

1 • *Mountain Birds and Their Habitats*

DAN CHAMBERLAIN, ALEKSI
LEHIKOINEN, DAVIDE SCRIDEL
AND KATHY MARTIN

Mountains are high relief habitats that occur across all continents. Their impressive features define landscapes and human societies. These high elevation,¹ topographically complex habitats provide key ecosystem services (Körner & Ohsawa 2006), host high levels of diversity and endemism (Antonelli *et al.* 2018), and are characterized by many specialized and charismatic species, in addition to many generalist species that are distributed across broad elevation gradients (Boyle & Martin 2015). Mountain regions are highly valued by people in terms of their natural beauty and wildlife, and they are common tourist destinations year-round. However, these regions are under threat from a range of factors (Alba *et al.* 2022), including climate change (e.g., Gottfried *et al.* 2012; Freeman *et al.* 2018), changes in livestock management (MacDonald *et al.* 2000; Laiolo *et al.* 2004), increasing pressure from tourism and recreational activities (Rixen & Rolando 2013), and exploitation of natural resources, including renewable energy (Svadlenak-Gomez *et al.* 2013), all of which may have implications for mountain bird populations.

In this chapter, we first define our key terms of reference, including what we consider to be ‘mountains’ and ‘mountain birds’. We then summarize the importance of mountains to biodiversity in general and to birds in particular, focussing on key drivers of avian community assembly and variation along elevation gradients encompassing a wide range of habitats (i.e., from relatively low elevations to the highest mountain peaks). Subsequently, we provide an overview of the particular conditions faced by mountain birds at higher elevations, especially

¹ The term ‘elevation’ is used to represent the height of the ground above sea-level (e.g., a mountain summit); ‘altitude’ is the height above ground (e.g., a bird in flight). Both are expressed as metres above sea-level.

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at and above the treeline. Finally, we identify some of the key anthropogenic pressures that have shaped high elevation habitats historically. In so doing, we set the scene for the diversity of topics covered in the following chapters.

1.1 Defining a Mountain

What is a mountain? This is a simple question for which there is no simple answer. Several researchers have attempted to define methods and delineate estimates of regional or global mountain areas, typically involving the key characteristics of elevation and steepness of terrain (e.g., Kapos *et al.* 2000; Körner *et al.* 2011; Karagulle *et al.* 2017; Körner *et al.* 2017; Sayre *et al.* 2018), although the importance put on specific characteristics varies (Körner *et al.* 2021). The definition of Kapos *et al.* (2000) and Blyth *et al.* (2002) developed for the United Nations Environmental Programme (UNEP), is based on defining different mountain classes, largely in relation to elevation, the minimum being 300 m to be included as part of a mountain system. This classification (which we term K1 following Sayre *et al.* 2018), results in 24.3 per cent of global terrestrial surface being classed as mountainous (Plate 1). This does, however, exclude areas that have many ecological characteristics of mountains. Körner *et al.* (2011) developed a different classification (termed K2) for the Global Mountain Biodiversity Assessment, mostly based on terrain ruggedness, that resulted in the inclusion of a greater area at lower elevations (particularly coastal mountains), but an overall lower area of global mountain systems (12.3 per cent of global terrestrial surface) compared to Kapos *et al.* (2000). This was due to the exclusion of high elevation plateaus, intermontane valleys and hilly forelands (Plate 2).

Using a higher resolution (250 m versus 1,000 m), Karagulle *et al.* (2017) based their classification (termed K3) for the US Geological Survey on gentle slopes (a virtual mean inclination), ruggedness and profile type (the amount of gently sloping land in upland areas), resulting in an estimate of 30.4 per cent mountain cover of global terrestrial surface (Plate 3). Testolin *et al.* (2020) used an even higher resolution (30 m) to identify a global alpine zone (areas above the treeline) based on unfor- ested areas and modelled estimates of the limits of regional treelines, using the classification of Körner *et al.* (2011) as an initial template. Excluding Arctic and Antarctic mountains, this resulted in an estimated 2.6 per cent of the global terrestrial surface being covered by alpine zones which matches well the alpine areas defined in K2. Plate 4 shows

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the classification of Testolin *et al.* (2020) superimposed on a composite map of the other three main classifications (K1–K3; Kapos *et al.* 2000; Körner *et al.* 2011; Karagulle *et al.* 2017) and thus gives an estimate of the maximum extent of mountainous area combining different ‘mountain’ definitions.

It should be noted that only K1 includes all of Greenland or Antarctica. These areas were excluded from K2 (except for coastal mountains of Greenland) and K3 because their overall aims were not to identify ruggedness *per se* (a purely topographic view), but to apply the classifications to fields such as forestry (Kapos *et al.* 2000), biodiversity and climatic life zones on earth (Körner *et al.* 2011, 2017), and human populations living in or near mountains (Körner *et al.* 2021). We argue that Greenland and Antarctica should be included in future mountain mapping exercises as they hold relevant mountain features (high elevation sites at high latitudes), they host mountain birds (e.g., golden eagle *Aquila chysaetos* and rock ptarmigan *Lagopus muta* in Greenland, snow petrel *Pagodroma nivea* in Antarctica), and many ice-covered sites currently without birds are subject to fast ice-melting processes and are likely to become suitable in the near future.

Which of these methods is preferred depends on the objectives of a given study (Sayre *et al.* 2018), but there are situations where clear and objective definitions of mountain areas are needed (Körner *et al.* 2017). In this book, we focus on the ecology of the bird species that use these zones for at least a part of their life cycle. Our goals are most in line with the definition of Körner *et al.* (2011), that is, the K2 classification in Plate 2, in that we are primarily concerned with mountain biodiversity quantity and condition, species–habitat relationships and species–climate relationships. However, we do not formally adopt a strict and static definition of a ‘mountain’ which could risk the exclusion of important examples from low mountains (e.g., coastal, or where boreal mountains grade into arctic tundra) or from high elevation plateaus where species are still subject to many of the same constraints (in particular climatic) as mountain birds in steeper terrain. For example, the K2 classification does not include the whole Tibetan Plateau as it does not meet the requirements for terrain ruggedness, but ecologically we would consider this area as mountainous.

Our philosophy mirrors that of Nagy & Grabherr (2009) in that we are mainly concerned with areas that can be considered part of mountain systems from an ecological, rather than a topographic, point of view. In other words, mountain systems should have significant influences

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on the ecology of habitats and species due to factors associated with a combination of elevation and topography with respect to the surrounding landscape. For much of this book, we maintain a focus (albeit not exclusively) on areas above the natural elevational limit of continuous forest, where the treeline ecotone forms the lower limit of our main area of interest. Thus, the Testolin *et al.* (2020) classification probably matches that focus most closely. However, it does not include treeline ecotone areas, and in particular those that have been formed at elevations lower than the climatic limit of the treeline, which are also of interest (Chapter 4). It also underestimates the area of alpine zones that have less rock and bare ground, particularly in the tropics (Chapter 3).

1.2 Mountain Biodiversity

Mountainous areas tend to have disproportionately high biodiversity, covering around a quarter of the world's terrestrial surface (Kapos *et al.* 2000), supporting an estimated one-third of terrestrial biodiversity (Körner 2004), and harbouring almost 50 per cent of terrestrial biodiversity hot-spots globally (Myers *et al.* 2000). Mountain specialists (i.e., those dependent on and restricted to high elevation habitats for key parts of their annual cycle) often show very narrow geographic (and vertical) distributions. The range of individual species may sometimes be restricted to a single mountain or valley (Antonelli *et al.* 2018), or more typically a narrow elevational range, hence mountains are important centres of endemism (Körner *et al.* 2017) and speciation (Fjeldså *et al.* 2012; Rahbek *et al.* 2019). Mountains thus often harbour a greater proportion of threatened species than other habitats (Franzén & Molander 2012). Biodiversity is also increased by the upshifting of generalist species (those normally occurring over a wide range of elevations) that have lost their low elevation habitat due to anthropogenic impacts, such as farmland birds in France (Archaux 2007).

What drives the high biodiversity in mountains? From an evolutionary perspective, geological heterogeneity and its interaction with historical long-term fluctuations in climate has led to enhanced speciation rates and hence high diversity in mountainous regions (Rahbek *et al.* 2019). At a fairly large scale (1° latitude), tetrapod species richness is closely and positively correlated with temperature, precipitation and topographic relief (Antonelli *et al.* 2018), showing the importance of the complexity of mountain environments (evolutionary processes are considered further in Chapter 9). At finer scales, high biodiversity arises over relatively small

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spatial scales (e.g., one or a few kilometres) as a consequence of the steep terrain and subsequent zonation along elevation gradients (Section 1.2.1).

Species diversity, in particular species richness, varies strongly with elevation. There are competing hypotheses to explain such patterns, and typically these are linked closely to hypotheses explaining trends in relation to latitude. Moist, tropical regions have a more stable year-round climate which, over evolutionary time, may result in greater divergence and niche packing with fine-scale specialization. More fluctuating, higher latitude environments facilitate generalists with broad niches. Analogously, the more fluctuating climatic conditions at higher elevations may contribute to broader niches (Mermillon *et al.* 2022) and decreasing species richness along elevation gradients. However, the latitude gradient shows a fairly constant decrease in species richness towards the poles, whereas there is much more evidence of an intermediate peak in terms of elevation patterns, suggesting that latitudinal and elevational trends are driven, at least in part, by different factors (Rahbek 1995).

Temperature is in general the most important factor driving biodiversity trends along elevation gradients (Peters *et al.* 2016; Laiolo *et al.* 2018). Ambient temperature varies with elevation, or more strictly air pressure, in a fairly predictable way termed the adiabatic lapse rate. Typically, there is an approximately 0.6°C decrease for every 100 m increase in elevation, with local variation caused by humidity, wind exposure, cloud cover and other factors (e.g., Dillon *et al.* 2006; Colwell *et al.* 2008). Since temperature may constrain the number of organisms that a given area can support, the decrease in temperature at higher elevations may limit the richness of a given community and affect its community structure (White *et al.* 2019). Water availability (precipitation, soil water retention and evaporation) is an additional critical climatic factor (McCain 2009; Antonelli *et al.* 2018), influencing, for example, tree formation at high elevation. Primary productivity, which decreases with temperature (and hence elevation) and is also affected by precipitation, is integrated with these two abiotic drivers. High elevations have lower productivity, hence there is insufficient energy to support species rich communities (Newton 2020; Schumm *et al.* 2020). Indeed, there is evidence that bird species richness is closely correlated with measures of productivity (e.g., Acharya *et al.* 2011; Abebe *et al.* 2019). However, these relationships show considerable geographic variation – stability, *in situ* speciation and accumulation of species over a long time are considered to be more important drivers of species richness within regions with high landscape complexity (Rahbek *et al.* 2019).

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A range of other hypotheses have been proposed to explain variations in species richness with elevation. Rapoport's rule states that the latitudinal range size of animals and plants is greater at higher latitudes (Stevens 1989). This has been extended to range sizes in relation to elevation, that is, species of higher elevations show a greater elevational range as they are adapted to a wider range of conditions (Stevens 1992). This results in greater species richness at lower elevations as higher elevation species are more likely to 'spill down' to lower elevations (Acharya *et al.* 2011). There are also hypotheses that are more related to spatial effects, rather than biological effects *per se*. For example, some have argued that lower species richness at higher elevations in mountains is due to the species-area relationship and the fact that a 'typical' conical-shaped mountain has a greater area at the base than close to the summit (Şekercioğlu *et al.* 2012). An alternative hypothesis is the Mid-Domain Effect (Colwell & Lees 2000), which proposes that the ranges of species are randomly distributed within a given area, thus more ranges will overlap near the middle of the area than at the edges, resulting in a mid-elevation species richness peak. There has been only limited support for Rapoport's rule (Gaston *et al.* 1998; Acharya *et al.* 2011), the species-area relationship (Elsen & Tingley 2015) and the Mid-Domain Effect (McCain 2009; Reynolds *et al.* 2021) for explaining patterns in species richness along elevation gradients. Environmental drivers (e.g., productivity and climate, in particular water and temperature) are thus likely to be more important (McCain 2009), although a range of complex factors interact to produce location-specific patterns (Reynolds *et al.* 2022).

Whilst much research on biodiversity trends along the elevation gradient has focussed on species richness, other studies have instead considered variations in functional diversity, that is, the role of organisms in communities and ecosystems (Petchey & Gaston 2006), usually expressed through the analysis of species traits (e.g., diet type, clutch size, foraging niche, migratory strategy). Trends in functional diversity along elevation gradients vary according to latitude. In the tropics, bird communities show a disproportionately high functional diversity in relation to their species richness (i.e., functional overdispersion) in stable lowland habitats, but the opposite pattern (functional clustering) in higher elevation habitats (Jarzyna *et al.* 2021). However, increasing functional overdispersion is shown in temperate and boreal bird communities at higher elevations (above *c.* 2,000 m, Martin *et al.* 2021). Temperate mountains are therefore functionally rich and distinctive ecosystems, despite their overall low species richness. These findings further suggest that higher

latitude mountains are disproportionately susceptible to the loss of critical ecological functions because they harbour species assemblages with high functional distinctiveness and low species richness (Jarzyńska *et al.* 2021).

1.2.1 Zonation Along the Elevation Gradient

Mountains are defined by their greater elevation with respect to the surrounding landscape, thus a key characteristic, in particular in relation to biodiversity, is the rapid change in environmental conditions along the elevation gradient – and obviously the steeper the gradient, the more rapidly conditions will change over a given spatial scale. The decrease in temperature with elevation is one of the key environmental factors that affects variation in biotic communities along elevation gradients (see earlier in section 1.2). Additionally, wind speed, air pressure, partial pressure of oxygen and UV radiation vary more-or-less predictably with elevation (Nagy & Grabherr 2009; Chapter 2).

The changing conditions over small spatial scales result in fairly distinct vegetation zones along the elevation gradient that are normally bounded by the upper limit of particular growth forms dictated by the environmental conditions. In a natural state (i.e., with little or minimal human influence), these correspond to the bioclimatic zones listed in Table 1.1. There are two features separating different zones that are of particular relevance to the scope of this book. First, the **timberline**, which is the upper limit of closed forest. Much of this book is concerned with the area above the timberline (i.e., it forms the lower limit of the bioclimatic zones considered). Second, the **treeline**, the approximate line that links the highest groups of mature trees, which is often limited by temperature (Körner & Paulsen 2004). The treeline typically represents an area of marked change in bird communities (e.g., Altamirano *et al.* 2020; Martin *et al.* 2021). Given the inconsistencies in the use of these terms to describe vegetation zones and boundaries around the treeline, we discuss them in more detail in Chapter 4.

The zones set out in Table 1.1 are, of course, generalizations – there are many situations where some of them are absent, often due to human activity (see Section 1.5), but also due to ecological or climatic conditions (e.g., the extent of treeline habitat for temperate mountains is often very limited; Nagy & Grabherr 2009). There are also regional or local climatic constraints that may influence zonation such as aspect. In dry climates, the forest may be largely absent (e.g., some central Asian ranges, Potapov 2004; the dry central Andes, Chapter 9). Furthermore, the limit of the

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Table 1.1 *Habitat zonation and key divisions between zones along the elevation gradient (based largely on Nagy & Grabherr 2009), as used in this book.*

Zone	Description
Lowland	Areas not classified as mountain.
Montane forest	Closed canopy forest, mature trees – note that transitions may occur between different types of forest within this zone (e.g., subtropical and temperate broad-leaved forest; Acharya <i>et al.</i> 2011).
Timberline	The line where the closed forest ends, marking the transition between montane forest and treeline ecotone.
Treeline ecotone	The zone between the timberline and the tree species line. Also sometimes termed the upper subalpine, this is typically characterized by a mosaic of trees, shrubs and meadows.
Treeline	The approximate line that links the highest growing groups of mature trees.
Tree species line	The maximum possible elevation of tree growth (including seedlings and saplings).
Alpine	The treeless area above the tree species line that is dominated by dwarf-shrub communities (sometimes termed lower alpine) and grassland, steppe-like and meadow communities (sometimes termed upper alpine).
Snowline	The elevation at which there is permanent snow cover (often considered equal to the upper limit of the alpine zone; Körner 2012).
Nival	Patchy vegetation, often cushion or rosette plants, within a largely unvegetated landscape (some authors separate nival and subnival zones according to the snowline).
Aeolian	Beyond the elevation limit at which vascular plants grow. Wind is important in providing nutrient input and maintaining food chains.

alpine zone is influenced by slope exposure. For mountain ranges that are generally orientated from east to west (e.g., Himalayas, European Alps, Pyrenees), the alpine zone is typically lower on northern facing slopes in the northern hemisphere and on southern facing slopes in the southern hemisphere (Nagy & Grabherr 2009). There are oceanic influences on the treeline as well, mediated by precipitation patterns that influence the elevation of the different zones in major mountain chains that are orientated from north to south (e.g., the Andes, Chapter 9) and also mountains on islands. Zonation may also vary according to the geographic position of a particular location within a mountain range, whereby central areas have warmer temperatures and thus higher elevations for any given zone

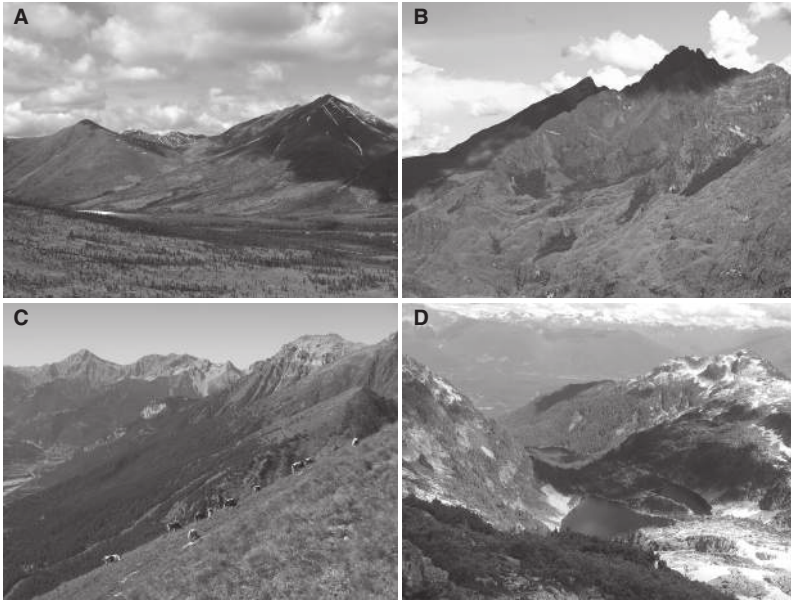


Figure 1.1 Examples of the elevation zones that are the main focus of this book. A. Suntar-Khayata Range, Eastern Siberia, showing gentle elevation gradients resulting in a wide treeline ecotone (Photo: E. Melikhova); B. Peruvian Andes, with patches of *Polylepis* woodland (Photo: S. Sevillano-Ríos). C. Gradient from montane forest to the alpine zone in the Italian Alps, where grazing has a major impact on vegetation structure and in particular on the elevation of the treeline ecotone (Photo: D. Chamberlain). D. A high elevation lake in the Tantalus Range, British Columbia, Canada, within a diffuse treeline ecotone transitioning into alpine shrubs and a rocky nival zone towards the peak (Photo: D.R. de Zwaan).

relative to external slopes (the mass elevation effect; Körner 2012). Some examples of elevation gradients in mountains from different geographic regions are shown in Figure 1.1. Despite these variations, the definitions in Table 1.1 serve as a useful reference for the typical zonation found along elevation gradients in many mountains.

At very high latitudes, Arctic mountains do not have a treeline as they are beyond the latitudinal limit of tree growth. Indeed, latitude is the main determinant of the elevation of these various zones (Table 1.1); the treeline in tropical mountains can occur at very high elevations (Nagy & Grabherr 2009), whereas in sub-arctic areas at high latitudes, the treeline is at sea-level. Furthermore, this classification does not apply in many areas due to human influence (see Section 1.5).

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1.3 Mountain Birds

1.3.1 What Is a Mountain Bird?

Defining a mountain is difficult, so it follows that defining a mountain bird is equally challenging. Objective definitions of mountain birds have been developed based on definitions of mountain areas as outlined above and their overlap with the range maps of the geographical distribution of species. In this way, mountain birds are identified as those with a large proportion of their range in mountain areas (e.g., Scridel *et al.* 2018; Lehtikoinen *et al.* 2019; Alba *et al.* 2022). However, such range maps are usually restricted to breeding season distributions and thus do not represent the use of mountains by birds throughout the year. The number of species that use mountains may be particularly high. One field study of temperate mountains in the Americas during the breeding season detected 44 to 63 per cent of the regional species pool in western Canada and southern Chile, respectively (Martin *et al.* 2021). At a continental level and including migrants, Boyle & Martin (2015) found that c. 35 per cent of the birds that breed in North America use mountains at some point in their annual life cycle.

In this book, we are interested in how mountain habitats are used by birds. We define a mountain bird in this book *as a bird species where at least some populations somewhere in their distribution spend at least one critical stage of their life cycle at or above the elevational limit of continuous forest (i.e., above the timberline)*. In doing so, we recognize that our knowledge of avian use of mountains is incomplete from a seasonal point of view (as research is biased towards breeding seasons) and from a geographic point of view (as many of the world's mountain ranges are under-researched – see Section 1.3.2).

1.3.2 Extent of Knowledge of Birds using Alpine Habitats Compared to Other Systems

Given the particular logistical challenges to mountain research, it has been suggested that knowledge of mountain birds is relatively poor compared to other major habitat types (European Environment Agency 2010; Chamberlain *et al.* 2012; Scridel *et al.* 2018). For example, nearly one quarter of all alpine breeding species have no nest records or have less than five nests described, in addition to deep data deficiency for most other basic life-history traits (Chapters 2 and 3). A systematic search of published articles in the Web of Science online database between