates on a per individual basis (Peacock et al. 2007), particularly because recent work has markedly different diversity estimates, likely due to per population calculation (Lewis et al. 2020). We did not reanalyze data for population structure; thus, any over- or underclustering of samples was accepted as the original authors interpreted their data. When the per-locus summary statistics were not available but genotypes had been published, we used Microsatellite Toolkit (Park 2002) to calculate A_r and H_e per locus.

For each paper we recorded the following metadata for each geographic site: bear species, microsatellite locus, number of samples genotyped, A_r, H_e, longitude, latitude, and citation. When data were reported as averages across loci instead of being listed per locus, we recorded the average A_r, H_e, and the associated standard errors. We recorded 4 Boolean variables: 3 for sample type collected

(tissue, feces, and hair) where a study could use ≥1 types, and 1 variable if data were averaged across loci or reported per locus. We calculated species-level diversity statistics from populations with >4 individuals sampled.

The yardstick analysis requires the standard error of A_r and H_e to be estimated for each population; however, not all studies reported these values. For studies where individual locus estimates were available, we calculated the standard error. For studies where diversity was averaged across all loci, we added standard error based on the total error observed across all the studies. The magnitude of the standard error increased with increasing A_r (slope = 0.39; $P < 0.001$) and H_e (slope = 0.15; $P < 0.001$); therefore, for populations without error noted in the paper, we added error based on the slope from the regression model (Pinsky and Palumbi 2014).

Analyses

Microsatellite description. We counted the number of studies that genotyped each microsatellite locus and summed across all studies and species within Program R v3.6.0 (R Core Team 2013). We also estimated the mean, median, and ranges for both the number of loci and number of sampling sites reported per study.

Spatial. To compare genetic variation between populations, we used a yardstick transformation (Skrbinšek et al. 2012). This method calculates genetic diversity from a single population with both large sample size and number of loci genotyped by resampling the number of individuals in the focal population for comparison at only the shared loci. Then using this newly computed estimate of allelic richness or heterozygosity, this method computes a ratio of diversity compared with the reference population, thereby allowing multiple populations to be compared with each other. This method gains power by having both large sample sizes and number of genotyped loci within the reference population. We selected the Shiretoko Peninsula population of the *U. arctos* data set (n = 837, loci = 21; Shimozuru et al. 2019) as the reference. We ran the subsample.gen and CalcDivRat functions in the *resamplediversity* package in R to complete the yardstick analysis. We visualized spatial patterns of genetic diversity of the untransformed data, including only sites with >4 individuals.

Results

Characterization of Ursidae microsatellite studies

We identified 161 studies using our keyword searches and retained 104 after screening for microsatellite summary statistics and removing papers that used previously published data sets. Within these papers, 284 unique geographic locations were studied, where 67 sites were sampled more than once by different authors. *Ursus americanus* appeared in 40 studies, followed by 32 papers with *U. arctos*. *Ursus thibetanus* and *U. maritimus* were studied in 15 and 14 papers, respectively. We analyzed 3 studies of *Ailuropoda melanoleuca,* 2 each of *U. ursinus* and *Tremarctos ornatus,* and 1 paper for *U. malayanus*. Some papers studied multiple species. Using author-defined geographic sites, a median of 2 sites (mean = 3.9, range = 1–61) were studied per published paper. Sample size of animals genotyped per geographic site varied from 1 to 2,945 bears, where the mean and median across all species were 59.6 and 30, respectively (Table S1, *Supplemental material*).

We identified 193 unique microsatellite markers used to study bears (Table S2, *Supplemental material*). Of these markers, 76 loci genotyped a single population of a single species; this was prevalent in *U. maritimus* and *U. thibetanus,* where 23 and 21 loci were used in a single publication. Further, none of the *A. melanoleuca* studies used loci that were also genotyped in another species. Across the 104 studies, bear researchers used a median of 12 microsatellite loci (mean = 12.8, range = 3–49; Fig. S1, *Supplemental material*).

Genetic diversity of Ursidae

Genetic diversity varied among species and throughout each species' range (Figs. 1–8). Allelic richness varied from 1 to 20 (median = 6, mean = 6.8) alleles per locus at a geographic site. We present species results from lowest to highest diversity, given available range-wide sampling only including populations genotyped at >4 samples (Table S1). *Tremarctos ornatus* had the lowest mean A_r of 2.56 alleles/locus and H_e of 0.44 (Fig. 3); H_e was largely stable across populations, whereas A_r showed lower values in southern populations. *Ursus malayanus* also had low overall diversity with mean A_r of 4.90 alleles/locus and H_e of 0.54 (Fig. 4); however, a fuller picture of genetic diversity was not available for this species because of the availability of only a single study. The studies of *A. melanoleuca* represent the entire extant range, where mean A_r was 4.94 alleles/locus and H_e was 0.56 (Fig. 5). Diversity was highest in the centrally located populations of the Minshan and Qionglai Mountains. *Ursus ursinus* had a mean A_r of 6.23 alleles/locus and H_e of 0.64 (Fig. 5). *Ursus thibetanus* populations had a mean A_r of 5.49 alleles/locus and H_e of 0.59 (Fig. 4). Populations across southern Asia had moderate to high diversity despite geographic isolation; populations in Korea and

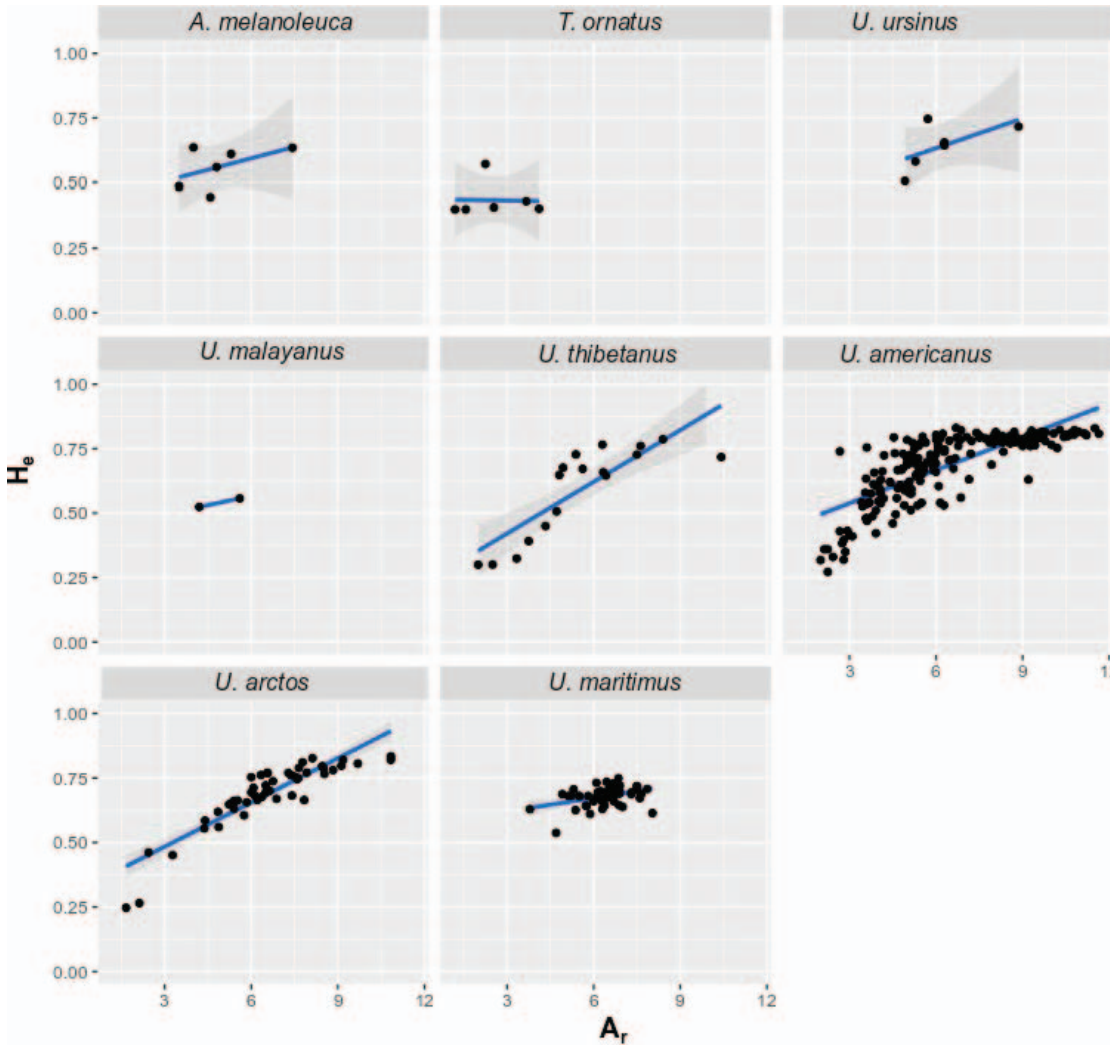

Fig. 1. Estimates of allelic richness (A_r) and expected heterozygosity (H_e) from the literature for populations (black dots) of the 8 species of Ursidae, with trend lines (blue) to highlight within-species variation between the variables.

Russia had high H_e although lower estimates of A_r. Across Japan, populations in the south had lower genetic diversity than in the north. *Ursus maritimus* has near complete range-wide sampling; we observed a narrow range of genetic diversity values, where mean A_r was 6.34 alleles/locus and H_e was 0.68 (Fig. 6). *Ursus arctos* had a mean A_r of 6.44 alleles/locus and H_e of 0.69 (Fig. 7). Genetic diversity was high in Finland and eastern Russia, and highly isolated populations in Spain and Mongolia had the lowest genetic diversity in the Eastern Hemisphere. North American populations had moderate diversity, and a distinct decrease in range edge populations could be observed, including the Greater Yellowstone Ecosystem and Kodiak Island, which had the lowest diversity. *Ursus americanus* had the most extensive sampling, allowing us to best compare the relationship between A_r and H_e (Fig. 1). For the species, the mean A_r was 6.25 alleles/locus and H_e was 0.69 (Fig. 8). Range edge and isolated populations had lower diversity, where populations along the Gulf Coast were particularly low; further, the Great Lakes region had the highest genetic diversity for the species.

To make directly comparable estimates of genetic diversity across all populations and species, we used a

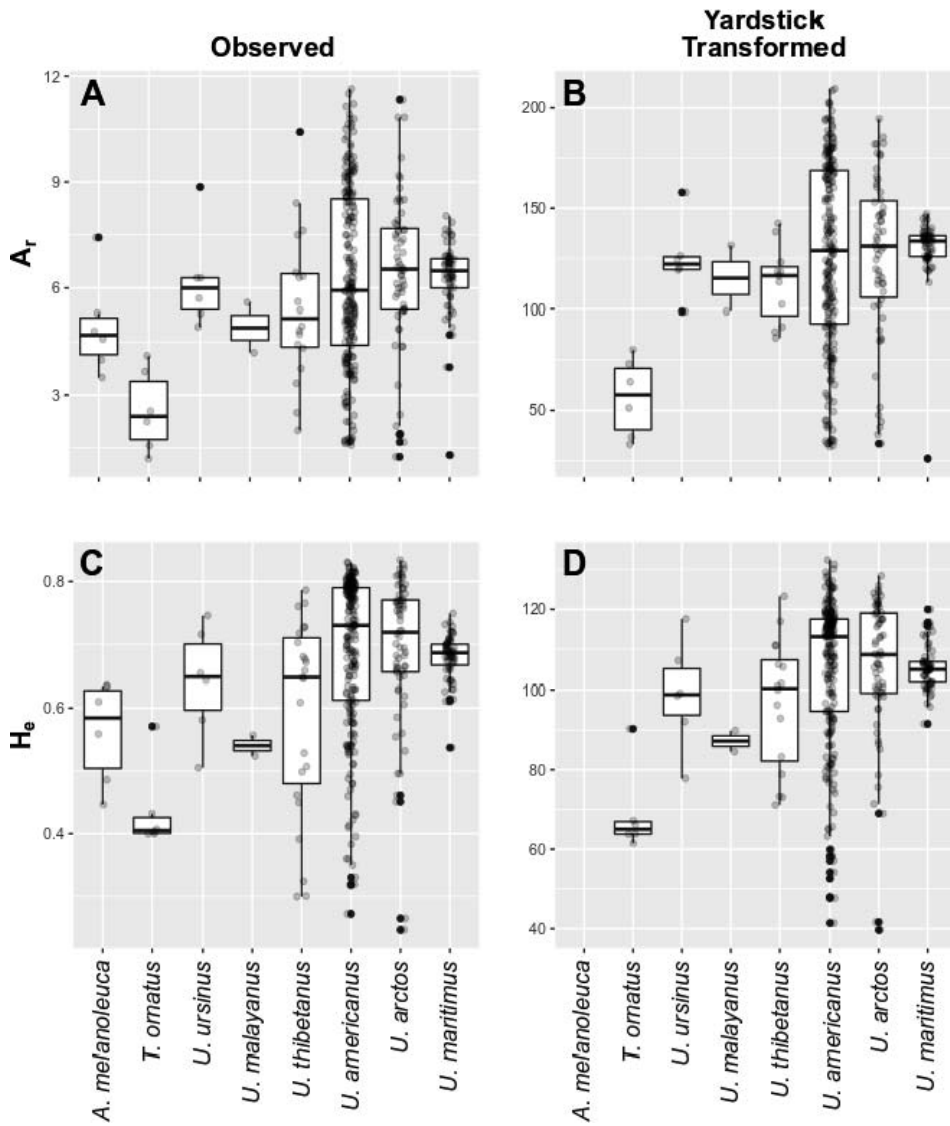

Fig. 2. Observed (A, C) and yardstick-transformed (B, D) estimates of allelic richness (A: alleles per locus per population; B: proportion change from reference population in %) and expected heterozygosity (C: diversity per population; D: proportion change from reference population in %) at the population level (light grey circles) in 8 species of Ursidae with boxplots showing the mean, first and third quantiles, and outliers in solid black circles.

population of *U. arctos* from Shiretoko Peninsula (A_r = 5.6; H_e = 0.67; Table S3, *Supplemental material*) as the reference in a yardstick analysis. No population of *A. melanoleuca* could be compared in the yardstick analysis because of the lack of shared loci (Table S2). The general trend was for species to maintain relative means among species between unadjusted and yardstick estimates (Fig. 2, Table S3); however, 2 species stood out in the yardstick analysis. In the raw data, *U. malayanus* had low genetic diversity; yet in comparison with the reference population, the Cambodian population of sun bears have 15% greater A_r but 12.5% lower H_e than the reference population, suggesting those populations were within the normal range of bear genetic diversity. In contrast, *T. ornatus* had a mean A_r and H_e that were 46% and 31% lower, respectively, than the reference population. Although the

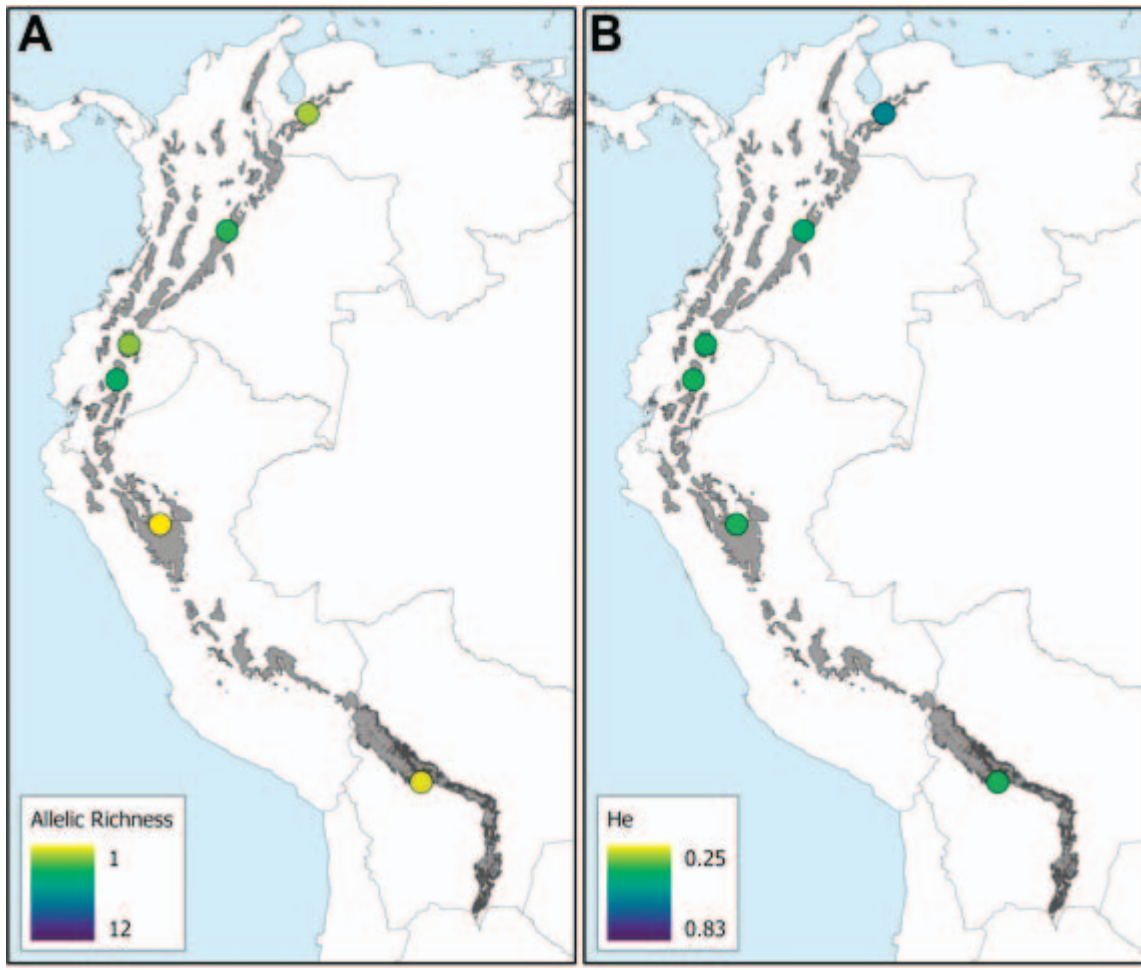

Fig. 3. Estimates of (A) allelic richness (A_r) and (B) expected heterozygosity (H_e) from the literature across the range (gray polygons) of *Tremarctos ornatus*. Note that scale bars are consistent among Figures 3–8 and represent the raw, not yardstick-transformed, data.

relative position of *T. ornatus* did not change between raw and yardstick estimates, we note the low diversity across the range.

Discussion

Our results have several implications for the conservation and management of bear populations. First, our maps make clear that North American populations, all populations of *A. melanoleuca,* and Japanese populations of *U. thibetanus* and *U. arctos* have been well-sampled for genetic diversity analyses, and that other species and geographic regions have been understudied in comparison. Although this disparity among species and/or countries is broadly known in the bear research community, our results highlight geographic regions that warrant study, and can be used to select populations both geographically isolated and with no nearby studies to prioritize collection of population genetic data.

Second, we encourage bear researchers beginning new projects to thoughtfully consider which loci to genotype. We identified 193 loci developed to study bears (Table S2), which excluded 43 developed by Shen et al. (2005) and 30 by Meredith et al. (2009, 2020). The most commonly used loci were the sets developed by Paetkau et al. (1995) and Taberlet et al. (1997). We acknowledge that population-specific allelic dropout and the presence of monomorphic loci will affect microsatellite marker

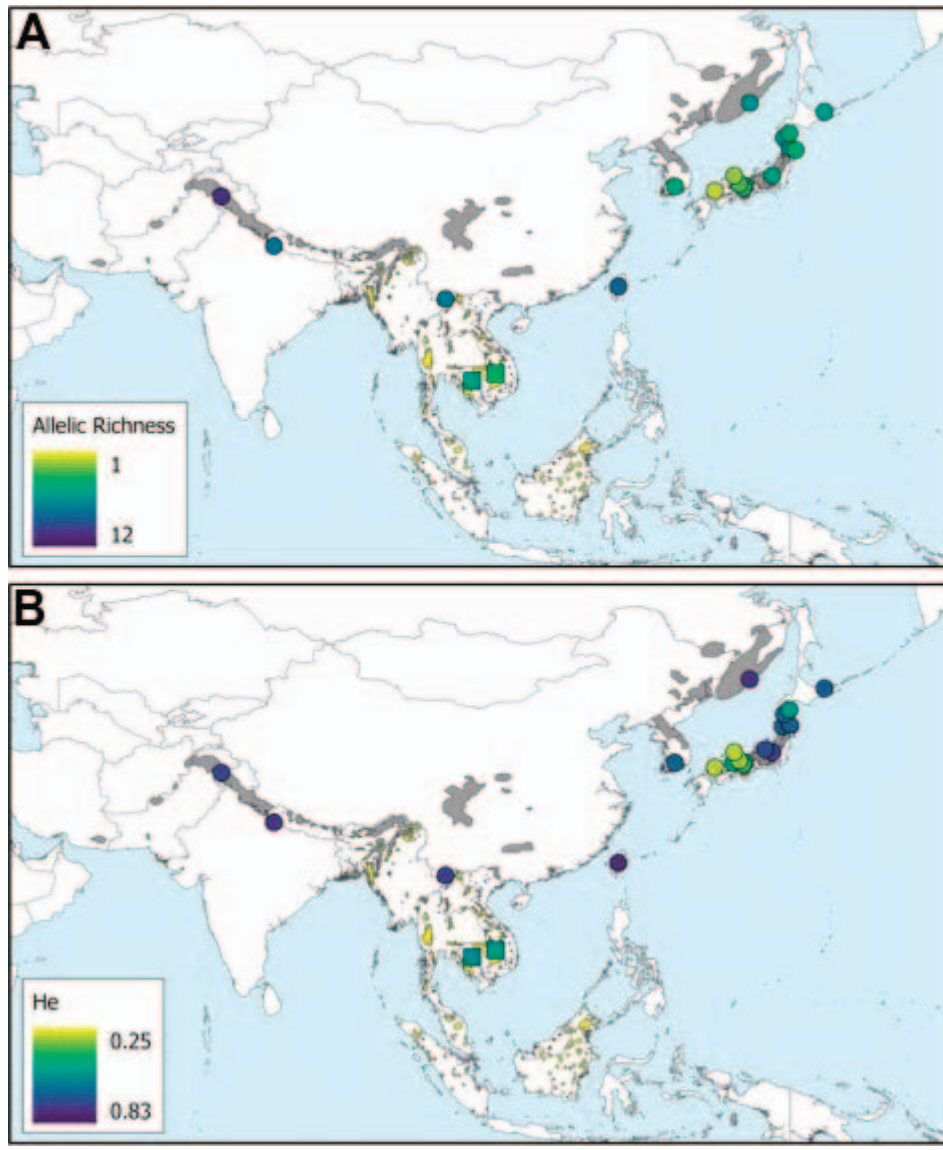

Fig. 4. Estimates of (A) allelic richness (A_r) and (B) expected heterozygosity (H_e) from the literature across the ranges of *Ursus thibetanus* (gray polygons; circle data points) and *Ursus malayanus* (yellow polygons; square data points). Note that scale bars are consistent among Figures 3–8 and represent the raw, not yardstick-transformed, data.

selection within a single study, and thus it is not always practical to use the most common markers. However, use of a common marker set and/or calibrating alleles based on genotyping reference samples from another study will enable more accurate comparisons among studies and facilitate use of new methods, such as the yardstick transformation (Skrbinšek et al. 2012). We feel that spending conservation monies to develop new microsatellite panels when so many loci have been developed and field-validated is not the best use of limited resources. We argue that those monies would be better spent collecting new data than developing new marker panels (although see discussion of *T. ornatus* below). That said, problems with ascertainment bias related to the development of markers in one species but low amplification, low allelic diversity, monomorphic loci, or dropout in another species could

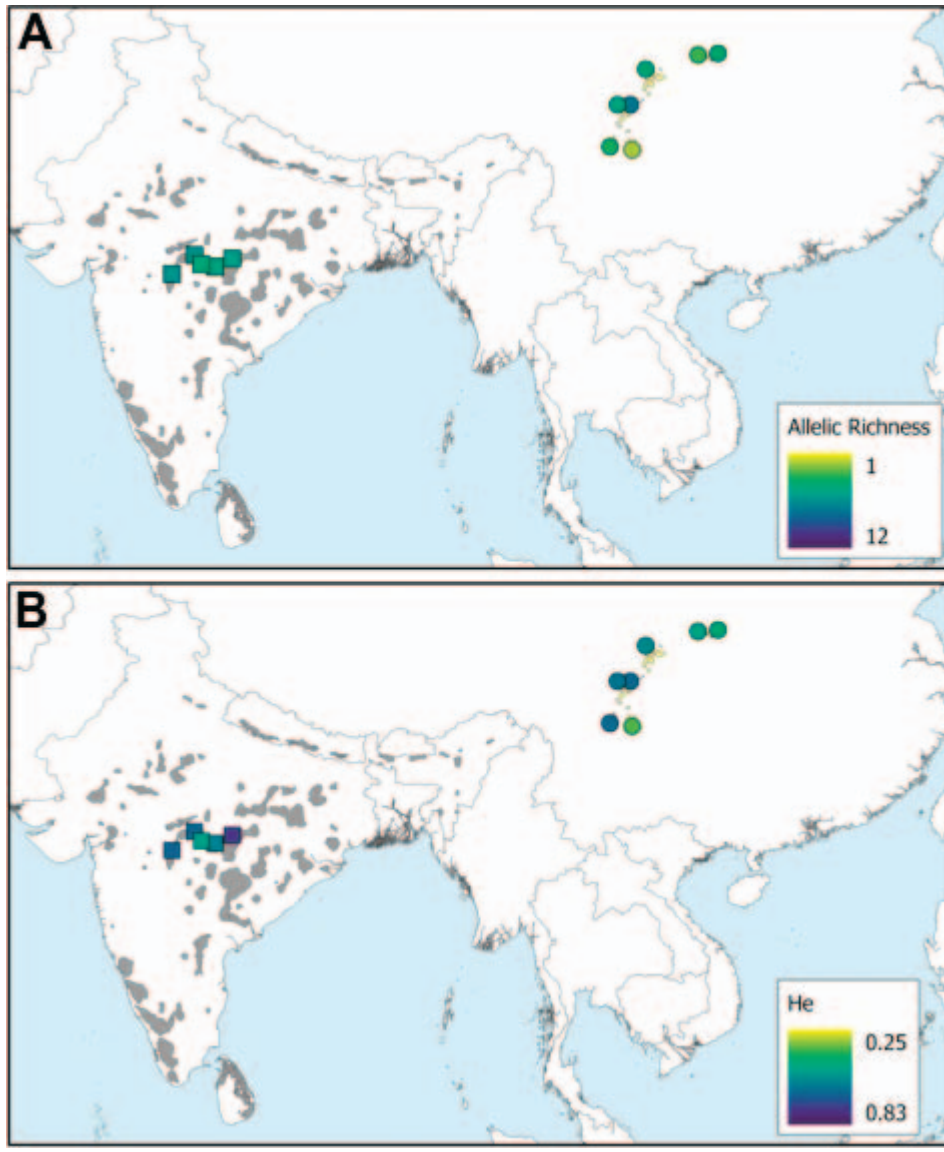

Fig. 5. Estimates of (A) allelic richness (A_r) and (B) expected heterozygosity (H_e) from the literature across the ranges of *Ailuropoda melanoleuca* (yellow polygons; circle data points) and *Ursus ursinus* (gray polygons; square data points). Note that scale bars are consistent among Figures 3–8 and represent the raw, not yardstick-transformed, data.

limit the utility of some markers and this effect may be species- and/or population-specific. When using primers for loci developed in another species, more recently diverged taxa will have lower rates of allelic dropout than those distantly related (Soulsbury et al. 2008). Thus, we may expect dropout to be higher for *A. melanoleuca* and *T. ornatus,* given that the most commonly used loci were developed in *Ursus*. *Ailuropoda melanoleuca* and *T. ornatus* diverged 19 and 12.8 Mya, respectively, whereas the 6 *Ursus* species diverged from each other within 5 Mya (Krause et al. 2008). Cross-species dropout or low amplification success has been observed for some loci among the 6 *Ursus* species (Uno et al. 2012, Sharma et al. 2013, Meredith et al. 2020). The yardstick transformation cannot remove the effects of ascertainment bias on diversity estimates from the focal population unless the locus

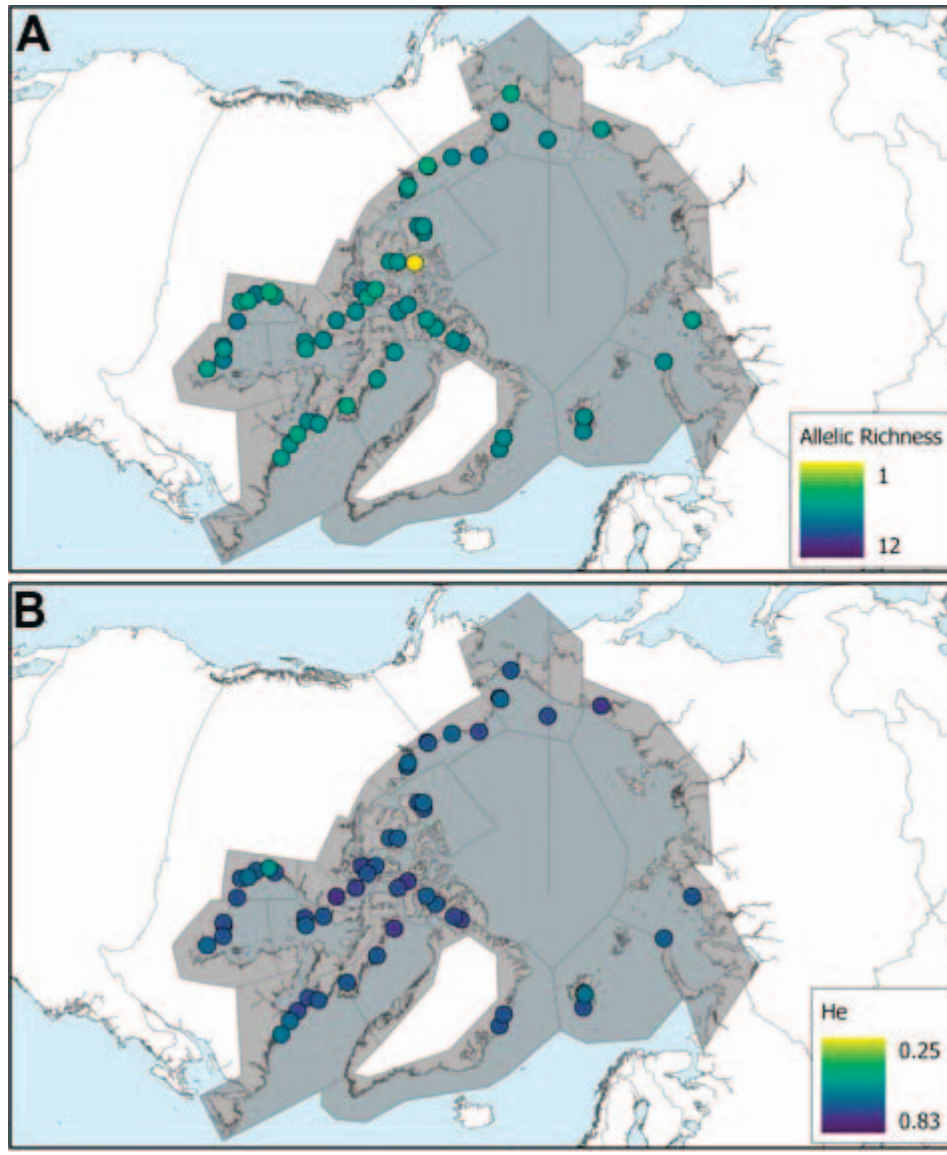

Fig. 6. Estimates of (A) allelic richness (A_r) and (B) expected heterozygosity (H_e) from the literature across the range of *Ursus maritimus*. Note that scale bars are consistent among Figures 3–8 and represent the raw, not yardstick-transformed, data.

containing the bias is not in the reference population. Further, ascertainment bias in the reference population would affect focal population estimates that shared the locus or loci.

Third, the cross-species data comparing A_r to H_e showed the range of variation in genetic diversity within bears (Fig. 1), as compared with theoretical limits on the number of microsatellite alleles in a species ranging between 40 and 60 (Cornuet et al. 2014) and heterozygosity bound 0 to 1. Caution is warranted when comparing microsatellite studies because of among-study variation; however, at the scale of the species' range, and with dense sampling as in this study, we believe our results reflect real patterns in spatial genetic diversity, even given variation in accuracy of individual studies. Our results are buttressed by instances of different research groups

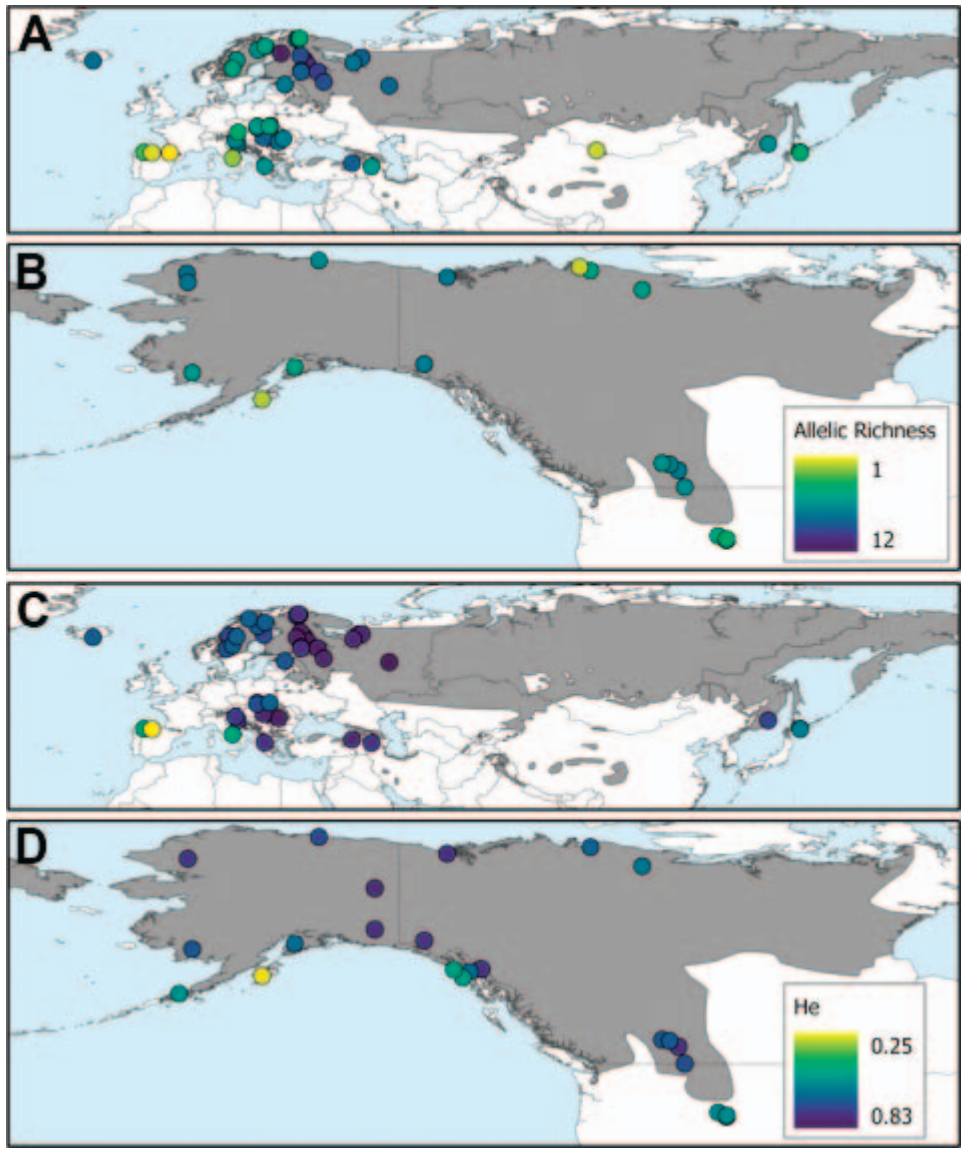

Fig. 7. Estimates of (A, B) allelic richness (A_r) and (C, D) expected heterozygosity (H_e) from the literature across the range (gray polygons) of *Ursus arctos*. Note that scale bars are consistent among Figures 3–8 and represent the raw, not yardstick-transformed, data.

studying the same population and returning similar values of A_r and H_e (Table S3). The high sampling density of *U. americanus* and *U. arctos* captured both the high and low ranges of within-species diversity, allowing us to observe practical (and not theoretical) limits on these values. Although individual loci had >12 alleles within a population, the mean upper bound in a multilocus study appears to be near 12 alleles. This was consistent with a study of microsatellite diversity across vertebrates, where in mammals 15 of 1,944 populations had a mean number of alleles >15/population (Lawrence et al. 2019). The *U. americanus* data suggest that H_e plateaus around 0.85 (Fig. 1) and that this high level of heterozygosity occurs across a range of A_r values. More important for conservation are the low-diversity populations. We show that diversity rarely decreases below 2 alleles/population and a heterozygosity of 0.25 (although it could, particularly if the population was in an extinction vortex). Moreover, the

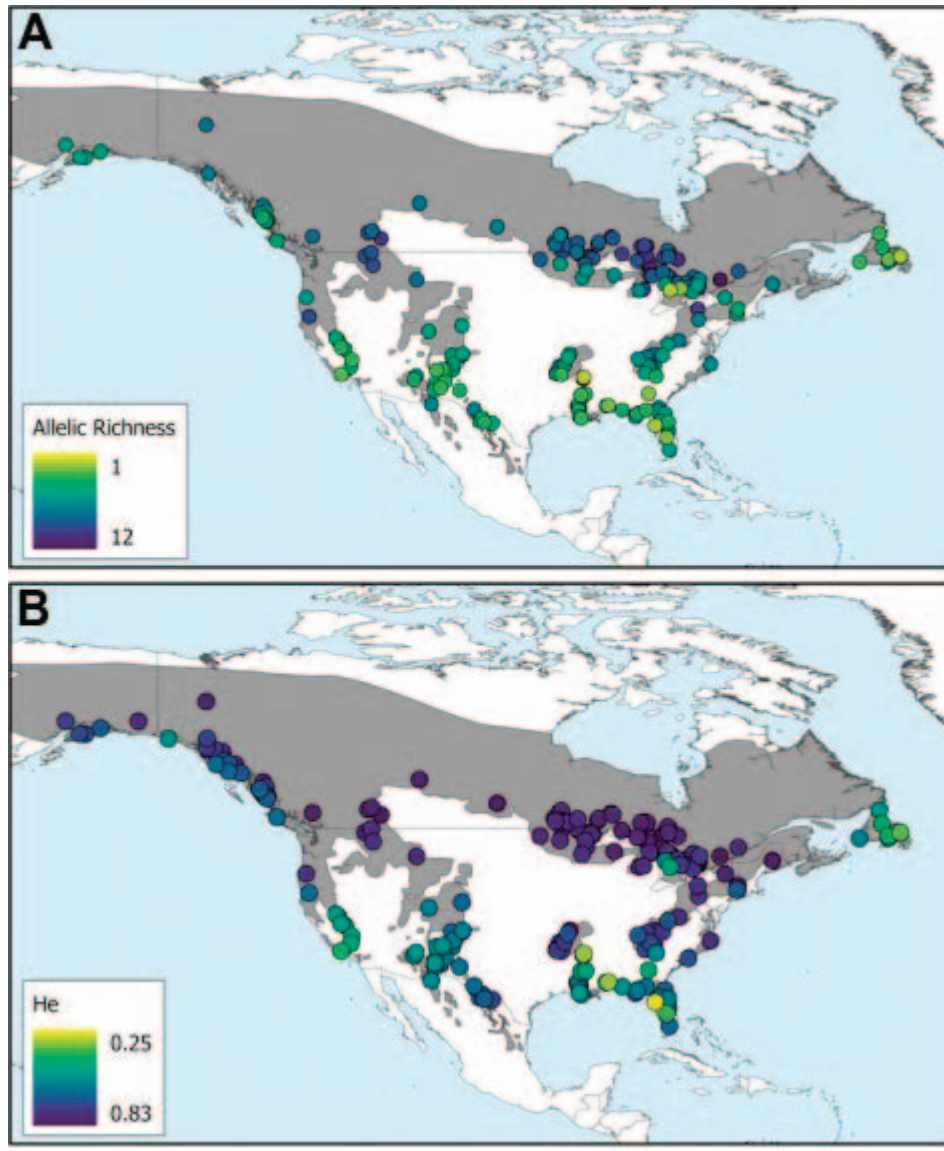

Fig. 8. Estimates of (A) allelic richness (A_r) and (B) expected heterozygosity (H_e) from the literature across the range (gray polygons) of *Ursus americanus*. Note that scale bars are consistent among Figures 3–8 and represent the raw, not yardstick-transformed, data.

removal of monomorphic loci ($A_r = 1$; $H_e = 0.0$) from a marker panel will inflate genetic diversity estimates. The compilation of these data allows us to quantitatively consider how to assign populations to "high," "average," and "low" diversity populations. Allelic richness declines faster than heterozygosity (Garza and Williamson 2001); thus, active genetic management should emphasize action for populations where both A_r and H_e are low, because H_e is a lagging indicator. Although the regression lines on Figure 1 were primarily to visualize patterns within each species' data (and would shift given more data), we could alternatively use them to identify populations where A_r and H_e have uncoupled. Populations above the regression have high H_e compared with A_r and are of lower conservation concern; whereas, populations below the regression have fewer alleles than expected, based on heterozygosity, and may be in early or late stages of genetic diversity loss. We note that using the regression

lines in this way does not make sense for all populations (e.g., high-diversity *U. americanus* populations near the limits of the diversity fall below the regression line) and that managers should consider habitat size, demographic decline, and local threats. However, if information was limited, we see value in comparing new data to that presented in Figure 1.

Geographic variation of bear genetic diversity

We compiled the largest data set of ursid genetic diversity and further scaled it to be comparable across species and populations. We end with a discussion of diversity for each species and where possible use mitochondrial or nuclear genomic information about within-species lineages to scaffold our understanding of spatial variation. Finally, we highlight priority research questions or areas for each species.

Ailuropoda melanoleuca. Markers were primarily or exclusively used for giant panda research, so we could not compare diversity with other ursids; therefore, our discussion is limited to the untransformed population estimates. Giant panda genetic diversity was lower than that of many other ursid species and likely reflects habitat fragmentation and small population sizes (Ma et al. 2018). Whole genome sequencing (WGS) data estimated nucleotide diversity of 1.13–1.37 $\times$ 10^{-3} (Zhao et al. 2013), which was similar to an estimate for *U. americanus* (1.43 $\times$ 10^{-3}), yet lower than *U. arctos* (2.49 $\times$ 10^{-3}), although there were methodological differences between these estimates (Hailer et al. 2012). Contemporary mitochondrial diversity forms a single clade that coalesces 65 kya (Barlow et al. 2019), and 3 subpopulations across 6 mountains ranges were identified based on patterns of nuclear genetic diversity (Zhang et al. 2007, Zhao et al. 2013). These subpopulations have limited gene flow, as a result of the highly mountainous terrain (Ma et al. 2018) and disconnected distribution between mountains. It is clear from fossil locations that the range contracted substantially, and aDNA results show loss of a mitogenome clade during the Pleistocene (Barlow et al. 2019).

We did not include microsatellite data from the captive breeding populations of giant panda (Shan et al. 2014) because we were interested in patterns of wild genetic diversity. However, based on their analysis of 19 loci, A_r in the captive populations ranged from 4.1 to 5.8 alleles/locus, and H_e from 0.58 to 0.67, suggesting that captive genetic diversity is within the range of wild populations.

Tremarctos ornatus. Our analysis identified Andean bears as the species with the lowest genetic diversity across its range when compared with other ursids, where this pattern held when adjusted to a reference population. Andean bears also had the lowest diversity within Ursidae in a study of nuclear introns (Kutschera et al. 2014), although WGS observed heterozygosity levels similar to polar and sloth bears when compared with all other species (Kumar et al. 2017); however, both studies utilized captive individuals, which may have reduced diversity. The low diversity across the Andean bear range may either be due to real ecological and evolutionary process that resulted in lost diversity, or ascertainment bias within microsatellite loci as previously proposed (Viteri and Waits 2009). Despite our aforementioned concerns about resource use for microsatellite development, the Andean bear would be a strong candidate to compare species-specific versus currently available loci to determine whether bias has affected diversity estimates. If low genetic diversity is not a result of marker choice, then opportunities for the management and conservation of genetic diversity may warrant consideration.

Ursus ursinus. With a range covering the Indian Subcontinent, Himalayas, and Sri Lanka, only tiger (*Panthera trigris*) reserves within central India have been studied to date (Sharma et al. 2013, Dutta et al. 2015), where evidence suggests the reserves form a single population with east–west substructure. This population has moderate A_r and slightly reduced H_e compared with worldwide ursid populations (Table S3). Whole genome sequencing data suggest sloth bear diversity is equally low to that of polar and Andean bears (Kumar et al. 2017), yet this was from a single zoo individual and may not reflect range-wide diversity. Thus, geographically diverse sampling of the sloth bear range to assess genetic diversity and the presence or absence of within-species lineages should be the highest priority for population genetic research in this species.

Ursus malayanus. The sun bear has received the least work on its population genetics and broader lineage divergence. Whole genome sequencing data suggest 2 independent evolutionary histories (Kumar et al. 2017), and mitochondrial haplotypes suggest 3 lineages (Paetkau and Strobeck 1996), although neither study can be associated with geography; further, each study found the number of unique lineages equal to sample size, and thus there are likely $\geq$3 lineages of sun bears. Given the geography of the sun bear range, range expansion and isolation onto Borneo and Sumatra may have occurred during the Pleistocene, which is further suggested by a possible divergence time of 100 kya in the WGS data. When we yardstick adjusted the microsatellite data, A_r was in the range of other ursids (Fig. 2), although H_e remained low for the Cambodian population. Priority genetics questions in this species include identifying lineages or evolution-

arily significant units, then estimating genetic diversity across the range to see whether particular regions would benefit from genetic management.

Ursus thibetanus. We observed high variability in genetic diversity across the Asiatic black bear range. Our sources either did not report summary statistics or used markers not shared with the reference population, so our interpretation of the yardstick results was limited. That said, yardstick values were in the range of other species for both A_r and H_e (Fig. 2). Genetic diversity was well-estimated across Japan, and showed a decline in diversity, particularly H_e, from the north to the south (Fig. 4). Estimates from Korea and Russia had lower A_r than other continental populations, which had moderate to high diversity, despite fragmentation, which likely prevents gene flow across the range. Results of high diversity in this species were also observed for genome-wide heterozygosity estimates for a zoo individual (Kumar et al. 2017). Given the high level of habitat fragmentation for this species, much of the range has been sampled.

Work on the range-wide phylogeography of Asiatic black bears has concentrated on the eastern portion of the range. Mitogenome data estimate the lineage that colonized Japan diverged approximately 1.5 Mya yet diversified more recently (Wu et al. 2015). Mitogenome signatures also suggest a recent northward range expansion that colonized the Korean Peninsula and eastern Russia (Wu et al. 2015). Thus, future work on range-wide genetics should incorporate the western portion of the species' range, and also expand nuclear data, because mito-nuclear discordance is known to influence phylogenetic patterns within and among bear species.

Ursus americanus. Genetic diversity was highly variable across the range of the American black bear. Specifically, southern populations had low A_r and H_e (Fig. 8), regardless of belonging to either the eastern or western lineage (Puckett et al. 2015). We interpret the low levels of genetic diversity in the south as a consequence of high levels of habitat fragmentation, despite southern geographies having been identified as glacial refugia with the expectation that diversity would be elevated in these areas. We further interpret the high diversity across Canada as due to multiple factors, including large census sizes, low levels of habitat fragmentation, and gene flow between the eastern and western lineages, which creates admixture, a process known to increase genetic diversity (Petit et al. 2003). Admixture was also identified in the northern Rocky Mountains and Southeast Alaska, USA, which may extend along the coast of British Columbia, Canada, but direct studies are needed. The lower diversity along the Pacific Coast may indicate that the complex coastal geography limits gene flow with inland populations, which is suggested by mitochondrial (Stone and Cook 2000, Puckett et al. 2015) and nuclear (Peacock et al. 2007, Lewis et al. 2020, Service et al. 2020) data. Given the extensive sampling of this species, the highest priority for research includes evaluation of populations in Mexico, from which very limited data are available. Several American black bear populations could be candidates for genetic rescue, particularly in areas where A_r and H_e are very low.

Ursus arctos. Analysis of brown bear genetic diversity outside of Europe and North America was limited (Fig. 7). Although analyses of mitochondrial data have a greater geographic breath (Hirata et al. 2013), nuclear genome studies remain lacking across large parts of the range, notably central and eastern Russia and China. Continental Europe had moderate genetic diversity, except for highly isolated populations, such as those in Spain and central Italy. Southern European populations show moderate A_r but high H_e, suggesting more recent losses of genetic diversity. Scandinavian populations also had moderate A_r and higher H_e although nearby Finland and western Russia had higher diversity. Scandinavia has a complex history that should affect genetic diversity estimates. Specifically, the presence of mitogenome clades 1 and 3a in the south and north, respectively (Miller et al. 2006), could result in historical admixture, although barriers to gene flow also act across the latitudinal gradient (Schregel et al. 2017). Further, intense persecution in the 1800s generated a genetic bottleneck, and demographic recovery since the mid-1970s would be expected to increase diversity (Swenson et al. 1995). Thus, Scandinavia presents an interesting case between the relationship of A_r and H_e because the lower allelic diversity does not appear to represent a recent loss of diversity, but a time lag in the generation of new private alleles.

North American brown bears showed moderate to low A_r and highly variable H_e in both the observed and yardstick-transformed data sets (Figs. 2, 7). There were not strong geographic patterns of genetic diversity in North America, except that isolated range edge populations, specifically Yellowstone National Park, Kodiak Island, and the Alaskan Peninsula, had low diversity, where diversity in Kodiak should be of particular conservation concern.

We suggest the highest priority for genetic diversity research in brown bears would include a global nuclear phylogeographic analysis. Although the mitogenome phylogeography has been well-studied, frequent instances of mito-nuclear discordance in mammals would help refine the patterns and timing of range expansions and define

evolutionarily significant units relevant for future conservation. We emphasize that Chinese and Gobi populations would be important to this analysis, given hypotheses about Asian origins of the species (McLellan and Reiner 1992).

Ursus maritimus. The evolutionary and demographic history of polar bears has been extensively studied (Hailer et al. 2012, Liu et al. 2014). The species has highly consistent levels of genetic diversity across its range, although some islands have lower diversity (Fig. 6). Our analysis showed that A_r and H_e were moderate compared with other bear species. We acknowledge that the inclusion of related individuals in some of the large polar bear studies may have affected the accuracy of individual data points. Across the 19 management units, the most recent data suggest 6 genetic clusters (Malenfant et al. 2016b), although we interpret their results as better supportive of a single cluster with isolation-by-distance across the range. Whole genome sequencing data have consistently shown that polar bear diversity is low when compared with European brown bear populations (Hailer et al. 2012, Liu et al. 2014, Benazzo et al. 2017, Kumar et al. 2017). Long-term low population size likely contributed to the large number of short runs of homozygosity observed in this species (Benazzo et al. 2017). Thus, microsatellite and WGS data present contrasting pictures of the level of genetic diversity in polar bears; yet, preliminary data (Malenfant et al. 2015) suggest that the geographic similarity in diversity estimates will remain as animals across the range are resequenced. Genetic management is likely less important than demographic management and habitat protection for this species.

Concluding remarks

Our results show the range of genetic variation within and among bear species. We see utility in this information for conservation planning, particularly to identify low-diversity populations and also to pair with evolutionary lineage information to identify high-diversity populations that may serve as sources for managed translocations. The development of genomic resources (including reference genomes, gene annotations, resequencing panels, single nucleotide polymorphism arrays, and transcriptomic data) is ongoing for most bear species; yet, we see continued utility in the collection of microsatellite data to answer conservation and management questions. For future studies to have the greatest impact, researchers should choose to genotype loci that are commonly used for their study species to better enable comparison and expanded inference. Alternatively, the bear research community could develop a set of standard DNA samples that could be used to calibrate individual research lab results, thereby enabling direct comparison across studies instead of the yardstick approach.

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Supplemental material

Fig. S1. Number of genotyped microsatellite loci per study ($n = 104$) over time in Ursidae studies. Regression line has a signification ($P = 0.039$) slope at a rate of 0.237 loci/year.

Table S1. Summary statistics for the 104 papers (some papers included >1 species) and theses identified that reported genetic diversity estimates using microsatellites for any of the 8 bear species. The number of publications identified, number of total geographic sites studied within the publications, sample size of genotyped individuals per population (mean, median, minimum, and maximum for any individual population), and allelic richness (A_r) and expected heterozygosity (H_e) mean or standard deviation of populations with >4 individuals genotyped.

Table S2. Counts of the number of geographic sites for which each of 193 microsatellite loci have been genotyped in for each of 8 bear species.

Table S3. Observed and yardstick-transformed estimates of allelic richness (A_r) and expected heterozygosity (H_e), and number of individuals sampled (*N*) for each geographic site analyzed from each paper (Reference) for all 8 species of bears. Standard errors were either recorded from the paper (s.e. Added = 0) or added (s.e. Added = 1) based on a model that related number of loci to error. If yardstick estimates were not performed because of missing observed data or lack of shared loci with the reference panel, NA is shown in the table. The number of microsatellite loci shared between the reference (n = 21) and focal populations and a reference to the original study are also shown.