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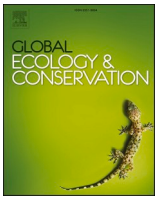

Avian ecology and community structure across elevation gradients: The importance of high latitude temperate mountain habitats for conserving biodiversity in the Americas

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ABSTRACT

Mountains are excellent systems for studying biodiversity as they promote rapid species turnover across relatively short elevational distances. Most research on biogeographic patterns in mountains has focused on tropical regions; far less is known about diversity across elevational gradients and their relative contribution to conservation in temperate mountains, particularly at high latitudes. To better understand the composition, ecology, and evolutionary history of high-latitude temperate mountain bird communities, we evaluated species richness, functional redundancy, and phylogenetic diversity across three elevation-specific habitats (upper montane, subalpine, alpine) in north temperate (9 mountains in British Columbia, Canada; 54°N) and south temperate (10 mountains in Chile; 39°S) regions representing distinct biogeographic origins. North temperate mountains had greater absolute species richness (77 versus 63 species), while south temperate mountains supported a greater proportion of the regional species pool (63% versus 44%). North temperate species richness increased with elevation to an ecotonal peak at treeline and then declined (subalpine = 58, alpine = 30 species), while the highest richness in south temperate mountains occurred at and above treeline (41 species). Similar species turnover patterns were observed in both systems with alpine habitats supporting the most distinct avifauna. Functional traits varied between regions with proportionally more migrants in the north, compared to more habitat specialists and cavity nesters in the south, particularly in the alpine. North temperate bird communities exhibited lower functional redundancy and higher total phylogenetic diversity, indicating a community susceptible to losing ecosystem functions and evolutionary potential. Southern communities contained greater functional redundancy and more evolutionarily isolated species, consistent with convergent evolution in challenging, high elevation habitats. Overall, in north temperate mountains, greater species richness and phylogenetic diversity, coupled with lower functional redundancy, particularly below treeline, highlights the importance of montane forests for biodiversity. In south temperate mountains, a distinct, speciose community at and above treeline, in combination with supporting a large proportion of the regional species pool, indicates a unique system with disproportionate conservation value. One-third of birds detected in north temperate mountains are considered of national or international conservation concern, compared to 9.5% of southern mountain birds. However, only 18% of the

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63 species observed in the south temperate Andes (and only 5% of alpine species) have had a conservation status assessment. With increasing climate change and habitat loss pressures across elevations, temperate mountains in the Americas have significant conservation value and appear particularly important for maintaining regional biodiversity.

1. Introduction

As microcosms of biogeography, mountains represent excellent natural systems to investigate patterns of biodiversity. Distinct gradients of biotic and abiotic factors distributed over relatively short elevational distances can shape the structure and function of wildlife communities (Kapos et al., 2000; Sanders and Rahbek, 2012; Laiolo et al., 2018). A range of environmental and evolutionary conditions interact within mountain ecosystems, including compressed climatic zones within narrow elevational bands, resource gradients (e.g., insect diversity, nest cavity availability), high habitat fragmentation, and an evolutionary history punctuated by climatic and glaciation events (Nagy and Grabherr, 2009; Cadena et al., 2012; White et al., 2019; Schumm et al., 2020). These conditions have facilitated speciation and rapid community turnover both along elevational gradients (i.e., parapatric speciation) and among adjacent mountains (allopatric speciation; Jankowski, 2009; Cadena et al., 2012; Pigot et al., 2016; Steinbauer et al., 2016). In fact, while mountains comprise only about 25% of the earth's surface, they support more than one third of terrestrial biodiversity and half of biodiversity hotspots globally (Körner and Paulsen, 2004; Körner and Ohsawa, 2006; Sayre et al., 2020). Thus, mountain habitats often harbour diverse and endemic species that represent disproportionately high conservation value.

Mountains, at all latitudes, exhibit strong turnover of climatic conditions across elevation (i.e., climatic zonation), imposing rapid changes in ecological constraints and resource availability (Janzen, 1967; Jankowski et al., 2009; Fjeldså, 2018a; Rahbek et al., 2019; Jarzyna et al., 2021). Such effects on avian community structure are influenced by interactions with latitude as avifauna in high-latitude temperate mountains experience a greater range of climatic conditions in seasonal environments, and therefore occupy broader thermal niches (Buckley and Jetz, 2008; Cadena et al., 2012; Quintero and Jetz, 2018). In contrast, low-latitude (tropical) mountain communities exhibit greater overlap in habitat and thermal niches among phylogenetically related species, suggesting evolutionary conservatism has restricted dispersal and promoted greater speciation with an accumulation of similar species within habitats (Cadena et al., 2012; Pigot et al., 2016). As a result, avian communities of high-latitude temperate mountains are less diverse overall, but support generalist species that may have a greater capacity to respond to environmental change.

Patterns of diversity within and among mountain ranges are shaped by interacting geological, climatic, and evolutionary factors (Hoorn et al., 2018; Quintero and Jetz, 2018; Tobias et al., 2020). In a global analysis, McCain (2009) described four diversity patterns with increasing elevation: 1) linear decrease, 2) low-elevation plateau followed by a sharp decline, 3) low-elevation plateau with a mid-elevational peak, and 4) a unimodal mid-elevational peak. Mountains with higher precipitation tended to exhibit the first two patterns with monotonic decreases in diversity, and drier mountains the latter two patterns with a mid-elevation peak (McCain, 2009). Quintero and Jetz (2018) demonstrated that mid-elevation peaks in diversity were produced by overlapping elevational ranges among species. In some systems, this may occur when range limits overlap at an 'ecotone'—the interface between two adjacent habitat types (Terborgh, 1971; Kark, 2013; Elsen et al., 2017). In temperate mountain habitats, treeline represents an ecotonal transition zone that can have abrupt or diffuse edges (Wilson and Martin, 2005; Guo et al., 2013; Quintero and Jetz, 2018; Bader et al., 2021), above which there is a decrease in avian diversity but a potential increase in the proportion of habitat specialists due to harsher conditions (Chamberlain et al., 2016; Altamirano et al., 2020; García-Navas et al., 2020).

The influence of climatic conditions and evolutionary history in structuring bird communities across elevation underlines the importance of considering species richness in combination with functional and phylogenetic diversity. Functional diversity is the range and density of behavioural, morphological, and physiological traits (e.g., breeding strategy, diet) in ecological communities, providing a mechanistic link between organisms and ecosystem function (Díaz and Cabido, 2001; Devictor et al., 2010). The decoupling of species richness and functional diversity across elevational gradients indicates the level of functional redundancy within a community (Flynn et al., 2009; Mayfield et al., 2010). Communities with high functional redundancy support species that occupy similar niche space (i.e., niche packing) and are thus more resilient to extirpations (Pigot et al., 2016). On the other hand, phylogenetic diversity reflects the accumulated evolutionary history of different genotypes and phenotypes that persists within lineages (Devictor et al., 2010; Mouquet et al., 2012). Total evolutionary history among species or the evolutionary distinctiveness of individual species (i.e., isolation) can identify trait diversity, unique species, and evolutionary potential within avian communities (Jetz et al., 2012; Tucker et al., 2017). In combination, functional and phylogenetic diversity can therefore be used to evaluate the eco-evolutionary processes that shape avian communities across environmental gradients, as well as to highlight the conservation value of high elevation habitats (Devictor et al., 2010; Tucker et al., 2017; Jarzyna et al., 2021).

Globally, about one quarter of high mountain habitats occur in temperate regions, located primarily in Europe, Asia, and the Americas (Kapos et al., 2000; Nagy and Grabherr, 2009). However, despite their extensive distribution, diversity patterns within temperate mountains systems and their contribution to global biodiversity have received comparatively little study. High-latitude temperate mountains in North and South America are cold, highly seasonal environments with a deep snowpack in winter and north-south orientations (Nagy and Grabherr, 2009; Perrigo et al., 2020). While we might expect similarities in avian community structure and function, key differences may arise due to region-specific climates, vegetation composition, and evolutionary histories. For example, continental variation in broad-scale climate patterns due to reversed land-ocean ratios at high latitudes in the Americas may over-ride the effect of latitude and elevation on local temperatures (Veblen et al., 2007; Fjeldså et al., 2012). Time is also

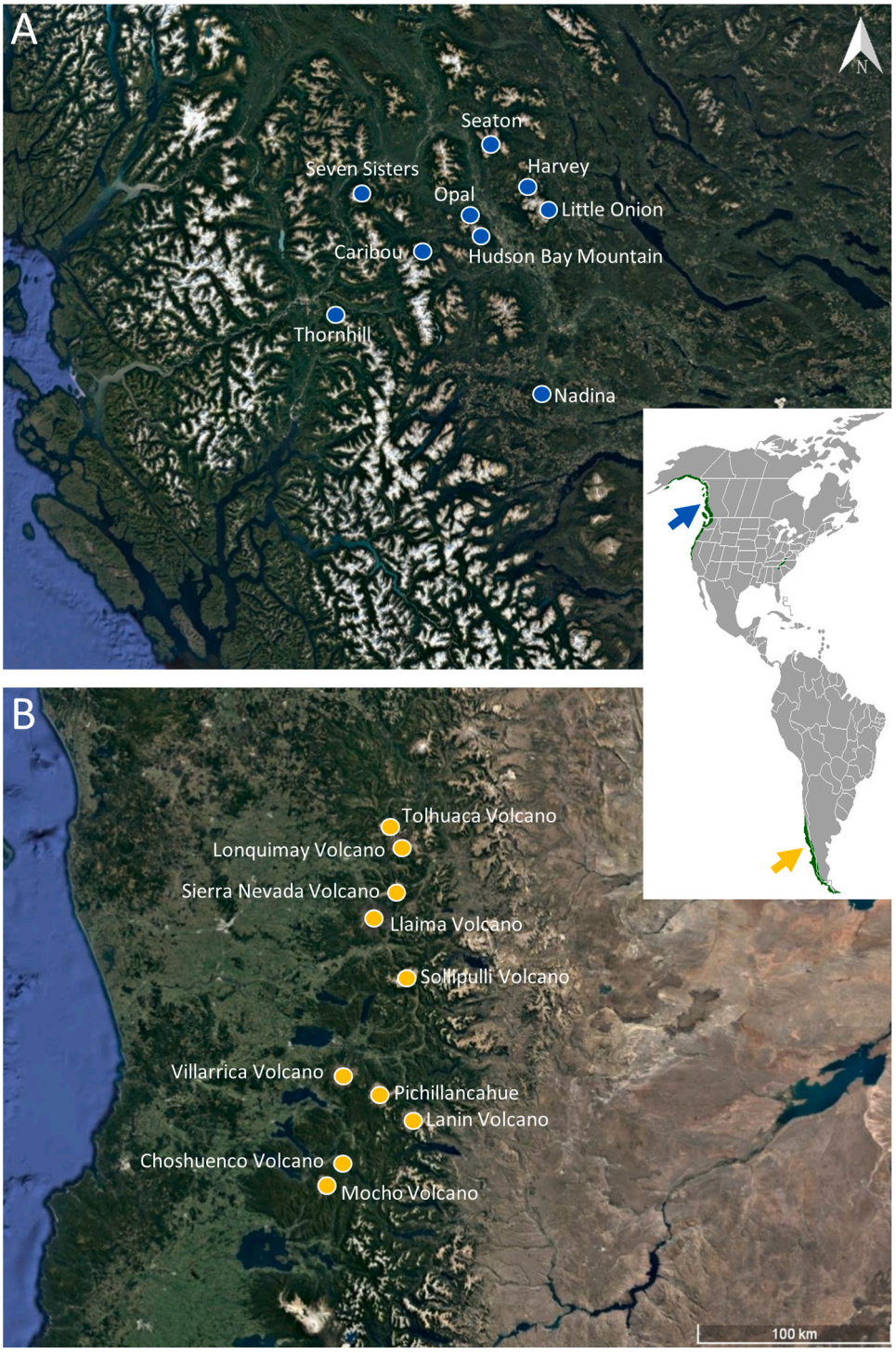

Fig. 1. Map of the study regions, including (A) the 9 mountains surveyed in British Columbia, Canada (spanning 117 km of latitude) and (B) 10 mountains surveyed in Chile (178 km of latitude). Base map © Google Earth. Map inset shows the two study regions in North and South America (blue and yellow arrows, respectively) with the temperate mountain habitats indicated in green.

important for the development of biodiversity (Quintero and Jetz, 2018). In the North American Cordillera, the last uplift occurred between 80 and 55 million years ago (mya; English and Johnston, 2004) compared to ~5.5–3.5 mya in the Andean Cordillera (Hoorn et al., 2018). With more recent regional isolation, Andean bird communities may have characteristics of an island biota, such as relatively low diversity (Vuilleumier, 1985; Jarzyna et al., 2021), while north temperate mountain communities may be more diverse

Table 1
Comparisons among temperate mountains ranges with respect to geographic location, elevation, climate, and breeding season duration within the study regions in North and South America.

Variable	North temperate	South temperate
Location	British Columbia, Canada	Southern Chile
Region	Bulkley Valley, Kitimat-Stikine	La Araucanía, Los Rios
Latitude distance (km, range)	117 (54.1–55.2° N)	178 (38.5–40.0° S)
Longitude distance (km, range)	106 (−128.4°– −126.8° W)	60 (−72.1° – −71.5° W)
Distance to coast (mean, range)	212 km (136 – 260)	148 km (112 – 178)
Elevation (m)		
Upper montane	1000–1557	1119–1495
Subalpine	1169–1658	1225–1690
Alpine	1319–1801	1377–1768
Treeline elevation (mean, range)	1543 (1288–1632)	1432 (1302–1618)
Climate		
Mean daily temperature: °C ± SE (range)		
Annual (region)	1.3 ± 0.4	6.0 ± 1.2
Breeding season (region)	6.6 ± 0.4	9.3 ± 1.0
Breeding season (local)		
Upper montane	10.6 ± 0.3 (2.4 – 21.3)	10.5 ± 0.2 (1.7 – 20.1)
Subalpine	11.4 ± 0.3 (1.3 – 22.7)	11.7 ± 0.3 (1.7 – 23.0)
Alpine	11.2 ± 0.4 (2.2 – 23.9)	12.4 ± 0.3 (2.0 – 23.2)
Mean total precipitation: mm ± SE (range)		
Annual	934 ± 64	1343 ± 193
Breeding season	129 ± 3	141 ± 9
Breeding season: *length (date range)*		
Alpine	74 d (17 May – 29 Jul)	111 + d (~8 Nov – 31 Jan)

with broader habitat niches given species dispersal from lowlands and glacial refugia over longer time-periods. For functional and phylogenetic diversity, south temperate mountains may more closely resemble tropical than temperate bird assemblages (i.e., high functional redundancy) due to similar clades from a more recently shared evolutionary history (Ghalambor and Martin, 2001; White et al., 2019). Alternatively, convergent evolution in comparable high elevation habitats may produce similar patterns in north and south temperate mountains, such as low functional redundancy and high phylogenetic diversity (Pigot et al., 2020; Jarzyna et al., 2021).

We investigated hemisphere-specific patterns of avian habitat use in high-latitude mountains of North and South America to characterize avifaunal communities, contrast respective biodiversity patterns, and highlight the conservation value of temperate high mountain habitats. Specifically, we conducted multi-year parallel field studies from these comparable but distant ecosystems (>11,500 km), representing distinct biogeographic regions and species pools, to identify convergent and divergent diversity patterns along elevational gradients which encompass montane forest, subalpine (treeline ecotone), and alpine habitats. We first compared general geophysical, biotic, and abiotic characteristics of temperate mountain systems in North and South America. Across habitat-specific elevational gradients, we then assessed patterns of: 1) community composition (species richness and turnover, habitat specialization, life-history traits), 2) functional redundancy and phylogenetic diversity metrics to address niche diversity and evolutionary history, and 3) conservation status of high elevation breeding birds.

2. Materials and methods

The terminology for mountain habitat types varies regionally. We use terminology provided by Grabherr (2000): 'upper montane' for mountain regions of higher elevation forest (above 1000 m), 'subalpine' or 'treeline ecotone' for the uppermost forest belt (open forest typically limited in extent; Nagy and Grabherr, 2009), and 'alpine' for the treeless zone above treeline.

2.1. Study areas

We selected a set of high latitude coastal mountains located within the Coast Mountains and the Andean Cordillera in North and South America, respectively (Fig. 1). Both temperate mountain systems are in long, north-south mountain chains formed by oceanic-continental plate tectonics and multiple uplift episodes. The mountain landscapes in Canada were shaped by the North American Plate and experienced more glaciation events, while the younger Chilean mountains were shaped by the Nazca Plate and more volcanism (Veblen et al., 2007; Hoorn et al., 2018). Both systems are strongly influenced by the Pacific Ocean. The south Andean mountains experience stronger oceanic influences given their larger ocean-to-land mass ratio and the influence of the Humboldt current that generates a more maritime climate with moderate temperatures and high precipitation, whereas the northern mountains have stronger continental influences given their lower ocean-to-land mass relationship (Veblen et al., 2007).

We classified our study areas into three habitat categories reflecting distinct vegetation structures: *upper montane,* high elevation forests consisting of relatively continuous, open-canopy forest of trees averaging 15 m or more in height (>50% tree cover), *subalpine* (treeline ecotone) of dry and wet meadows of herbaceous plants and shrubs interspersed with sparse tree patches and krummholz (5–50% tree cover), and *alpine* areas supporting hardy perennial herbaceous plants, sub-shrubs, and few or no trees (0–5% tree cover;

Boyle and Martin, 2015; Altamirano et al., 2020). Montane forest vegetation was composed primarily of old growth coniferous trees in the north and broad-leaf *Nothofagus* mixed with *Araucaria* conifers in the south. In both systems, all habitats were in relatively natural conditions with limited anthropogenic activities (e.g., hiking trails, some ski runs).

For the north temperate region, we surveyed nine mountains (1000–1801 m elevation) in British Columbia, Canada (54°N) spanning a maximum of 117 km in latitude and 106 km in longitude among transects and encompassing five biogeoclimatic zones: Coastal Mountain Hemlock, Mountain Hemlock, Engelmann Spruce-Subalpine Fir, Boreal Altai-Fescue Alpine, and Coastal Mountain-heather Alpine (British Columbia Ministry of Forests, Lands, Natural Resource Operations, and Rural Development, 2018; Fig. 1; Table 1). Characteristic trees of upper montane and subalpine habitats included subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmanni*), with an understory or ground cover of woody shrubs, grasses, and perennial herbs. Alpine habitats were characterized by few or no trees, dwarf woody shrubs such as mountain heathers or low-profile *Salix* spp, perennial herbaceous plants, grasses, mosses, lichens, and bare rock or scree. These mountains have a strong coastal influence with cold winters and relatively high annual precipitation (rain and snow; MacKinnon et al., 1992).

For the south temperate region, we surveyed 10 mountains over a similar elevational range from upper montane forest to alpine (1119–1768 m) in the southern Andes of Chile, covering a latitudinal gradient of 178 kilometers. These mountains fall within the Moist Pacific Temperate Ecological Region and have slightly closer proximity to the coast than our north temperate mountain sites (Veblen et al., 2007; Fig. 1, Table 1). The upper montane landscape was dominated by relatively continuous mixed broadleaf-conifer forests which were primarily old growth (> 200 years old). These forests were characterized by a high and open canopy (> 15 m tree height) consisting of Chilean tepa (*Laurelipsis philippiana*), Prince Albert's yew (*Saxegothaea conspicua*), monkey puzzle tree (*Araucaria araucana*), lenga beech (*Nothofagus pumilio*), and Dombey's beech (*Nothofagus dombeyi*). Subalpine habitat was comprised of a mix of highland herbaceous meadows, shrubs, and sparse patches of trees and/or krummholz. Subalpine trees included montane species and Antarctic beech (*Nothofagus antartica*). Andean alpine habitats were characterized by perennial herbaceous plants, shrubs, few or no trees, bare rock, or scree. Alpine vegetation was dominated by Chaura (*Gaultheria pumila*), Magellan barberry (*Berberis microphylla*), heath barberry (*Berberis empetrifolia*), and Quinchamali (*Quinchamalium chilense*). Vegetation structure varied across elevation within- and among-mountains based mainly on natural disturbances (i.e., volcanic eruptions; Altamirano et al., 2020).

2.2. Avian surveys

We conducted avian surveys during the 2017–2019 breeding seasons (north temperate: June–July, south temperate: November–January). For each mountain site, we stratified survey effort by habitat and located transects within each of the three habitat types described above. Counts were restricted to elevations with some vegetation, and thus we did not survey the highest elevational extents (i.e., scree, nival zones). Each mountain was surveyed using one transect of 5 point count stations per habitat type (for a total of 15 point count stations per mountain), with each point count 6 min in duration and separated by at least 200 m. We walked transects passively (no playbacks) between sunrise (± 30 min) and 10:00 h to encompass peak bird activity. We recorded the species and the number of individuals of every bird species identified by sight and sound. The distance to each detection was recorded within 3 distance intervals of the observer (0– 25 m, 26–50 m, 51–100 m). In addition to species detected during point counts, we recorded all new species observed along the transect (0 to >100 m) while walking between points, and while returning to the start of the transect; hereafter referred to as 'transect data'. We repeated each transect three times across each of two breeding seasons (once every 2 weeks) to incorporate seasonal variation in avian activities.

2.3. Weather data

Since we lacked consistent annual weather data for our high mountain sites in both regions, we used WorldClim data (Fick and Hijmans, 2017) to estimate mean daily temperature and total precipitation (snow and rain) during the breeding season and annually using interpolation from surrounding weather stations. To do so, we estimated the mid-point of each of our 19 study mountains in both regions and then interpolated monthly minimum temperature (°C), maximum temperature, and total precipitation (mm) within a 1 km radius from January 2016 to December 2018. Mean monthly temperature was then calculated from the minimum and maximum temperatures. Mean monthly temperature and precipitation were averaged and summed across all months, respectively, to determine mean annual temperature, total annual precipitation, breeding season temperature, and breeding season precipitation at each mountain site. For each region we present the overall mean with standard error calculated from the standard deviation across study sites. Comparable data on seasonal snow fall or snowmelt were not available.

To assess comparative ambient temperatures for north and south temperate mountains during the breeding season, we also installed temperature loggers (HOBO MX2201 pendant; Onset Computer Co., Pocaset, MA, USA) on three mountains in both Chile and B.C. (n = 6 loggers per mountain; 2 in each habitat). Temperature was recorded every 10 min as an average of the five preceding 2 min intervals and then we calculated the hourly average within day (24 hr) to produce mean daily temperatures during our survey periods.

2.4. Data analysis and avian diversity measures

We used point count data only for statistical comparisons so that we could control for survey effort and bird density. For community-level descriptive summaries and phylogenetic analyses, we used the total of species detected from the larger transect data set. To categorize species by habitat specialization and functional life-history traits, we used species-level data from the published literature and unpublished knowledge from local experts, complemented by our field observations (see Altamirano et al., 2020).

2.4.1. Habitat use and species richness

For each species detected, we developed a 'breeding habitat specialization' classification based on whether a species breeds in only one (i.e., specialist) or more (generalist) of our three high mountain habitat types. We included all species detected on our mountain transects and incidental observations (i.e., incidental observations involve rare or low detectability species, not detected on our surveys; n = 10 and 7 additional species for northern and southern regions, respectively). Where possible, this assignment was determined for our specific regions (approximate latitude and longitude).

To improve comparisons of species richness among regions and habitats, we accounted for differences in the assemblage coverage (total species detected per habitat) achieved by point counts using iNEXT analyses (Chao et al., 2014; Hsieh et al., 2016). Using sampling-unit-based incidence data, we generated species accumulation curves in iNEXT for each habitat and region combination using interpolation/extrapolation, and then obtained richness values at an equivalent assemblage coverage of 99.0%. Our survey effort obtained greater assemblage coverage than 99.0% in all habitats except for the alpine in the north temperate, thus only richness in this habitat was extrapolated and the values reported for the remaining five habitats are the product of interpolation. Although interpolated values are lower than our raw counts, they can be compared directly with the extrapolated value for the northern alpine (Chao and Jost, 2012). After controlling for effort, the resulting estimates were used to assess whether species richness (α-diversity) differed among habitats (i.e., if the 95% confidence intervals did not overlap). Additionally, we calculated the Jaccard dissimilarity index to measure species turnover (β-diversity) across habitat types within mountains.

2.4.2. Functional richness and redundancy

To assess patterns of functional richness (i.e., the relative volume of niche space filled by species in a community) we measured both discrete and continuous species traits (Petchey and Gaston, 2006; Ibarra and Martin, 2015). We used presence of avian species derived from our point count data and six functional traits: 1) habitat breadth, or the number of habitats (n = 1, 2, or 3) a species was detected in, 2) nest type (cavity, open cup), 3) foraging guilds, 4) foraging substrate, 5) migratory status, and 6) body mass. These functional traits reflect spatial and temporal resource use (i.e., response traits), as well as ecosystem function across elevational gradients (effect traits; Lavorel and Garnier, 2002). The range of habitat use across elevations is a spatial metric of resource use within mountain habitats. Nest location and type indicates breeding site selection and different species interactions (e.g., commensal networks; Altamirano et al., 2017). Diet expresses trophic linkages in ecological networks and can be associated with habitat productivity, as well as the extent of ecological processes such as predation, seed dispersion, and pollination, while foraging substrate reflects fine-grained habitat associations (Laiolo et al., 2018; Ikin et al., 2019). Migratory status accounts for temporal dynamics of bird communities regarding whether birds use mountains year-round or during a single season (breeding, post-breeding; Boyle and Martin, 2015; Barbe et al., 2018). Body mass is related to thermal and energetic constraints and interspecific competition (Brown et al., 2004; Woodward et al., 2005).

Functional richness was calculated for each habitat type using species traits and the estimated species richness (99% coverage) per point count with the R package 'FD' (Laliberté and Legendre, 2010; Laliberté et al., 2014). The degree of functional redundancy was determined by evaluating the association between functional richness and the log of species richness. A greater incremental increase in functional richness for every added species indicates lower functional redundancy. The non-linear association was also evaluated to determine when the asymptote was reached for each community (i.e., number of species to fill relative niche space).

2.4.3. Phylogenetic richness and turnover

We randomly sampled 1000 possible trees from a larger set of 10,000 produced by Jetz et al. (2014) which estimates the phylogeny of 9993 global species (Hackett backbone). We subset each tree based on the total species list from the north and south temperate communities (transect data; Table A1), and then further divided phylogenies into birds observed above (alpine), and below treeline (upper montane, subalpine). Species observed in all three habitats (generalists) were included in both categories. We separated species in this way to focus on phylogenetic turnover at treeline by assessing the difference in phylogenetic structure between tree-dependent and tree independent communities; below and above treeline, respectively. For each phylogeny (total, above, and below treeline), we created majority rule consensus trees based on a 50% threshold.

We calculated metrics for phylogenetic richness and turnover. For phylogenetic richness, we compared total phylogenetic diversity (PD; branch length) and evolutionary distinctiveness (ED; phylogenetic isolation) to test for continental differences between avian communities of high-latitude mountains. PD and ED were calculated for each of the original 1000 phylogenetic trees and then averaged to produce a mean and standard deviation for the total mountain (i.e., consensus metric), as well as the below and above treeline habitats. For phylogenetic turnover within mountains, we estimated 'PhyloSor' to assess the proportion of shared evolutionary history between the avian communities above and below treeline for each temperate region (i.e., shared branch lengths). Phylogenetic analyses were conducted using the 'PhyloMeasures' package (Tsirogiannis and Sandel, 2017) in R 4.0.2 (R Core Team, 2020).

3. Results

3.1. Environmental comparisons

Although our two temperate mountain systems were > 11,500 km apart and our southern latitude site was about 16 degrees closer to the equator (Fig. 1), the mountain range orientation (N–S), average treeline elevation, and elevation range for each of the major habitat types were comparable (Table 1). Average breeding season temperatures were also similar between regions for upper montane and subalpine habitats, but the alpine in the southern region was > 1 °C warmer than in the north. Regional climate interpolation

Table 2
Summary statistics of avian species diversity and selected functional traits (i.e., nest type, diet, migration status, breeding habitat specialization), and conservation status for north and south temperate mountains of the Americas. Values are derived from transect surveys, incorporating species seen during point counts and between counts along the transect (see Table A1).

Variable	North temperate	South temperate
Species diversity		
Number of species (families)	77 (28)	63 (22)
Regional species pool (# species)[a]	175	100
Functional traits		
Nest type: cavity/open cup[b]	21 / 56	32 / 31
Nest type: M/S/A (% cavity)[c]	27.1 / 16.1 / 13.3	48.7 / 56.5 / 43.6
Diet (top 3 in rank order)[d]	I, G, H	I, C, G
Migrant / resident spp[e]	63 / 14	35 / 28
Habitat specialists: n (%)[f]	48 (55%)	38 (54%)
Conservation status		
Species of concern[b]	22	6[g]

[a] Regional species pool: North temperate: Bulkley Valley bird list. South temperate: Martinez and Gonzalez 2021, Medrano et al. (2018).
[b] Absolute number of species nesting in cavities or open cup.
[c] Calculated from Table A.1 using transect data. % of species using cavity nests there were detected within each habitat: M = upper montane, S = subalpine, A = alpine).
[d] I: Insectivore; G: Granivore, H: Herbivore; C: Carnivore.
[e] Absolute number of migrant (M) and year-round resident (R). Includes altitudinal migrants.
[f] Calculated from Fig. 2. See text (methods) for assignment criteria.
[g] Includes endemic species (Slender-billed parakeet *Enicognathus leptorhynchus*).

indicated that the south temperate mountains were warmer and wetter than the north temperate for both the breeding season and annually (Table 1). Despite high levels of precipitation in Chile (largely occurring as snow in winter), the breeding season for alpine passerines was at least five weeks longer in the southern Andes than in our north temperate site in Canada (Table 1).

3.2. Avian communities in high mountains

3.2.1. North temperate

We observed a total of 77 bird species on 9 mountains: 59 species in upper montane forests, 57 species in subalpine (treeline ecotone), and 31 species in alpine habitats (transect data; 6308 total detections; Table A1a). This represented 44% of the 175 species of birds recorded breeding across all elevations in the region (Table 2). Most high mountain species (73%) use open cup nests, but nesting guild varied across habitats with open-cup nesting species dominating higher elevations. Migrants made up 82% of species compared to residents. Twenty-two species (29%) are listed on a national or international program of conservation concern; three of which use alpine habitats extensively and the rest use montane forests.

3.2.2. South temperate

We observed a total of 63 bird species on 10 mountains, including one range-restricted endemic (slender-billed parakeet *Enicognathus leptorhynchus*): 39 species in upper montane forests, 46 in subalpine, and 39 in alpine habitats (7968 total detections; Table A1b). This represents 63% of the 100 species of birds recorded breeding across all elevations in the region (Table 2). In contrast to the north, 51% of high mountain species used rock or tree cavities for nesting. Although there is uncertainty about the migratory status of some species, about 44% were residents and 56% of species were migratory (25% latitudinal migrants; 31% likely altitudinal migrants). The conservation status of mountain birds is not well established for Chile, but six species (9.5%) are listed on a national or international program of conservation concern; five of which are raptors that use alpine habitats (Table A1b).

3.3. General habitat breadth

From our field data, about 23% of species from both regions used all three habitats for feeding or nesting activities (Table A1). Comparable numbers of species were detected using both upper montane and subalpine habitats (31% in BC vs. 25% in Chile), whereas in southern mountains, 24% of species were detected in both subalpine and alpine habitats compared to only 10% in the north.

3.4. Breeding habitat: specialists and generalists

We found dramatically different patterns for breeding habitat specialization between north and south temperate mountain birds, despite the proportion of habitat breeding specialists being just over 50% for each region (Table 2). In the Andes, habitat specialization was strongest in birds breeding in alpine habitats, with 87% of the 31 species detected on our alpine surveys classified as breeding only above treeline (Fig. 2). This contrasted with the north temperate alpine that had a predominance of habitat generalist breeding birds (65%). In the north temperate, upper montane habitats had the highest proportion of specialist breeders (67%). Despite high richness

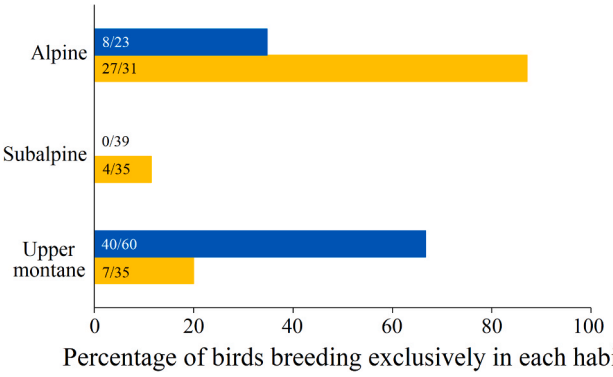

Fig. 2. Bird species classified as breeding exclusively within elevational habitats in north (top blue bars) and south (bottom yellow bars) temperate mountains based on published literature, field observations (this study), and expert knowledge. Total species detected for each region (north temperate: n = 87 species; south temperate: n = 70) include species observed during point counts, study transects, and incidental sightings from 2017 to 2019 in each mountain region. The numerator in each bar indicates the number of species known to breed exclusively in each habitat within a mountain context, while the denominator indicates the total number of species known to breed in that habitat (i.e., generalists and specialists). Bird specialization sources: North temperate (Boyle and Martin, 2015; Davidson et al., 2015; Billerman et al., 2020), South temperate (Billerman et al., 2020; Martinez and Gonzalez, 2021).

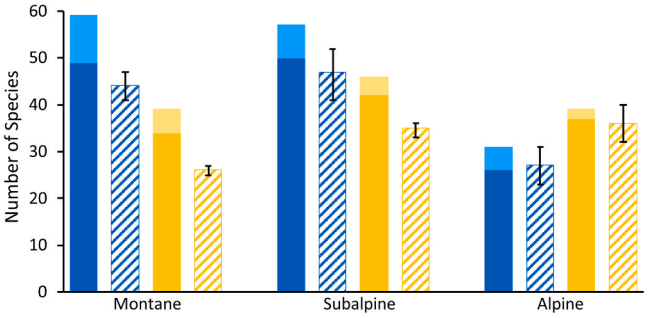

Fig. 3. Species richness with increasing elevation in upper montane, subalpine, and alpine habitats in north (left two blue bars; 2017–2019; 65 surveys) and south temperate mountains (right two yellow bars; 2017–2019; 60 surveys) using point count data only (bottom darker segment) and totals combining point counts and transect data (full bar). Total number of species detected on point count surveys across habitats was 65 and 55 for north and south temperate mountains, respectively, increasing to 77 and 63 species when including transect observations. Hatched bars depict the interpolated richness estimates at 99% sampling coverage using program iNEXT (Hsieh et al., 2016), with 95% confidence intervals as the error bars. Only the north temperate alpine required extrapolation to achieve 99% coverage (see Methods; Fig. A1).

in the subalpine, this habitat had the lowest proportion of specialist breeders in both hemispheres; none in the north and only four species in the south. We note some birds classified as alpine or treeline specialists also breed at low elevations in other open-country habitats, such as grasslands. For example, species identified as breeding specialists in a mountain habitat context, such as the Savannah sparrow (*Passerculus sandwichensis)* or buff-winged cinclodes (*Cinclodes fuscus*), also breed in open or agricultural areas at low elevations.

3.5. Species richness and turnover for north and south temperate mountains

Over the study, the total sample of point counts for the 3 years (pooled) varied from 290 to 323 for each habitat in the north, and 300 counts for each habitat in the south. At this level of effort, we obtained 4210 individual detections at north temperate sites and 5566 individual detections in the south temperate mountains. In the north, adjusting species richness estimates to an equivalent assemblage coverage of 99%, we obtained interpolated richness values of 44 (84% CI: 42–46) species for the upper montane, 47 (43−50) for subalpine, and an extrapolated value of 27 (24−30) species for the alpine (Fig. 3; Fig. A1). Thus, northern montane and subalpine habitats had comparable species richness estimates (confidence intervals overlapped), and both were significantly more diverse than the alpine (hatched bars, Fig. 3). In the south, we obtained interpolated richness values of 26 (84% CI: 25–27) species for the upper montane, 35 (33−36) for subalpine, and 36 (33−38) species for the alpine (hatched bars, Fig. 3, Fig. A1). In the south, the alpine and subalpine had comparable estimates of species richness, with both significantly more diverse than the upper montane forests.

Species turnover among habitat types (i.e., within mountains) was consistently greater in the north temperate (Fig. 4), but the

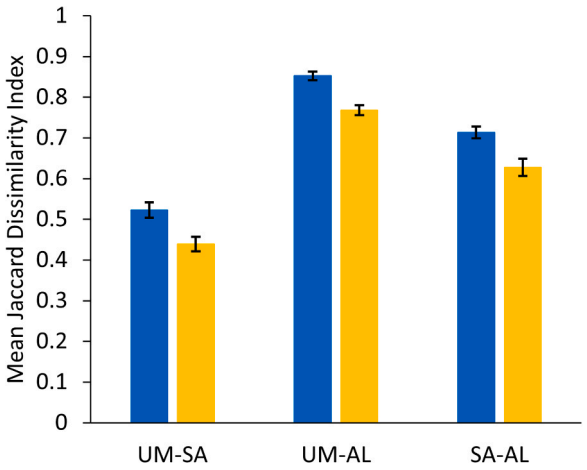

Fig. 4. Mean Jaccard Dissimilarity Index values for comparisons of species detected during point counts among upper montane (UM), subalpine (SA) and alpine (AL) habitats (all mountains pooled). North temperate surveys are depicted on the left in blue (65 transect surveys, 2017–2019) and south temperate mountains in yellow on the right (60 surveys, 2017–2019). Error bars represent 95% confidence intervals.

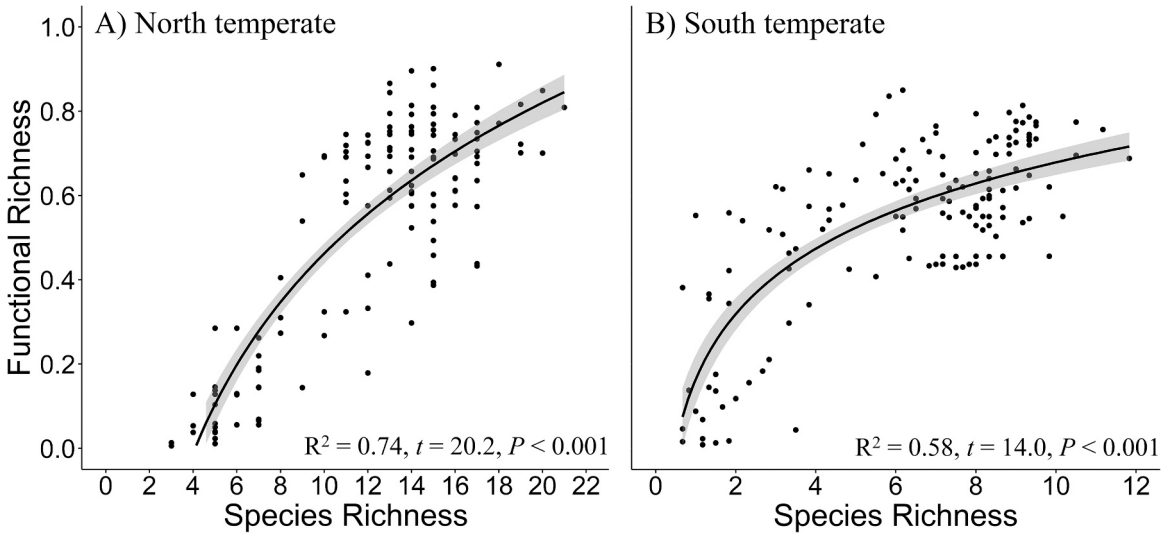

Fig. 5. Fitted curve depicting the relationship between functional richness and species richness detected from point count data in (A) north and (B) south temperate mountain ranges. Each point represents a point count located within a specific mountain and habitat, averaged over the entire survey period for each region (north = 3 breeding seasons, 2017–2019; south = 2, 2017–2019). The number of surveys used to generate point count averages ranged from 7 to 9 in north temperate (1–3 per year) and 6 in south temperate mountains (3 per year). Functional richness was calculated using seven functional traits: nest substrate, nest type, diet, foraging substrate, migratory status, mass, and habitat breadth (see Table A.1 for traits). The R2 value represents the proportion of variance explained. The test statistics refer to the strength of the relationship between functional richness and the log of species richness. The shaded band indicates the 95% confidence interval.

general patterns were comparable between regions. In both hemispheres, the greatest difference in turnover was between upper montane forest and alpine habitats, followed by subalpine and alpine habitats, with the lowest turnover (highest similarity) between upper montane and subalpine communities (Fig. 4). The subalpine therefore consists of species from both upper montane and alpine communities, with a greater representation of montane forest species.

3.6. Functional richness and redundancy

We found strong and positive non-linear associations between species richness and functional richness (north: $R^2 = 0.74$, south: $R^2 = 0.58$) that did not saturate over the species richness values observed at either of our sites (Fig. 5). Northern mountains had the highest complement of species exhibiting different traits (i.e., functional richness), but neither site reached a plateau with our current sampling effort (north: n = ~936, south: n = 900 counts). Surprisingly the southern mountains, with a smaller species pool, had

Table 3
Phylogenetic richness and turnover for north and south temperate mountains. Phylogenetic diversity (PD) and evolutionary distinctiveness (ED) for above treeline, below treeline, and the total mountain are calculated from 1000 phylogenetic trees. Values represent mean ± standard deviation, while habitat and region effects are Cohen's d effect sizes (values > 1.0 are considered strong effects). The 'phylosor' metric for β-diversity indicates the proportion of branch lengths shared between above and below treeline communities.

Species richness					
PD		Above	Below	Total	Habitat effect
	North	886.9 ± 50.9	2100.0 ± 106.0	2173.3 ± 109.9	−14.59
	South	1237.3 ± 63.6	1874.1 ± 90.6	1989.5 ± 98.0	−8.13
Region effect		−6.08	2.29	1.77	
ED		Above	Below	Total	Habitat effect
	North	29.6 ± 1.7	28.8 ± 1.5	28.2 ± 1.4	0.50
	South	31.7 ± 1.6	34.7 ± 1.7	31.6 ± 1.6	−1.80
Region effect		−1.30	−3.78	−2.25	
Species turnover					
		Shared branch lengths above and below treeline			
Phylosor	North	54.4%			
	South	72.1%			

greater functional redundancy than the northern region, as adding each new species in the north resulted in proportionately greater increases in functional richness than in the south.

3.7. High latitude temperate mountain phylogenetic clustering

We assessed phylogenetic diversity (total branch length) and evolutionary distinctiveness (phylogenetic isolation) to test for continental differences in avian communities in high latitude temperate mountains. Total phylogenetic diversity was greater in the north than the south temperate region, indicating northern mountains contained more absolute evolutionary history (Table 3). However, southern temperate mountains demonstrated greater evolutionary distinctiveness compared to the north, indicating that the average species in the south is more isolated phylogenetically and represents more unique evolutionary history. The most evolutionarily distinct north temperate species were band-tailed pigeon, black swift, and Bonaparte's gull, while in the south, the ashy-headed goose, Chilean pigeon, band-winged nightjar, and black-faced ibis were most distinct (Table A1).

3.8. Phylogenetic species richness and turnover above and below treeline

Phylogenetic diversity (PD) above treeline contained a greater proportion of the total mountain PD in the southern region (1237.3/1989.5 = 62.2%) compared to the north (886.9/2173.3 = 40.8%; Table 3). Evolutionary distinctiveness did not differ above and below treeline in the north, but in the south the avian community below treeline contained species that were on average more phylogenetically isolated than communities above treeline. In terms of species turnover, the above and below treeline communities shared more evolutionary history in the south (72.1% of all branch lengths) compared to the north (54.4%; Table 3; Fig. A2). Thus, in addition to supporting more evolutionarily distinct species in the south, avian communities in the southern Andes were more closely related above and below treeline than in north temperate mountains.

4. Discussion

Our north and south temperate study regions are located at opposite latitudinal extremes and support biota with distinct evolutionary histories within the Nearctic and Neotropical zoogeographic biomes, respectively. Despite this, the comparable landscape complexity and climatic conditions of our two study regions present excellent replicates in which to address avian community structure and function in temperate high mountain habitats. Within this comparative framework, we identified key similarities in avian assemblages as well as divergent patterns across elevational gradients. Species richness was highest at and below treeline in the north, but at and above treeline in south temperate mountains. Overall, north temperate mountains were more diverse, characterized by greater species richness, lower functional redundancy, and greater phylogenetic diversity, particularly below treeline. Within both regions, alpine habitats supported the most unique bird communities. However, the south temperate alpine community had comparatively more pronounced breeding habitat specializations, as well as greater phylogenetic diversity and evolutionary distinctiveness, highlighting the uniqueness of the southern Andes alpine habitat.

4.1. Species richness and community turnover

In both north and south temperate regions, the treeline ecotone supported the highest avian diversity. However, while there was a clear reduction in species richness above treeline in northern mountains, in the southern Andes we observed comparably high species richness in subalpine and alpine habitats. An ecotonal peak at treeline contrasts with observations in the north temperate Swiss Alps and global expectations for species distribution across elevation (i.e., mid-elevation peak or monotonic decline; McCain, 2009; Quintero and Jetz, 2018; García-Navas et al., 2020). While we did not survey the entire elevational range, these global models would

predict a decline in species richness from the montane forest (approximately mid-elevation) to the alpine. High species richness at treeline followed by a sharp decline as observed at our northern site is consistent with recent studies in the south temperate Andes (Altamirano et al., 2020) and dry tropical Andes of northern Chile (19°S), where species diversity increased up to 3500 m (treeline) and then declined (Araneda et al., 2018), indicating similar diversity patterns at these two sites in Chile despite dramatically different climatic conditions. However, our finding that subalpine and alpine habitats had comparably high species richness in the southern Andes contrast those of Altamirano et al. (2020), likely because they assessed average richness at the point count level, while we assessed species richness of the total community observed among mountains and over time. This may indicate that alpine species are more uncommon, spatially dispersed, or cryptic, leading to lower values of richness per count on average as observed by Altamirano et al. (2020) despite high overall richness. Regardless, our study of community composition reveals a pattern of higher species richness at and above treeline that has not been reported previously in any mountain type (Quintero and Jetz, 2018), indicating a uniquely diverse alpine community.

Since we only detected four subalpine habitat specialists between regions (north: $n = 0$, south: $n = 4$), an ecotonal peak at treeline reflects overlapping elevational ranges of montane forest and alpine species. In both regions, species were more commonly shared between upper montane and subalpine habitats which resulted in the greatest species turnover occurring at treeline. In high-latitude temperate mountains, treeline represents the most significant shift in climate and associated resource availability across elevation and may also delineate different evolutionary lineages, leading to abrupt community turnover (Bader et al., 2019; Jarzyna et al., 2021). An extreme example occurs in the subtropical eastern Himalayan mountains where a sharp change in the avian community occurs at the freezing line, representing a shift from tropical communities at low elevation to temperate-like communities at high elevation (White et al., 2019). Interestingly, turnover rate was consistently higher in the north temperate, suggesting avian communities of the southern Andes are more similar among high elevation habitats. This may be driven by regional differences in habitat structure or evolutionary history, such as more shrubs or volcanic-formed rock cavities above treeline in the south temperate which could facilitate species use of below and above treeline habitats, or a more recent common ancestor. Future assessments of species and phylogenetic turnover within and among mountains in association with fine-scale differences in habitat structure could shed light on this regional variation.

4.2. *Functional traits and phylogenetic diversity*

Several key life-history traits that determine how species interact with their surrounding environment differed between regions, such as breeding season duration, nesting behaviour, and migration strategies. For example, with a breeding season that is 50% shorter in north temperate mountains, species are more likely to be migratory. The warmer, wetter climate (i.e., milder) in the south likely promotes an extended breeding season, and perhaps also explains the reduced proportion of seasonal migration movements in the Andes. Interestingly, we observed major differences in nest traits with a high proportion of south temperate alpine birds nesting in rock cavities, particularly among the passerine species, versus a predominance of open cup ground nests for north temperate birds. It is unclear whether this propensity for cavity nesting may be shaped by environmental forces (e.g., snowmelt, predation pressure) or perhaps is the result of different ancestral traits (i.e., phylogenetic differences). While 13 families were detected in both regions, species assemblages were distinct with only one shared species (American kestrel; *Falco sparverius*), indicating fundamentally different phylogenies that could shape the prevalence of certain life-history strategies simply based on different environmental drivers through history (Pienaar et al., 2013).

Longer breeding seasons and more resident species in south temperate birds may result from a more recent shared evolutionary history with the Neotropical avifauna. For example, nearly 30% of species detected in the south were members of Tyrannidae ($n = 9$) and Furnariidae ($n = 9$); two hyper-diverse families that predominately occur in the Neotropics and have experienced relatively recent adaptive radiations around ~16–11mya and ~6mya, respectively (Seeholzer et al., 2017; Fjeldså et al., 2018b). Parts of the Andes doubled in size between 10 and 6mya and completed uplift ~5.5–3.5mya (Gregory-Wodzicki, 2000; Hoorn et al., 2018), suggesting that rapid niche diversification occurred around the same time as high elevation niche creation. Greater diversification rates can lead to greater niche packing, or more species within limited niche space (Ricklefs, 2012; Belmaker and Jetz, 2015; Schumm et al., 2020). This may indicate why south temperate mountain communities exhibited greater functional redundancy compared to the north temperate. This also may explain the high propensity for cavity nesting above treeline in the south (primarily Tyranids and Furnarids), as tree cavity nesting species may have radiated to occupy available rock cavity niche space above treeline. In fact, avian communities in south temperate mountains shared more evolutionary history between communities above and below treeline (72.1% versus 54.4%), indicating a more recent common ancestor. In contrast, the Coast Mountains in the north temperate completed uprising between 80 and 55mya (English and Johnston, 2004). This older, slower rate of mountain formation represents a longer period for species to disperse from low elevation habitats and glacial refugia, as well as for high elevation communities to experience more extirpation events. In line with this hypothesis, avian communities in high elevation habitats in the north were characterized by both higher functional and phylogenetic diversity.

High-latitude mountain habitats exhibit greater rates of diversification at high elevations, particularly those with a history of fluctuating climatic conditions (Quintero and Jetz, 2018). We found regional-scale differences in species richness, functional redundancy, and phylogenetic diversity that support global studies characterizing temperate mountains as functionally rich and distinctive ecosystems, despite their overall low species richness (Quintero and Jetz, 2018; Jarzyna et al., 2021). Recently the relationship between phylogenetic and functional diversity has been questioned because phylogenetic signals can be masked by convergent evolution under similar environmental constraints (Pigot et al., 2020). For example, temperate high elevation habitats in general have low functional redundancy, indicating communities that are vulnerable to the loss of ecosystem function; yet this low redundancy is accompanied by high phylogenetic relatedness (Jarzyna et al., 2021). Relative to north temperate communities which

had low redundancy, we found that south temperate communities exhibited greater functional redundancy and evolutionary distinctiveness. The observed patterns in the north therefore align with expectations of decoupled functional and phylogenetic diversity at high elevation in temperate mountains (Jarzyna et al., 2021). Patterns of functional redundancy and phylogenetic diversity in the south are more consistent with convergent evolution under a harsh, high elevation climate (Pigot et al., 2020). Interpreting these intriguing inter-hemispheric differences requires considering additional metrics of functional and phylogenetic diversity that could help identify the underlying eco-evolutionary processes acting on high-latitude mountain communities (Devictor et al., 2010; Mouquet et al., 2012).

4.3. Conservation implications

Under a changing climate, temperate mountain habitats are experiencing suppressed snow dynamics, advancing treelines, and increasingly stochastic weather, in combination with direct habitat loss from increasing land-use (Jackson et al., 2016; Martin et al., 2017; Scridel et al., 2018). During the last century, global surface air temperature increased by 0.87 °C (IPCC, 2018). By contrast, mountainous regions at high latitudes have experienced a temperature increase of 1.8 °C over the last 50 years, highlighting greater sensitivity to global climate change than low elevation habitats at similar latitudes (Wang et al., 2016). Habitat loss and current land-use practices in many mountains, including our temperate sites, have influenced the elevational range of some mountain bird species as most primary forests in the valley bottoms of South and Central America have been lost or degraded, requiring habitat specialists to move to higher elevations to track available niche space (Ibarra and Martin, 2015; Freeman et al., 2018; Neate-Clegg et al., 2018; Altamirano et al., 2020). Range contractions are considered a high risk for cold-adapted species in north temperate mountains (Braunisch et al., 2014; Jackson et al., 2015; Scridel et al., 2018), but few studies have examined montane biodiversity responses to climatic and vegetational changes in south temperate mountain ecosystems (Harris et al., 2014).

Comprising one quarter of the global land-base (Blyth et al., 2002) but supporting nearly one third of terrestrial species (Körner and Paulsen, 2004), mountains are disproportionately important for maintaining global biodiversity. High mountain habitats in both north and south temperate regions contained a large proportion of the regional species pools (44% and 63%, respectively). In the north temperate, this proportional contribution to regional biodiversity is greater than the average of 33–35% of North American birds reported using mountain habitats for both breeding and fall migration (Boyle and Martin, 2015).

The relatively high representation of species from the regional pool in high-latitude mountain habitats highlights an important conservation role for temperate mountains in maintaining local biodiversity (Boyle et al., 2016). Notably, we also detected a high proportion (29%) of at-risk species in north temperate systems, many of which are open-country species in decline at lower elevations. Of concern, only 18% of all high elevation species detected in the south temperate Andes have had conservation status assessments at the regional or national level; a value which declines to 5% for alpine specialists (Altamirano et al., 2020). Due to poor understanding of the distribution and conservation status of high elevation birds, we strongly recommend prioritizing research and formalized species assessments to better evaluate the conservation value of high elevation habitats in the south temperate Andes. In sum, temperate mountains contain disproportionately high species richness, as well as unique functional traits and evolutionary history, with strong implications for conservation and management strategies that justify prioritizing the protection of these reservoirs of diversity (Jetz et al., 2014; Altamirano et al., 2020).

5. Conclusions

Despite the importance for conservation, distributions of bird species across high elevation habitats are poorly understood in general; a critically important knowledge gap given current unprecedented levels of climatic and land-use change in temperate mountain areas (Lehikoinen et al., 2019; Scridel et al., 2018). Birds inhabiting temperate mountains appear resilient to environmental change given their broad elevational and thermal niches that allow them to persist in these highly variable seasonal environments (Cadena et al., 2012; Martin et al., 2017; Altamirano et al., 2020; Schumm et al., 2020). Still, we show that particularly in the north temperate, a combination of low functional redundancy and high phylogenetic diversity makes temperate mountain bird communities susceptible to functional collapse or to the loss of significant evolutionary potential if environmental perturbations lead to species extirpation (Jetz et al., 2012; Jarzyna et al., 2021). Thus, our positive findings that high-latitude temperate mountains support a large proportion of at-risk species should not be cause for complacency, as most current environmental risk assessments do not include the high elevation habitats used by birds for breeding and migratory stopovers. This is a critical oversight, due in part to a misconception that high elevation habitats have limited ecological value. Combining targeted monitoring, autonomous recording units (ARUs), and community science initiatives may address some of these gaps (Drake et al., 2021). However, given the importance of understanding species diversity patterns across elevational gradients and the potential conservation value of high mountain habitats to maintain biodiversity, the limited state of ecological knowledge for many avian species in the temperate mountains of the Americas, particularly the Andean alpine, is a significant concern.

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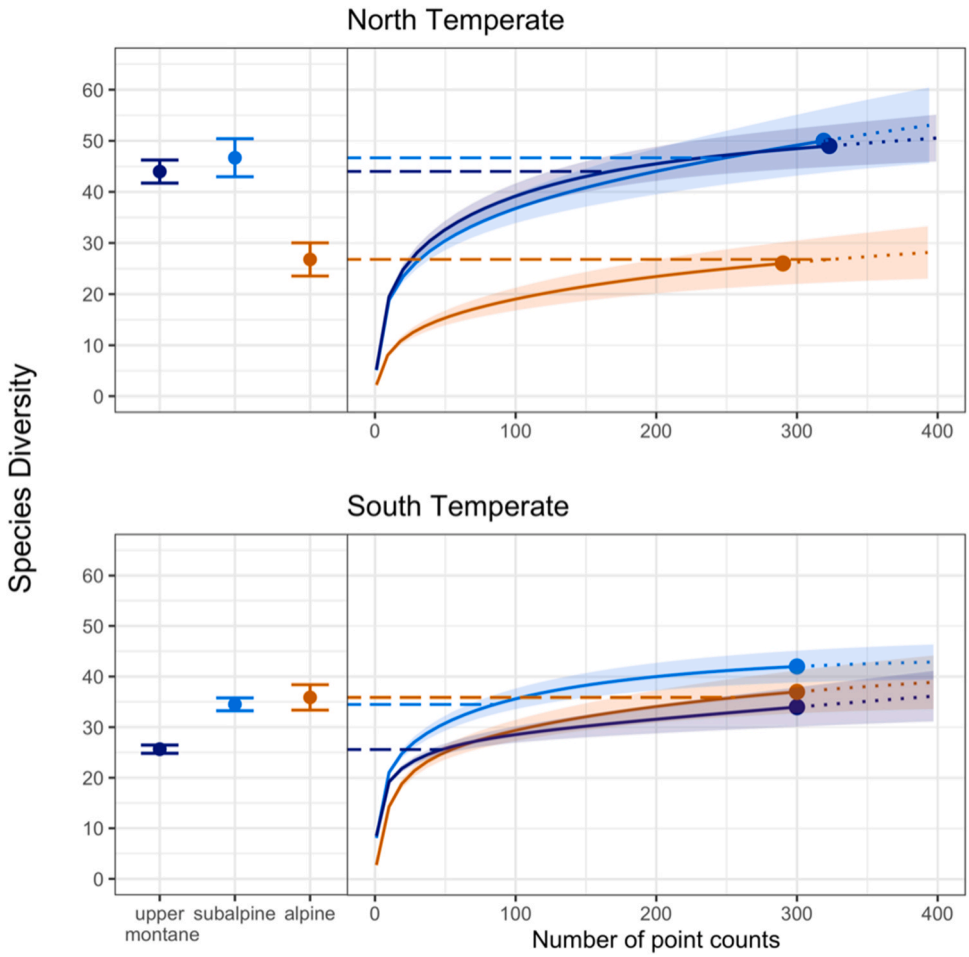

Fig. A1. Species richness (Hill number q=0) accumulation curves by effort for north and south temperate mountain habitats (+/- 95% CI). Curves were produced using program iNEXT (Hsieh et al., 2016) and species incidence frequencies within point count datasets. Solid lines are interpolated from the dataset. Given survey effort in the north temperate, we achieved 99.0% sample completeness in the upper montane (167 point counts required) and subalpine (249 point counts required) but not within alpine habitats which would have required 324 counts (only 290 counts available). In the south, our sampling effort of 300 counts/habitat was more than sufficient to achieve 99.0% sample completeness in montane, subalpine and alpine habitats with 48, 85, and 256 point count samples required, respectively. Dashed lines are extrapolated from the dataset up to double the sampling effort conducted in the field.

sources were not involved in the study design; in the collection, analysis and interpretation of data; in the writing of the manuscript; nor in the decision to submit the article for publication.

CRediT authorship contribution statement

KM, DRD, and TAA conceived the ideas and designed the methodology, with input from SW; KM, DRD, and TAA carried out the analyses with support from KH and SW. KM and DRD led the writing of the manuscript. All authors made substantial contributions to the interpretations of results and editing the manuscript.

Declaration of Competing Interest

All authors declare no conflicts of interest in the execution or submission of this study.

Data accessibility

Data and code will be made available in a public repository upon publication.

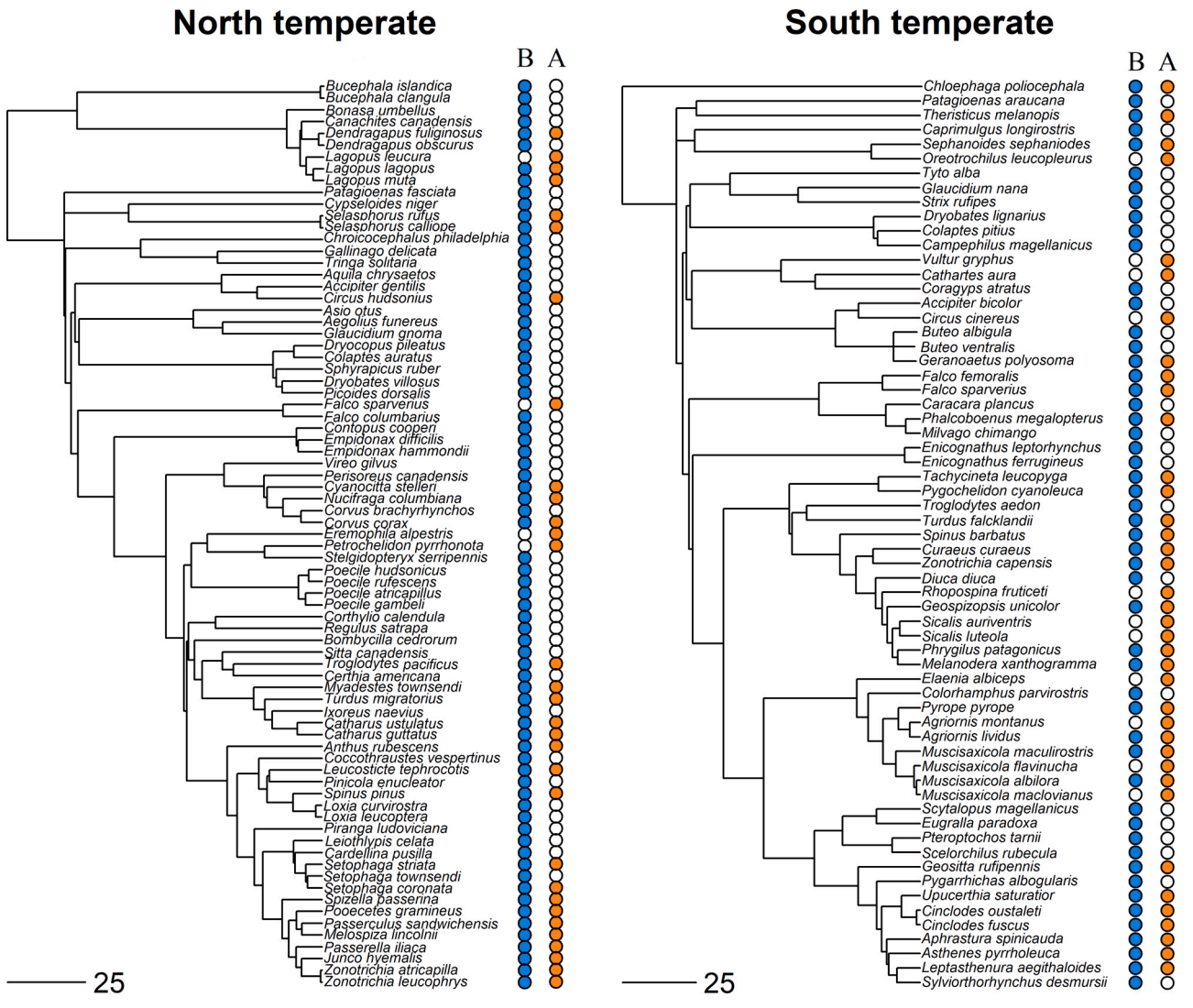

Fig. A2. Majority rule consensus trees for north and south temperate mountain ranges. The scale represents 25 million years of evolutionary history. Coloured dots represent whether a species was observed below treeline (B) or above treeline (A). White dots mean species were not observed in these habitats.

Table A1
Avifauna observed in temperate mountains during point counts or while walking between point count stations (i.e., transect sightings) from 2017 to 2019 seasons in (A) northern British Columbia, Canada, and (B) southern Chile. Symbols behind each species indicated conservation concern classifications (see footnotes). Habitat of observation indicates a 1 for presence and 0 for absence in upper montane forest (M), subalpine (S), and alpine (A). Under nest, nest substrate (T–tree, G–ground, S–shrub, and R–rock) precedes nest type (C–cavity, O–open cup). For example, T/C uses tree cavity nest and R/C = rock cavity nest. Diet includes: P–piscivore, H–herbivore, F–frugivore, I–insectivore, N–nectarivore, C–carnivore, O–omnivore, G–granivore, and V–vermivore. Foraging substrates (FS) are: W–water, F–foliage, G–ground, A–air, and B–bark. Migratory status (MS) distinguishes between migrants (M), altitudinal (A), and resident (R). For species in British Columbia, migrants are further divided into short (M_S) and long distance (M_L). Short distance migrants remain within southern Canada and the United States during winter, while long distance migrants winter in South and Central America. Mass is in grams and ED refers to evolutionary distinctiveness (this paper).

Species	Habitat (M,S,A)	Nest	Diet	FS	MS	Mass	ED
A) British Columbia							
Anatidae							
Common goldeneye *(Bucephala clangula)*	1,0,0	T/C	P	W	M_S	982	45.6
Barrow's goldeneye *(Bucephala islandica)*	1,1,0	T/C	P	W	M_S	910	45.6
Phasianidae							
Ruffed grouse *(Bonasa umbellus)*$^{\Delta}$	1,0,0	G/O	H	F	R	587	51.0
Spruce grouse *(Falcipennis canadensis)*$^{\Delta}$	1,1,0	G/O	H	F	A	600	18.1
Willow ptarmigan *(Lagopus lagopus)*	0,1,1	G/O	H	G	A	533	10.3
Rock ptarmigan *(Lagopus muta)*	0,1,1	G/O	H	G	A	550	10.3
White-tailed ptarmigan *(Lagopus leucura)*$^{\Delta}$	0,0,1	G/O	H	G	A	348	17.4
Dusky grouse *(Dendragapus obscurus)*	1,1,0	G/O	H	F	A	1088	9.9
Sooty grouse *(Dendragapus fuliginosus)*,$^{\Delta}$*	1,1,1	G/O	H	G	A	1088	9.9
Accipitridae							
Northern harrier *(Circus cyaneus)*	0,1,1	G/O	C	A	M_S	420	38.6
Northern goshawk *(Accipiter gentilis)*,	1,0,0	T/O	C	A	R	950	38.6
Golden eagle *(Aquila chrysaetos)*	0,1,0	T/O	C	A	R	4575	56.6
Scolopacidae							
Solitary sandpiper *(Tringa solitaria)*	1,1,0	T/O	I	T	M_L	511	53.0
Wilson's snipe *(Gallinago delicata)*	0,1,0	G/O	I	G	M_L	100	53.0
Laridae							
Bonaparte's gull *(Chroicocephalus philadelphia)*	1,0,0	T/O	P	W	M_S	211	72.5
Columbidae							
Band-tailed pigeon *(Patagioenas fasciata)*$^{\Delta *B}$	1,1,0	T/O	F	F	M_S	340	91.6
Strigidae							
Northern pygmy-owl *(Glaucidium gnoma)*	1,0,0	T/C	I	A	R	70	46.0
Long-eared owl *(Asio otus)*	1,0,0	T/O	C	A	R	260	60.2
Boreal owl *(Aegolius funereus)*	1,0,0	T/C	C	A	R	135	46.0
Species	Habitat (M,S,A)	Nest	Diet	FS	MS	Mass	ED
Apodidae							
Black swift *(Cypseloides niger)*$^{\Delta BB}$	1,0,0	R/O	I	A	M_L	46	76.9
Trochilidae							
Rufous hummingbird *(Selasphorus rufus)*$^{\Delta}$*	1,1,1	T/O	N	F	M_L	4	38.8
Calliope hummingbird *(Selasphorus calliope)*	0,1,1	T/O	N	F	M_L	3	38.8
Picidae							
Red-breasted sapsucker *(Sphyrapicus ruber)*	1,0,0	T/C	I	B	M_S	49	31.2
Hairy woodpecker *(Leuconotopicus villosus)*$^{\Delta}$	1,0,0	T/C	I	B	A	66	22.0
Am. three-toed woodpecker *(Picoides dorsalis)*	1,1,0	T/C	I	B	R	55	22.0
Northern flicker *(Colaptes auratus)*$^{\Delta}$	1,0,0	T/C	I	G	R	158	28.4
Pileated woodpecker *(Hylatomus pileatus)*	1,0,0	T/C	I	B	A	290	28.4
Falconidae							
American kestrel *(Falco sparverius)*	0,0,1	T/C	I	A	M_S	117	46.7
Merlin *(Falco columbarius)*	0,1,0	T/O	C	A	M_S	190	46.7
Tyrannidae							
Olive-sided flycatcher *(Contopus cooperi)*$^{\Delta *B}$	1,1,0	T/O	I	A	M_L	32	41.0
Hammond's flycatcher *(Empidonax hammondii)*	0,1,0	T/O	I	A	M_L	10	24.3
Pacific-slope flycatcher *(Empidonax difficilis)*	1,0,0	T/C	I	A	M_L	11	24.3
Vireonidae							
Warbling vireo *(Vireo gilvus)*	1,0,0	T/O	I	F	M_L	12	46.6
Corvidae							
Canada jay *(Perisoreus canadensis)*	1,1,0	T/O	O	G	R	70	32.6
Steller's jay *(Cyanocitta stelleri)*$^{\Delta}$	1,1,0	T/O	O	G	A	128	25.1
Clark's nutcracker *(Nucifraga columbiana)*	1,1,1	T/O	G	F	A	130	18.8
American crow *(Corvus brachyrhynchos)*	1,1,0	T/O	O	G	R	450	12.8
Common raven *(Corvus corax)*	1,1,1	T/O	O	G	R	1200	12.8
Alaudidae							
Horned lark *(Eremophila alpestris)*$^{\Delta}$	0,0,1	G/O	G	G	M_S	32	42.1
Hirundinidae							
N rough-winged swallow *(Stelgidopteryx serripennis)*	0,1,0	G/C	I	A	M_L	15	30.3

(*continued on next page*)

Table A1 (*continued*)

Species	Habitat (M,S,A)	Nest	Diet	FS	MS	Mass	ED
Cliff swallow *(Petrochelidon pyrrhonota)*	0,0,1	R/C	I	A	M_L	22	30.3
Paridae							
Black-capped chickadee *(Poecile atricapillus)*	1,0,0	T/C	I	F	R	11	16.4
Mountain chickadee *(Poecile gambeli)*	1,1,0	T/C	I	F	A	11	16.4
Chestnut-backed chickadee *(Poecile rufescens)*$^{\Delta *}$	1,1,0	T/C	I	F	A	10	15.9
Boreal chickadee *(Poecile hudsonicus)*$^{\Delta}$	1,1,0	T/C	I	F	R	10	15.9
Sittidae							
Red-breasted nuthatch *(Sitta canadensis)*	1,1,0	T/C	I	B	A	10	36.3
Certhiidae							
Brown creeper *(Certhia americana)*	1,0,0	T/C	I	B	A	8	32.3
Troglodytidae							
Pacific wren *(Troglodytes pacificus)*	1,1,1	T/C	I	G	A	9	32.3
Species	Habitat	Nest	Diet	FS	MS	Mass	ED
Regulidae	(M,S,A)						
Golden-crowned kinglet *(Regulus satrapa)*	1,1,0	T/O	I	F	R	6	39.8
Ruby-crowned kinglet *(Regulus calendula)*	1,1,0	T/O	I	F	M_S	7	39.8
Turdidae							
Townsend's solitaire *(Myadestes townsendi)*	1,1,1	G/O	I	A	A	34	31.3
Swainson's thrush *(Catharus ustulatus)*	1,1,1	S/O	I	F	M_L	31	14.2
Hermit thrush *(Catharus guttatus)*	1,1,1	G/O	I	G	M_S	31	14.2
American robin *(Turdus migratorius)*	1,1,1	T/O	V	G	M_S	77	24.8
Varied thrush *(Ixoreus naevius)*$^{\Delta}$	1,1,0	T/O	I	G	M_S	78	20.4
Motacillidae							
American pipit *(Anthus rubescens)*	0,1,1	G/O	I	G	M_S	21	39.3
Bombycillidae							
Cedar waxwing *(Bombycilla cedrorum)*	1,1,0	T/O	I	F	M_S	32	43.2
Parulidae							
Orange-crowned warbler *(Vermivora celata)*	1,1,0	G/O	I	F	M_L	9	16.2
Blackpoll warbler *(Setophaga striata)*$^{\Delta}$	1,1,1	T/O	I	F	M_L	13	8.8
Yellow-rumped warbler *(Setophaga coronate)*	1,1,1	T/O	I	F	M_S	12	6.8
Townsend's warbler *(Setophaga townsendi)*	1,1,0	T/O	I	F	M_L	9	6.8
Wilson's warbler *(Cardellina pusilla)*$^{\Delta}$	1,1,1	G/O	I	F	M_L	7	12.4
Passerellidae							
Chipping sparrow *(Spizella passerine)*	1,1,1	T/O	G	G	M_L	12	18.0
Vesper sparrow *(Pooecetes gramineus)*$^{\Delta R}$	0,1,1	G/O	G	G	M_L	26	11.3
Savannah sparrow *(Passerculus sandwichensis)*	0,1,1	G/O	O	G	M_L	26	8.9
Fox sparrow *(Passerella iliaca)*	1,1,1	G/O	I	G	M_S	32	11.3
Lincoln's sparrow *(Melospiza lincolnii)*	1,1,1	G/O	I	G	M_S	17	8.9
White-crowned sparrow *(Zonotrichia leucophrys)*	1,1,1	S/O	O	G	M_S	29	4.7
Golden-crowned sparrow *(Zonotrichia atricapilla)*	1,1,1	G/O	G	G	M_S	29	4.7
Dark-eyed junco *(Junco hyemalis)*	1,1,1	G/O	G	G	A	19	9.0
Cardinalidae							
Western tanager *(Piranga ludoviciana)*	0,1,0	T/O	I	F	M_L	28	27.5
Fringillidae							
Gray-crowned rosy-finch *(Leucosticte tephrocotis)*	0,1,1	R/C	G	G	M_S	27	19.4
Pine grosbeak *(Pinicola enucleator)*$^{\Delta}$	1,1,0	T/O	G	F	A	56	19.5
Red crossbill *(Loxia curvirostra)*	1,1,0	T/O	G	F	M_S	37	8.7
White-winged crossbill *(Loxia leucoptera)*	1,1,0	T/O	G	F	M_S	27	8.7
Pine siskin *(Spinus pinus)*$^{\Delta}$	1,1,1	T/O	G	F	M_S	15	15.5
Evening grosbeak *(Coccothraustes vespertinus)*$^{\Delta *}$	1,1,0	T/O	G	F	M_S	60	26.7
Transect total = 77 species	**59,57,31**						
B) Southern Chile							
Species	Habitat	Nest	Diet	FS	MS	Mass	ED
Anatidae	(M,S,A)						
Ashy-headed goose *(Chloephaga poliocephala)*	1,1,1	G/O	H	G	A	2234	101.3
Columbidae							
Chilean pigeon *(Patagioenas araucana)*	1,1,0	T/O	F	G	R	280	83.7
Caprimulgidae							
Band-winged nightjar *(Systellura longirostris)*	1,0,0	G/O	I	A	M	52	84.0
Trochilidae							
Green-backed firecrown *(Sephanoides sephaniodes)*	1,1,1	S/O	N	F	M	5	50.3
White-sided hillstar *(Oreotrochilus leucopleurus)*	0,0,1	R/O	N	F	M	8	50.3
Threskiornithidae							
Black-faced ibis *(Theristicus melanopis)*	1,1,1	T/O	I	G	A	1250	83.7
Cathartidae							
Andean condor *(Vultur gryphus)*^{R,NT}	0,1,1	R/C	C	G	R	11500	63.3
Black vulture *(Coragyps atratus)*	1,1,0	G/O	C	G	R	1600	49.3

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Table A1 (*continued*)

Species	Habitat (M,S,A)	Nest	Diet	FS	MS	Mass	ED
Turkey vulture *(Cathartes aura)*	0,0,1	G/O	C	G	R	1425	49.3
Accipitridae							
Cinereous harrier *(Circus cinereus)*	0,0,1	G/O	C	A	A	413	37.4
Bicolored hawk *(Accipiter bicolor)*[R]	1,0,0	T/O	C	G	R	387	37.4
Variable hawk *(Geranoaetus polyosoma)*	1,1,1	T/O	C	G	R	980	30.3
White-throated hawk *(Buteo albigula)*[R]	1,0,0	T/O	C	G	M	475	30.5
Rufous-tailed hawk *(Buteo ventralis)*[R,V]	1,1,0	T/O	C	G	R	1045	29.8
Tytonidae							
Barn owl *(Tyto alba)*	1,0,0	T/C	C	G	R	368	72.1
Strigidae							
Rufous-legged owl *(Strix rufipes)*[R,NT]	1,0,0	T/C	C	G	R	350	56.6
Austral pygmy-owl *(Glaucidium nana)*	1,1,0	T/C	C	G	R	78	56.6
Picidae							
Striped woodpecker *(Dryobates lignarius)*	1,1,0	T/C	I	B	R	37	48.0
Magellanic woodpecker *(Campephilus magellanicus)*[R,V]	1,1,0	T/C	I	B	R	320	31.2
Chilean flicker *(Colaptes pitius)*	1,1,0	T/C	I	B	R	132	31.2
Falconidae							
Southern caracara *(Caracara plancus)*	1,1,0	T/O	C	G	R	1375	34.8
Mountain caracara *(Phalcoboenus megalopterus)*	0,1,1	R/O	C	G	A	795	19.8
Chimango caracara *(Milvago chimango)*	1,1,0	T/C	C	G	R	235	19.8
American kestrel *(Falco sparverius)*	0,1,1	T/C	C	G	R	123	35.4
Aplomado falcon *(Falco femoralis)*	0,1,1	T/O	C	A	R	334	35.4
Psittacidae							
Austral parakeet *(Enicognathus ferrugineus)*	1,1,0	T/C	G	F	R	155	42.4
Slender-billed parakeet *(Enicognathus leptorhynchus)*[E]	1,0,0	T/C	G	F	R	193	42.4
Species	Habitat (M,S,A)	Nest	Diet	FS	MS	Mass	ED
Rhinocryptidae							
Black-throated huet-huet *(Pteroptochos tarnii)*	1,1,0	T/C	I	G	A	159	23.6
Chucao tapaculo *(Scelorchilus rubecula)*	1,1,0	T/C	I	G	A	48	23.6
Ochre-flanked tapaculo *(Eugralla paradoxa)*	1,0,0	S/O	I	G	A	27	26.3
Magellanic tapaculo *(Scytalopus magellanicus)*	1,1,0	T/C	I	G	A	12	26.3
Furnariidae							
Rufous-banded miner *(Geositta rufipennis)*	0,1,1	R/C	I	G	M	40	35.1
White-throated treerunner *(Pygarrhichas albogularis)*	1,1,0	T/C	I	B	R	24	24.9
Patagonian forest earthcreeper *(Upucerthia saturatior)*	0,1,1	G/C	I	G	A	46	12.6
Buff-winged cinclodes *(Cinclodes fuscus)*	0,1,1	T/C	I	G	A	31	6.9
Gray-flanked cinclodes *(Cinclodes oustaleti)*	0,1,1	R/C	I	G	A	27	6.9
Thorn-tailed rayadito *(Aphrastura spinicauda)*	1,1,0	T/C	I	F	R	12	15.2
Des Murs' wiretail *(Sylviorthorhynchus desmursii)*	1,1,0	S/O	I	F	R	10	10.4
Plain-mantled tit-spinetail *(Leptasthenura aegithaloides)*	1,1,1	T/C	I	F	A	9	10.4
Sharp-billed canastero *(Asthenes pyrrholeuca)*	0,1,1	S/O	I	F	A	13	12.9
Tyrannidae							
White-crested elaenia *(Elaenia albiceps)*	1,1,1	S/O	I	F	M	16	42.2
Spot-billed ground-tyrant *(Muscisaxicola maculirostris)*	0,0,1	G/O	I	G	M	14	14.7
Ochre-naped ground-tyrant *(Muscisaxicola flavinucha)*	0,0,1	R/C	I	G	M	25	8.4
Dark-faced ground-tyrant *(Muscisaxicola maclovianus)*	0,1,1	R/C	I	G	M	24	4.8
White-browed ground-tyrant *(Muscisaxicola albilora)*	0,1,1	R/C	I	G	M	23	4.8
Black-billed shrike-tyrant *(Agriornis montanus)*	0,0,1	R/C	C	G	M	63	8.9
Great shrike-tyrant *(Agriornis lividus)*	0,1,1	S/O	C	G	R	99	8.9
Fire-eyed diucon *(Pyrope pyrope)*	1,1,1	S/O	I	A	R	35	14.3
Patagonian tyrant *(Colorhamphus parvirostris)*	1,0,0	S/O	I	F	M	11	29.9
Hirundinidae							
Blue-and-white swallow *(Pygochelidon cyanoleuca)*	1,1,1	R/C	I	A	M	35	36.4
Chilean swallow *(Tachycineta leucopyga)*	1,1,1	T/C	I	A	M	18	36.4
Troglodytidae							
House wren *(Troglodytes aedon)*	1,1,1	T/C	I	F	R	12	44.7
Turdidae							
Austral thrush *(Turdus falcklandii)*	1,1,1	T/C	I	F	R	104	44.7
Thraupidae							
Greater yellow-finch *(Sicalis auriventris)*	0,0,1	R/C	G	G	A	55	9.4
Grassland yellow-finch *(Sicalis luteola)*	0,0,1	G/O	G	G	A	16	9.4
Patagonian sierra finch *(Phrygilus patagonicus)*	1,1,1	T/O	G	G	M	23	9.7
Mourning sierra finch *(Rhopospiza fruticeti)*	0,0,1	S/O	G	G	A	39	17.8
Plumbeous sierra finch *(Geospizopsis unicolor)*	0,1,1	R/C	G	G	A	22	14.4
Yellow-bridled finch *(Melanodera xanthogramma)*	0,1,1	R/C	F	G	A	36	9.7
Common diuca-finch *(Diuca diuca)*	0,1,1	S/O	G	G	R	33	22.7
Passerellidae							
Rufous-collared sparrow *(Zonotrichia capensis)*	1,1,1	G/O	G	G	M	24	23.1

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Table A1 (*continued*)

Species	Habitat (M,S,A)	Nest	Diet	FS	MS	Mass	ED
Icteridae							
Austral blackbird *(Curaeus curaeus)*	1,1,1	T/O	O	G	R	83	23.1
Species	Habitat	Nest	Diet	FS	MS	Mass	ED
Fringillidae	(M,S,A)						
Black-chinned siskin *(Spinus barbatus)*	1,1,1	S/O	G	F	M	16	39.1
Transect total = 63 species	**39,46,39**						

(A) British Columbia: $^{\Delta}$Species considered common, but in rapid decline; *Species of highest conservation concern across North America (Partners in Flight Watch List); ^{R}Species considered endangered or threatened in British Columbia (i.e., Red listed); ^{B}Species of special concern in British Columbia (i.e., Blue listed).

(B) Southern Chile: ^{R}Species considered Rare according to the Reglamento de la Ley de Caza(CAZA) by the Ministerio de Agricultura de Chile (MINAGRI); ^{E}Endemic to Chile; ^{NT}Species are considered locally nearlythreatened according to the Reglamento de Clasificación de Especies (RCE) bythe Ministerio Secretaría General de la Presidencia or globally by the IUCN RedList; ^{V}Species are considered locally vulnerable by CAZA or globally by IUCNRed List.

Data sources for (A) North temperate: Order of species according to North American Classification Committee, American Ornithological Society (Chesser et al. 2020); Migratory status retrieved from Pacific Bird Summary British Columbia (Canadian Wildlife Service, excel file) and Boyle and Martin (2015); Diet, foraging substrate, nest type, and nest substrate retrieved from Pacific Bird Summary BC,and Birds of the World Online (Billerman et al. 2020), accessed 25 June 2020.

Data sources for (B) South temperate: Order of species according to South American Classification Committee, American Ornithological Society (Remsen et al. 2021); Migratory status, nest, diet, foraging substrate, and mass (Jaksic and Feinsinger 1991, Martínez and González 2021, Cofre et al. 2007, Ibarra et al. 2010, Billerman et al. 2020); Endemic species according to Martínez and González 2021.

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Declaration of competing interest

All authors declare no conflicts of interest in the execution or submission of this study.

Appendix

See Figs. A1, A2 and Table A1 here.

References

Altamirano, T.A., Ibarra, J.T., Martin, K., Bonacic, C., 2017. The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforests. Biodivers. Conserv. 26, 2453–2472. https://doi.org/10.1007/s10531-017-1369-x.

Altamirano, T.A., de Zwaan, D.R., Ibarra, J.T., Wilson, S., Martin, K., 2020. Treeline ecotones shape patterns of avian species richness and functional diversity in south temperate mountains. Sci. Rep. 10, 1–13. https://doi.org/10.1038/s41598-020-75470-2.

Araneda, P., Sielfeld, W., Bonacic, C., Ibarra, J.T., 2018. Bird diversity along elevational gradients in the Dry Tropical Andes of northern Chile: the potential role of Aymara indigenous traditional agriculture. PLoS One 13, e0207544. https://doi.org/10.1371/journal.pone.0207544.

Bader, M.Y., Llambí, L.D., Case, B.S., Buckley, H.L., Toivonen, J.M., Camarero, J.J., Cairns, D.M., Brown, C.D., Wiegand, T., Resler, L.M., 2021. A global framework for linking alpine-treeline ecotone patterns to underlying processes. Ecography 44, 265–292. https://doi.org/10.1111/ecog.05285.

Barbe, L., Morel, R., Rantier, Y., Lebas, J.F., Butet, A., 2018. Bird communities of a temperate forest: spatio-temporal partitioning between resident and migratory species. J. Ornithol. 159, 457–469. https://doi.org/10.1007/s10336-017-1523-y.

Belmaker, J., Jetz, W., 2015. Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. Ecol. Lett. 18, 563–571. https://doi.org/10.1111/ele.12438.

Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. (Eds.), 2020. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/home.

Blyth, S., Groombridge, B., Lysenko, I., Miles, L., Newton, A.C., 2002. Mountain Watch: Environmental Change and Sustainable Development in Mountains. UNEP-WCMC Biodiversity Series, Cambridge, UK, pp. 1–88.

Boyle, W.A., Martin, K., 2015. The conservation value of high elevation habitats to North American migrant birds. Biol. Conserv. 192, 461–476. https://doi.org/10.1016/j.biocon.2015.10.008.

Boyle, W.A., Sandercock, B.K., Martin, K., 2016. Patterns and drivers of intraspecific variation in avian life history along elevational gradients: a meta-analysis. Biol. Rev. 92, 469–482. https://doi.org/10.1111/brv.12180.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., Bollmann, K., 2014. Temperate mountain forest biodiversity under climate change: compensating negative effects by increasing structural complexity. PLoS One 9, e97718. https://doi.org/10.1371/journal.pone.0097718.

British Columbia Ministry of Forests, Lands, Natural Resource Operations, and Rural Development, 2018. Biogeoclimatic Zones of British Columbia, 2018. Forest Analysis and Inventory Branch, Victoria, BC. https://www.for.gov.bc.ca/hre/becweb/resources/maps/CurrentVersion.html.
Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789. https://doi.org/10.1890/03-9000.
Buckley, L.B., Jetz, W., 2008. Linking global turnover of species and environments. PNAS 105, 17836–17841. https://doi.org/10.1073/pnas.0803524105.
Cadena, C.D., Kozak, K.H., Gomez, J.P., Parra, J.L., McCain, C.M., Bowie, R.C., Graham, C.H., 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proc. R. Soc. B 279, 194–201. https://doi.org/10.1098/rspb.2011.0720.
Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P., Rolando, A., 2016. Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions. Oecologia 181, 1139–1150. https://doi.org/10.1007/s00442-016-3637-y.
Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547.
Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. https://doi.org/10.1890/13-0133.1.
Chesser, R.T., Billerman, S.M., Burns, K.J., Cicero, C., Dunn, J.L., Kratter, A.W., Winker, K., 2020. Checklist of North American Birds (online). American Ornithological Society. http://checklist.americanornithology.org/taxa.
Cofre, H.L., Bohning-Gaese, K., Marquet, P.A., 2007. Rarity in Chilean forest birds: which ecological and life-history traits matter? Divers. Distrib. 13, 203–212.
Davidson, P.J.A., Cannings, R.J., Couturier, A.R., Lepage, D., Di Corrado, C.M., 2015. The Atlas of the Breeding Birds of British Columbia, 2008–2012. Bird Studies Canada,, Delta, BC. http://www.birdatlas.bc.ca.
Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. Ecol. Lett. 13, 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x.
Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2.
Drake, A., de Zwaan, D.R., Altamirano, T., Wilson, S., Hick, K., Bravo, C., Ibarra, J.T., Martin, K., 2021. Combining point counts and autonomous recording units improves survey efficacy across elevational gradients on two continents. Ecol. Evol. https://doi.org/10.1002/ece3.7678.
Elsen, P.R., Tingley, M.W., Kalyanaraman, R., Ramesh, K., Wilcove, D.S., 2017. The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds. Ecology 98, 337–348. https://doi.org/10.1002/ecy.1669.
English, J.M., Johnston, S.T., 2004. The Laramide orogeny: what were the driving forces? Int. Geol. Rev. 46, 833–838. https://doi.org/10.2747/0020-6814.46.9.833.
Fick, S.E., Hijmans, R.J., 2017. Worldclim2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.
Fjeldså, J., 2018a. Mountains and the Diversity of Birds. In: Hoorn, C., Perrigo, A., Antonelli, A. (Eds.), Mountains, Climate and Biodiversity. John Wiley & Sons, West Sussex, UK, pp. 245–256. Ch. 18.
Fjeldså, J., Bowie, R.C., Rahbek, C., 2012. The role of mountain ranges in the diversification of birds. Annu. Rev. Ecol. Evol. Syst. 43, 249–265. https://doi.org/10.1146/annurev-ecolsys-102710-145113.
Fjeldså, J., Ohlson, J.I., Batalha-Filho, H., Ericson, P.G.P., Irestedt, M., 2018b. Rapid expansion and diversification into new niche space by fluvicoline flycatchers. J. Avian Biol. 49, jav-01661. https://doi.org/10.1111/jav.01661.
Flynn, D.F., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecol. Lett. 12, 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x.
Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V., Fitzpatrick, J.W., 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. PNAS 115, 11982–11987.
García-Navas, V., Sattler, T., Schmid, H., Ozgul, A., 2020. Temporal homogenization of functional and beta diversity in bird communities of the Swiss Alps. Divers. Distrib. 26, 900–911. https://doi.org/10.1111/ddi.13076.
Ghalambor, C.K., Martin, T.E., 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292, 494–497. https://doi.org/10.1126/science.1059379.
Grabherr, G., 2000. Biodiversity of mountain forests. In: Price, M.F., Butt, N. (Eds.), Forests in Sustainable Mountain Development: A State-of-Knowledge Report for 2000. CAB International, Wallingford, UK, pp. 28–37.
Gregory-Wodzicki, K.M., 2000. Uplift history of the central and northern andes: a review. Geol. Soc. Am. Bull. 112, 1091–1105.
Guo, Q., Kelt, D.A., Sun, Z., Liu, H., Hu, L., Ren, H., Wen, J., 2013. Global variation in elevational diversity patterns. Sci. Rep. 3, 1–7. https://doi.org/10.1038/srep03007.
Harris, J.B.C., Dwi Putra, D., Gregory, S.D., Brook, B.W., Prawiradilaga, D.M., Sodhi, N.S., Fordham, A., 2014. Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Divers. Distrib. 20, 773–785. https://doi.org/10.1111/ddi.12180.
Hoorn, C., Perrigo, A., Antonelli, A. (Eds.), 2018. Mountains, Climate and Biodiversity. John Wiley & Sons, West Sussex, UK.
Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613.
Ibarra, J.T., Martin, K., 2015. Beyond species richness: an empirical test of top predators as surrogates for functional diversity and endemism. Ecosphere 6, 1–15. https://doi.org/10.1890/ES15-00207.1.
Ibarra, J.T., Altamirano, T., Gálvez, N., Rojas, I., Laker, J., Bonacic, C., 2010. Avifauna de los bosques templados de Araucaria araucana del sur de Chile. Ecol. Austral 20, 33–45.
Ikin, K., Barton, P.S., Blanchard, W., Crane, M., Stein, J., Lindenmayer, D.B., 2019. Avian functional responses to landscape recovery. Proc. R. Soc. B 20190114. https://doi.org/10.1098/rspb.2019.0114.
IPCC, 2018. Summary for policymakers. In: Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P.R., et al. (Eds.), Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission pathways, in the Context of Strengthening the Global response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty. World Meteorological Organization, Geneva, Switzerland.
Jackson, M.M., Gergel, S.E., Martin, K., 2015. Effects of climate change on habitat availability and configuration for an endemic coastal alpine bird. PLoS One 10, e0142110. https://doi.org/10.1371/journal.pone.0142110.
Jackson, M.M., Topp, E., Gergel, S.E., Martin, K., Pirotti, F., Sitzia, T., 2016. Expansion of subalpine woody vegetation over 40 years on Vancouver Island, British Columbia, Canada. Can. J. . Res. 46, 437–443. https://doi.org/10.1139/cjfr-2015-0186.
Jaksic, F.M., Feinsinger, P., 1991. Bird assemblages in temperate forests of North and South America: a comparison of diversity, dynamics, guild structure and resource use. Rev. Chil. Hist. Nat. 64, 491–510.
Jankowski, J.E., Ciecka, A.L., Meyer, N.Y., Rabenold, K.N., 2009. Beta diversity along environmental gradients: Implications of habitat specialization in tropical montane landscapes. J. Anim. Ecol. 78, 315–327. https://doi.org/10.1111/j.1365-2656.2008.01487.x.
Janzen, D.H., 1967. Why mountain passes are higher in the tropics. Am. Nat. 101, 233–249. https://doi.org/10.1086/282487.
Jarzyna, M.A., Quintero, I., Jetz, W., 2021. Global functional and phylogenetic structure of avian assemblages across elevation and latitude. Ecol. Lett. 24, 196–207. https://doi.org/10.1111/ele.13631.
Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448. https://doi.org/10.1038/nature11631.
Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K., Mooers, A.O., 2014. Global distribution and conservation of evolutionary distinctness in birds. Curr. Biol. 24, 919–930. https://doi.org/10.1016/j.cub.2014.03.011.
Kapos, V., Rhind, J., Edwards, M., Price, M.F., Ravilious, C., 2000. Developing a map of the world's mountain forests. In: Price, M.F., Butt, N. (Eds.), Forests in Sustainable Mountain Development: A State-of-Knowledge Report for 2000. CAB Intl, Wallingford, UK, pp. 4–9.

Kark, S., 2013. Ecotones and ecological gradients. In: Leemans, R. (Ed.), Ecological Systems. Springer, New York, USA, pp. 147–160. https://doi.org/10.1007/978-1-4614-5755-8_9.
Körner, C., Ohsawa, M., 2006. Mountain systems. In: Hassan, R., Scholes, R., Ash, N. (Eds.), Ecosystem and Human Well-being: Current State and Trends, Vol. 1. Millennium Ecosystem Assessment, Island Press, Washington, USA, pp. 681–716.
Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31, 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x.
Laiolo, P., Pato, J., Obeso, J.R., 2018. Ecological and evolutionary drivers of the elevational gradient of diversity. Ecol. Lett. 21, 1022–1032. https://doi.org/10.1111/ele.12967.
Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1.
Laliberté, E. , Legendre, P. , Shipley, B. , Laliberté , M.E., 2014. Package 'FD'. Measuring functional diversity from multiple traits, and other tools for functional ecology.
Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x.
Lehikoinen, A., Brotons, L., Calladine, J., Campedelli, T., Escandell, V., Flousek, J., Trautmann, S., 2019. Declining population trends of European mountain birds. Glob. Chang. Biol. 25, 577–588. https://doi.org/10.1111/gcb.14522.
MacKinnon, A., Pojar, J., Coupe, R., 1992. Plants of Northern British Columbia. BC Ministry of Forests & Edmonton, AB: Lone Pine Publishing, Victoria, BC.
Martin, K., Wilson, S., MacDonald, E.C., Camfield, A.F., Martin, M., & Trefry, S.A. (2017). Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success. Auk Ornithol. Adv. 134: 696–709. https://doi.org/10.1642/AUK-16-271.1.
Martinez, D.E., Gonzalez, G.E., 2021. Field Guide to the Birds of Chile. Helm Field Guides, New York, USA.
Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S., Vesk, P.A., 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Glob. Ecol. Biogeogr. 19, 423–431. https://doi.org/10.1111/j.1466-8238.2010.00532.x.
McCain, C.M., 2009. Global analysis of bird elevational diversity. Glob. Ecol. Biogeogr. 18, 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x.
Medrano, F., Barros, R., Norambuena, H.V., Matus, R., Schmitt, F., 2018. Atlas de las aves nidificantes de Chile. Red de Observadores de Aves y Vida Silvestre de Chile, Santiago, Chile.
Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.F., Chave, J., Thuiller, W., 2012. Ecophylogenetics: advances and perspectives. Biol. Rev. 87, 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x.
Nagy, L., Grabherr, G., 2009. The Biology of Alpine Habitats. Oxford University Press, New York, NY.
Neate-Clegg, M.H., Jones, S.E., Burdekin, O., Jocque, M., Şekercioğlu, Ç.H., 2018. Elevational changes in the avian community of a Mesoamerican cloud forest park. Biotropica 50, 805–815. https://doi.org/10.1111/btp.12596.
Perrigo, A., Hoorn, C., Antonelli, A., 2020. Why mountains matter for biodiversity. J. Biogeogr. 47 (315), 25.
Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.
Pienaar, J., Ilany, A., Geffen, E., Yom-Tov, Y., 2013. Macroevolution of life-history traits in passerine birds: adaptation and phylogenetic inertia. Ecol. Lett. 16, 571–576. https://doi.org/10.1111/ele.12077.
Pigot, A.L., Trisos, C.H., Tobias, J.A., 2016. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. Proc. R. Soc. B 283, 20152013. https://doi.org/10.1098/rspb.2015.2013.
Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T.P., Freeman, B.G., Roll, U., Tobias, J.A., 2020. Macroevolutionary convergence connects morphological form to ecological function in birds. Nat. Ecol. Evol. 4, 230–239. https://doi.org/10.1038/s41559-019-1070-4.
Quintero, I., Jetz, W., 2018. Global elevational diversity and diversification of birds. Nature 555, 246–250. https://doi.org/10.1038/nature25794.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., Nogues-Bravo, D., Fjeldså, J., 2019. Building mountain biodiversity: geological and evolutionary processes. Science 365, 1114–1119. https://doi.org/10.1126/science.aax0151.
Remsen, J.V., Areta, J.I., Bonaccorso, E., Claramunt, S., Jaramillo, A., Pacheco, J.F., Zimmer, K.J., 2021. A classification of the bird species of South America. American Ornithological Society. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm.
Ricklefs, R.E., 2012. Species richness and morphological diversity of passerine birds. PNAS 109, 14482–14487. https://doi.org/10.1073/pnas.1212079109.
Sanders, N.J., Rahbek, C., 2012. The patterns and causes of elevational diversity gradients. Ecography 35, 1–3. https://doi.org/10.1111/j.1600-0587.2011.07338.x.
Sayre, R., Karagulle, D., Frye, C., Boucher, T., Wolff, N.H., Breyer, S., Touval, J., 2020. An assessment of the representation of ecosystems in global protected areas using new maps of World Climate Regions and World Ecosystems. Glob. Ecol. Conserv 21, e00860. https://doi.org/10.1016/j.gecco.2019.e00860.
Schumm, M., White, A.E., Supriya, K., Price, T.D., 2020. Ecological limits as the driver of bird species richness patterns along the east Himalayan elevational gradient. Am. Nat. 195, 802–817. https://doi.org/10.1086/707665.
Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., Rolando, A., 2018. A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. Ibis 160, 489–515. https://doi.org/10.1111/ibi.12585.
Seeholzer, G.F., Claramunt, S., Brumfield, R.T., 2017. Niche evolution and diversification in a Neotropical radiation of birds (Aves: Furnariidae). Evolution 71, 702–715. https://doi.org/10.1111/evo.13177.
Steinbauer, M.J., Field, R., Grytnes, J.A., Trigas, P., Ah-Peng, C., Attorre, F., De Sanctis, M., 2016. Topography-driven isolation, speciation and a global increase of endemism with elevation. Glob. Ecol. Biogeogr. 25, 1097–1107. https://doi.org/10.1111/geb.12469.
Terborgh, J., 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52, 23–40. https://doi.org/10.2307/1934735.
Tobias, J.A., Ottenburghs, J., Pigot, A.L., 2020. Avian diversity: speciation, macroevolution, and ecological function. Annu. Rev. Ecol. Evol. Syst. 51, 533–560. https://doi.org/10.1146/annurev-ecolsys-110218-025023.
Tsirogiannis, C. , Sandel, B. , 2017. PhyloMeasures: Fast and exact algorithms for computing phylogenetic biodiversity measures. https://CRAN.R-project.org/package=PhyloMeasures.
Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., Mazel, F., 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol. Rev. 92, 698–715. https://doi.org/10.1111/brv.12252.
Veblen, T.T., Young, K.R., Orme, A.R., 2007. The Physical Geography of South America. Oxford University Press, New York, NY.
Vuilleumier, F., 1985. Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. Ornithol. Monogr. 36, 255–304. https://doi.org/10.2307/40168287.
Wang, Q., Fan, X., Wang, M., 2016. Evidence of high-elevation amplification versus Arctic amplification. Sci. Rep. 6, 1–8. https://doi.org/10.1038/srep19219.
White, A.E., Dey, K.K., Mohan, D., Stephens, M., Price, T.D., 2019. Regional influences on community structure across the tropical-temperate divide. Nat. Commun. 10, 1–8. https://doi.org/10.1038/s41467-019-10253-6.
Wilson, S., Martin, K., 2005. High elevation habitat associations of birds during fall migration. Ecoscience 12, 561–568.
Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., Warren, P.H., 2005. Body size in ecological networks. Trends Ecol. Evol. 20, 402–409. https://doi.org/10.1016/j.tree.2005.04.005.