

7 · *Subalpine Coniferous Forests of Europe*

Avian Communities in European High-Altitude Woodlands

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7.1 Forest Ecosystem

7.1.1 Introduction

Subalpine coniferous forests cover higher-altitudinal zones in various mountain ranges of Europe, notably in the Alps, Pyrenees and Carpathians, as well as some lower-elevation massifs in central and south-east Europe (defined as category 3 by the European map of natural vegetation; Bohn *et al.* 2000). These forests are characterised by a dominance of coniferous trees, compared to the lower-altitude montane forests, which are mainly composed of broadleaved trees (Ott *et al.* 1997; Landolt 2003). This distinction between montane and subalpine forests is important, because bird species assemblages generally differ quite markedly between conifer and broadleaved woodlands (Fuller *et al.* 2012; see also Chapters 6 and 8). Montane forests provide habitats supporting very rich bird assemblages linked to the presence of both coniferous and broadleaved forest features and thereby resemble forests of the hemiboreal (boreonemoral) zone (Nilsson 1997). Although a few studies have focused specifically on bird assemblages of montane forests in the Carpathians (e.g., Kropil 1996; Korňan & Adamík 2014) and the Alps (e.g., Archaux & Bakkaus 2007), montane forests are not treated separately in this book. The reader can refer to Chapter 8 (and to some extent Chapter 6) for content of relevance to the bird assemblages of these forests. Conifers tend to become dominant over broad-leaved trees under harsher environmental conditions (Ellenberg 2009). The principal environmental drivers of subalpine coniferous forest tree

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species composition are altitude, topography, soil conditions and natural history, particularly the history of recolonisation of mountain ranges by tree species after the Pleistocene ice ages. More specifically, climatic and weather conditions, ambient temperature, precipitation regime and type (snow *vs* rain), frost occurrence, air moisture and solar radiation all tightly correlate with altitude, topography and continentality, playing crucial roles in forest dynamics, notably in rejuvenation processes. This chapter considers the entire subalpine coniferous zone, including the ecologically distinctive ecotone along the upper treeline.

Subalpine coniferous forests occur within a given altitudinal belt, typically between the montane mixed forests and alpine grasslands. The absolute altitude and altitudinal range of this belt vary among the different mountain massifs considered. It tends to be situated higher and to extend across a broader altitudinal amplitude in areas where the climate is warmer or drier. This is the case, for instance, in the inner valleys of the Alps, due to the protective effect of high mountain ridges, which locally create a more continental climate. Thus, the limit between montane and subalpine forests almost never follows isotherms and shows great altitudinal variation. This is because of the manifold relationships between local climatic conditions, topographic circumstances, altitude and slope exposure typically encountered in mountain ranges with a complex topography (Körner 1998).

At first glance, the upper altitudinal limit of subalpine forest distribution seems evident. Worldwide, in all high massifs, there is a treeline somewhere above which tree growth is no longer possible (Fig. 7.1). However, this treeline is rarely a sharp line; it usually forms an ecotonal zone with gradual opening of the canopy and steadily wider spacing of individual trees as altitude increases (Körner 2012). The treeline belt can stretch across only a few metres under very steep conditions, whereas it can extend over several hundred metres in rather flat terrain. This natural zonal habitat heterogeneity is accentuated by uneven terrain and the resulting heterogeneous distribution of soil types. It is further modified by natural disturbances such as snow avalanches and landslides. Finally, it has been greatly influenced by human activity, since both timber production and grazing were important for the economy of Old World traditional mountain societies across centuries, if not millennia (Bugmann 2001; Bätzing 2005; Körner 2012). Given their pronounced habitat and structural heterogeneity, treeline ecosystems are inhabited by a rich species community in general, and a unique bird community in particular

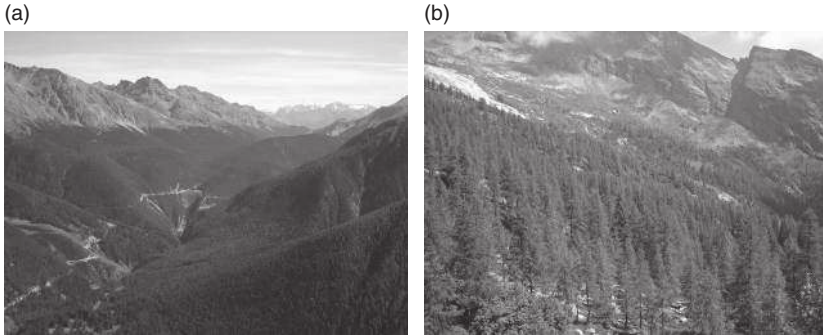


Figure 7.1 (a) Looked at from far away, the upper altitudinal limit of a subalpine forest seems to be a more or less clearly defined line. (b) In reality, it's rather an ecotonal zone, with gradual opening of the canopy and steadily wider spacing of individual trees as altitude increases or productivity of the soil decreases, even in forests with no signs of past human intervention. (a) Val dal Spöl, Grisons, Switzerland and (b) pure larch forest on very rocky soil in the southern Alps, close to Alpe Magnello, Ticino, Switzerland. Photos: P. Mollet.

(Mattes *et al.* 2005). Here, birds with mainly Mediterranean distributions may live in sympatry with boreo-alpine species, and typical forest species meet species that are adapted to very open land with scattered single trees and grassy field layers.

7.1.2 Forest Cover

Traces of exploitation of subalpine forests by humans have been documented from the second millennium BC onwards, but large-scale landscape changes, resulting from burning and systematic tree felling, primarily to increase the area of grazed or mown grasslands, apparently accelerated in the 9th or 10th century AD; at least this has been documented for the Alps (Burga & Perret 1998). Forest conversion and exploitation continued unabated throughout the Middle Ages and the modern epoch until the late 19th and early 20th centuries (Parolini 2012). Later, during the 20th century, traditional silvi-agricultural land-use systems were progressively abandoned due to profound socio-economic changes, but the magnitude of their effects depended on the geographic area or even the political system. Among other factors, the progressive reliance on petrol instead of wood fuel caused a dramatic release of the economic pressure formerly exerted upon subalpine forests. This development was paralleled by a progressive shift towards

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more sustainable forest management (see Johann 2006 for details), together resulting in an increase of forest extent and the stock of growing trees. Despite the abandonment of traditional agricultural and silvi-pastoral practices, the area covered by forest remains smaller today than what it would be naturally, i.e., without past human intervention. Some mountain areas, however, have recently undergone forestry intensification. In some regions of the Slovak and Romanian Carpathians, for instance, subalpine forests are being subjected to large-scale clearcutting by multinational companies, severely impacting the avifauna, as illustrated by the dramatic decline of local populations of capercaillie *Tetrao urogallus* (Mikoláš *et al.* 2015). A first crucial conservation issue is how a progressive reliance upon more renewable energy sources will affect subalpine forest management and its ecological community in the future. A second key issue is how land-use changes, notably the release of grazing pressure, will impact on species requiring semi-open and open grassy habitats (Chamberlain *et al.* 2013). These developments, and their consequences for subalpine birds, should be closely monitored.

7.1.3 Tree Species Composition

Tree species composition depends heavily on soil and local climate conditions. In general, European subalpine forests are dominated by four main tree species, while two additional species may be important locally. In the Alps and the Carpathians, Norway spruce *Picea abies* is the most widely distributed and most abundant tree. It is absent from the Pyrenees. After the last Pleistocene ice age, the Norway spruce recolonised the Alps and the Carpathians from the south-east (Burga & Perret 1998) and most likely never reached the Pyrenees. In many European subalpine forests, silver fir *Abies alba* is an important species, notably at lower altitudes and in rather humid and cool local climates. However, it rarely forms pure stands, being usually associated with other tree species, principally Norway spruce in subalpine conditions at higher altitudes. In inner alpine valleys, which are characterised by a pronounced continental climate (see above), the European larch *Larix decidua* may occupy vast areas. It requires very light conditions (i.e., it does not tolerate shade) and is usually associated with poor and shallow soils. Swiss stone pine *Pinus cembra* also covers wide areas at the treeline. This species is one of the most tolerant to cold temperatures and reaches the highest altitudes of any tree in the Alps, at slightly more than 2,500 m above sea level in

Valais, Switzerland. Stone pine can form pure, albeit mostly open or semi-open, stands, but is more often associated with larch. Neither the larch nor the stone pine occurs in the Pyrenees, but both have a fine-scale and spatially scattered distribution pattern in the Carpathians, including the High Tatra mountains.

Apart from these four dominant tree species, two other pines can be encountered in the subalpine zones of the Alps and on the southern slopes of the Pyrenees: Scots pine *Pinus sylvestris* and mountain pine *Pinus mugo* (var. *arborea*, ssp. *uncinata*, according to some sources), the latter in its upright growth form. In the Alps, however, they rarely cover large areas, occurring primarily on small patches of very poor soils, where they can break the dominance of the other four species. An exception is in the Swiss National Park, in south-east Switzerland next to the Italian border, where extensive pure stands of mountain pine dominate on a dolomitic substrate. On the southern slopes of the Pyrenees, where the climate is fairly dry (characterised by Mediterranean summers), the two species are widespread and predominant in subalpine woodlands. Mountain pine exists in another shrub-like form (var. *prostrata*, ssp. *mugo*, according to some sources), which covers large areas only in the eastern Alps and the Carpathians. Yet another potentially landscape-dominating element in the subalpine belt is the green alder *Alnus viridis*, a small bush-like tree that can form pure stands, particularly on cooler and steep slopes that are regularly exposed to snow avalanches.

At a local scale, tree-species composition depends not only on climatic and edaphic conditions, but also on historic and recent human activity. Silvi-agricultural land-use systems favour the larch over the Norway spruce (Mayer & Stöckli 2005), most probably due to both the enhanced light supply and the fact that many farmers spared the larches when cutting young trees (Janett 1943).

Finally, it is important to note that, in contrast to lower elevations, large-scale plantations of non-native tree species have never been important in subalpine forests, most likely as a consequence of the prevailing harsh climatic conditions.

7.1.4 Forest Structure

Structurally, subalpine forests can form two rather distinct types of stands. At lower elevations, close to the limits of montane woods, subalpine forests occasionally develop stands with a rather closed canopy, limited understorey and very scarce, if any, ground vegetation. At this elevation,



Figure 7.2 Typical subalpine forest stand with dominant conifers (*Picea abies*) in the tree layer at 1,200 m above sea level in Uaul Grond, Surselva, in Grisons, Switzerland. Microtopographic heterogeneity and disturbance agents support the development of semi-open stands with a well-developed ground layer and tree rejuvenation at microclimatic favoured sites. The avifaunistic diversity of such forests is high due to the availability of diverse ecological niches in the canopy, tree, shrub and ground layers. Photo: K. Bollmann.

more open stands only occur on poor soils or as a result of natural or anthropogenic disturbances such as avalanches, slope slides, fire, windthrow, bark beetle infestations or timber exploitation (Fig. 7.2).

In comparison, extensive closed stands are rare in the higher-altitude subalpine belt close to the treeline. Here, open stands predominate, typically accompanied by a rich understorey characteristic of early successional stages, consisting of small deciduous trees belonging to the genera *Betula*, *Sorbus*, *Salix* and *Alnus*, and dwarf shrubs such as *Vaccinium* ssp., *Rhododendron* ssp. and *Juniperus communis* (var. *saxatilis*). Many of these species provide important food resources for forest birds, notably various berries and buds (Turček 1961). Centuries-long grazing activity in those high-elevation forests, furthermore, has led to an even more open landscape, the woody vegetation being frequently intermixed with an extended grassy field layer (Fig. 7.3).

Human management of this zone has significantly lowered the treeline in many regions (Körner 2012). These profound structural differences between closed coniferous stands at lower elevations within the subalpine belt and very open vegetation in the treeline zone give rise to rather different bird assemblages, with typical forest guilds in the former and a dominance of ecotonal species in the latter habitat type.



Figure 7.3 Cattle grazing and browsing keep subalpine forests open through suppression of rejuvenation. Farmers sometimes also eliminate young trees actively. Forest with larch (*Larix decidua*), spruce (*Picea abies*) and some Scots pine (*Pinus sylvestris*) above Tschlin, Grisons, Switzerland. Photo: P. Mollet.

7.2 Bird Assemblages

7.2.1 Large-scale Variation in Species Richness and Abundance

Bird-species richness is lower in subalpine than in lowland and montane forests (Mosimann *et al.* 1987), which has been attributed to a decrease in net primary productivity – and therefore a decrease in the availability of ecological niches – with increasing altitude (Zbinden *et al.* 2010). According to presence-absence data from various breeding bird atlases (e.g., Dvorak *et al.* 1993; Niederfriniger *et al.* 1996; Schmid *et al.* 1998; Estrada *et al.* 2005), subalpine breeding bird assemblages are rather similar across European mountain ranges (Table 7.1), with a few noticeable exceptions:

- a) Some species with a typical boreo-alpine distribution are absent from the Pyrenees: hazel grouse *Tetrastes bonasia*, black grouse *Lyrurus tetrix*, three-toed woodpecker *Picoides tridactylus* and pygmy owl *Glaucidium passerinum*.
- b) Ural owl *Strix uralensis* is largely restricted to northern and eastern Europe, and in the Alps occurs only in Bavaria and in the far south-east of the massif.
- c) Some species which are widespread throughout northern, central and eastern Europe have their western distribution limits in central France, thus not reaching the Pyrenean massif, e.g., willow tit *Poecile montanus* and lesser whitethroat *Sylvia curruca*.
- d) Citril finch (*Serinus citrinella*) and western Bonelli's warbler *Phylloscopus bonelli* occur in south-western and southern Europe, respectively, but not in the Carpathians.

Table 7.1 Breeding bird species in European subalpine forests according to Catzeflis (1979), Estrada et al. (2005), Meier (1954), Mosimann et al. (1987), Müller-Buser (2002), Saniga (1995) and Schmid et al. (1998) and unpublished data by the authors. EU Bird Directive status according to Ddirective 2009/147/EC of the European Parliament and the Council of 30 November 2009 on the conservation of wild birds (http://ec.europa.eu/environment/nature/legislation/birdsdirective/index_en.htm, accessed 13 July 2015), SPEC categories according to Burfield and van Bommel (2004). All the species are classified as 'Least Concern' on the Red List (BirdLife International 2015).

English	Scientific	Pyrenees	Jura & Alps	Carpathians	EU Bird Directive Annex I	SPEC
1 Northern goshawk	<i>Accipiter gentilis</i>	Yes	Yes	Yes	No	Non-SPEC
2 Eurasian sparrowhawk	<i>Accipiter nisus</i>	Yes	Yes	Yes	No	Non-SPEC
3 Hazel grouse	<i>Tetrastes bonasia</i>	No	Yes	Yes	Yes	Non-SPEC
4 Black grouse	<i>Lyrurus tetrix</i>	No	Yes	Yes	Yes	SPEC 3
5 Western capercaillie	<i>Tetrao urogallus</i>	Yes	Yes	Yes	Yes	Non-SPEC
6 Eurasian woodcock	<i>Scolopax rusticola</i>	Yes	Yes	Yes	No	SPEC 3
7 Common cuckoo	<i>Cuculus canorus</i>	Yes	Yes	Yes	No	Non-SPEC
8 Eurasian pygmy owl	<i>Glaucidium passerinum</i>	No	Yes	Yes	Yes	Non-SPEC
9 Tengmalm's owl	<i>Aegolius funereus</i>	Yes	Yes	Yes	Yes	Non-SPEC
10 Long-eared owl	<i>Asio otus</i>	Yes	Yes	Yes	No	Non-SPEC
11 Ural owl	<i>Strix uralensis</i>	No	Partly	Yes	Yes	Non-SPEC
12 European green woodpecker	<i>Picus viridis</i>	Yes	Yes	Yes	No	SPEC 2
13 Black woodpecker	<i>Dryocopus martius</i>	Yes	Yes	Yes	Yes	Non-SPEC
14 Great spotted woodpecker	<i>Dendrocopos major</i>	Yes	Yes	Yes	No	Non-SPEC
15 Three-toed woodpecker	<i>Picoides tridactylus</i>	No	Yes	Yes	Yes	SPEC 3
16 Tree pipit	<i>Anthus trivialis</i>	Yes	Yes	Yes	No	Non-SPEC
17 Eurasian wren	<i>Troglodytes troglodytes</i>	Yes	Yes	Yes	No	Non-SPEC
18 Dunnock	<i>Prunella modularis</i>	Yes	Yes	Yes	No	Non-SPEC

19	European robin	<i>Eirithacus rubecula</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
20	Ring ouzel	<i>Turdus torquatus</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
21	Common blackbird	<i>Turdus merula</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
22	Fieldfare	<i>Turdus pilaris</i>	No	Yes	Yes	Yes	No	Non-SPEC
23	Song thrush	<i>Turdus philomelos</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
24	Mistle thrush	<i>Turdus viscivorus</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
25	Lesser whitethroat	<i>Sylvia curruca</i>	No	Yes	Yes	Yes	No	Non-SPEC
26	Garden warbler	<i>Sylvia borin</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
27	Blackcap	<i>Sylvia atricapilla</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
28	Western Bonelli's warbler	<i>Phylloscopus bonelli</i>	Yes	Yes	Yes	No	No	SPEC 2
29	Chiffchaff	<i>Phylloscopus collybita</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
30	Goldcrest	<i>Regulus regulus</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
31	Firecrest	<i>Regulus ignicapilla</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
32	Willow tit	<i>Poecile montanus</i>	No	Yes	Yes	Yes	No	Non-SPEC
33	Crested tit	<i>Lophophanes cristatus</i>	Yes	Yes	Yes	Yes	No	SPEC 2
34	Coal tit	<i>Periparus ater</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
35	Eurasian nuthatch	<i>Sitta europaea</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
36	Eurasian treecreeper	<i>Certhia familiaris</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
37	Eurasian jay	<i>Garrulus glandarius</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
38	Spotted nutcracker	<i>Nucifraga caryocatactes</i>	No	Yes	Yes	Yes	No	Non-SPEC
39	Common chaffinch	<i>Fringilla coelebs</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
40	Citril finch	<i>Serinus citrinella</i>	Yes	Yes	Yes	No	No	Non-SPEC
41	Eurasian siskin	<i>Carduelis spinus</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
42	Common linnet	<i>Carduelis cannabina</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
43	Common redpoll	<i>Carduelis flammea</i>	No	Yes	Yes	Yes	No	Non-SPEC
44	Common crossbill	<i>Loxia curvirostra</i>	Yes	Yes	Yes	Yes	No	Non-SPEC
45	Eurasian bullfinch	<i>Pyrrhula pyrrhula</i>	Yes	Yes	Yes	Yes	No	Non-SPEC

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In the lower subalpine forests (denser coniferous stands), most bird species are woodland generalists that occur in almost any type of forest, from the lowlands up to the treeline. Chaffinch *Fringilla coelebs* and coal tit *Periparus ater* are the two most widespread and abundant bird species of European subalpine forests, whether in the Jura (Catzeflis 1979), the Alps (Meier 1954; Mosimann *et al.* 1987; Schmid *et al.* 1998; Müller-Buser 2002), the Carpathians (Saniga 1995) or the Pyrenees (Estrada *et al.* 2005). Nevertheless, their populations can apparently undergo pronounced interannual demographic fluctuations (Müller-Buser 2002), most probably as a result of highly variable breeding success that might itself be dictated by variation in food supply. Another ubiquitous species, the blackbird *Turdus merula*, occurs at much lower abundance in subalpine than in montane and lowland forests. Although highly adaptable, since it occurs in private gardens and urban parks as well as in some treeline habitats, this species has its strongholds in deciduous forests.

Then there is a group of presumably more specialised species that are common in subalpine forests but absent or very rare in central European lowland and montane forests. Good examples are pygmy owl, three-toed woodpecker, citril finch and ring ouzel *Turdus torquatus*. As these species differ markedly in life history and foraging strategies (tree *vs* ground foraging), their preferences for coniferous forests probably have different ecological causes. Three-toed woodpecker and pygmy owl are emblematic inhabitants of conifer-dominated forests. They show a classical boreo-alpine distribution range in Europe, which is fairly congruent with the large-scale distribution of Norway spruce (Hess 1983). The three-toed woodpecker (Fig. 7.4) is a highly specialised forager that feeds on bark beetle larvae. It depends on high amounts of snags (Bütler *et al.* 2004) and often colonises forests after fires or heavy storms, which provide opportunities for massive bark beetle infestations. Its absence from most Norway spruce plantations at lower elevations in central Europe is therefore most likely due to an absence of sufficient natural forest disturbances and more intensive forest management (Glutz von Blotzheim & Bauer 1994). The pygmy owl prefers forest habitats with a pronounced vertical structure and high edge density (Braunisch *et al.* 2014), often occurring where coniferous stands are interspersed with clearings and grasslands (Brambilla *et al.* 2015). As a secondary cavity-nester, it also depends on the presence of rotting trees, snags and woodpecker cavities.

Subalpine and boreal ring ouzels belong to two phenotypically distinct subspecies: *T.t. alpestris* in central Europe and *T.t. torquatus* in Scandinavia



Figure 7.4 Three-toed woodpecker (*Picoides tridactylus*) is a common species in subalpine forests dominated by Norway spruce (*Picea abies*), as long as there is enough deadwood. As a highly specialised forager that feeds on bark beetle larvae, it usually does not occur in heavily managed Norway spruce stands in central European lowlands. Photo: M. Dorsch.

and the British Isles. The former is a typical inhabitant of semi-open subalpine conifer-dominated forests, while the latter prefers more open habitats such as heather-dominated moorland. The citril finch, endemic to Europe, is restricted to the Pyrenees, the Alps and some lower-elevation mountain ranges in Germany, France and Spain. Its typical habitat consists of open and semi-open coniferous stands and an extensive grassy field layer. Its large-scale distribution approximately coincides with that of the upright mountain pine, whose seeds indeed seem to be a crucial food source in winter (Borras *et al.* 2003), but its breeding range encompasses other woody formations, notably those dominated by larch and stone pine.

Treeline mosaics comprising very open coniferous stands and scattered trees within an extensive grass-shrub matrix represent other key habitats for bird species typical of semi-open habitats, such as black grouse (Signorell *et al.* 2010), fieldfare *Turdus pilaris*, lesser whitethroat and tree pipit *Anthus trivialis*. The latter was formerly widespread in lowland farmland (Schmid *et al.* 1998) but suffered large-scale decline due to agricultural intensification and now occurs mainly in semi-open subalpine areas. Some bird species that are not considered forest species can also be observed regularly in these semi-open habitats along the treeline. Black redstart *Phoenicurus ochruros*, for example, is quite widespread,

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at least in places where there are rocky outcrops between the trees. In rocky and very dry treeline habitats, rock bunting *Emberiza cia* is also not uncommon.

7.2.2 Fine-scale Variation and Seasonality in Species Richness and Abundance

Breeding bird species assemblages in subalpine forests seem to depend on forest structure and, to a lesser extent, edaphic conditions rather than on tree species composition (Mosimann *et al.* 1987; Müller-Buser 2002). However, as vegetation and soil structure are interlinked, it is difficult to disentangle the primary drivers of species' habitat selection. Important structural features in subalpine forests are similar to other forest types. Dense tree canopies provide abundant food supplies for needle-gleaners as well as varied nesting opportunities. Gaps in the canopy, in turn, allow ground vegetation to develop: pioneer trees, shrubs or grassy field layers represent crucial resources for foliage-gleaners, shrub-nesters and birds feeding on berries, and grass-dwelling arthropods, respectively (Signorell *et al.* 2010; Schäublin & Bollmann 2011; Patthey *et al.* 2012). Dense shrubs in clearings are inhabited by garden warbler *Sylvia borin*, blackcap *Sylvia atricapilla* and hazel grouse. Grassy field layers are important for ring ouzel, green woodpecker *Picus viridis*, tree pipit and citril finch. These ground foragers need free access to food resources, either invertebrates or seeds, and show a preference for patches with short grass or even bare soil, as do many insectivorous farmland birds (Schaub *et al.* 2010), although this preference still needs to be properly quantified for subalpine birds. Western Bonelli's warbler and, to a lesser extent, lesser whitethroat are principally found in relatively open and dry forests, with a predilection for sun-exposed areas. Among crucial forest structural features, old trees and snags are essential for woodpeckers and other cavity-breeders, either primary or secondary, such as pygmy owl, Tengmalm's owl *Aegolius funereus*, willow tit and crested tit *Lophophanes cristatus*.

Subalpine forests often offer very complex structured habitats, because they are regularly subjected to natural disturbances. Although fires remain rare in most subalpine coniferous forests, especially compared to Mediterranean pine woods, heavy winter snow cover and frequent storms cause branches, limbs and trunks to break. This offers fungi a portal to infect trees, weakening them and exposing them to bark beetle infestations, representing an accumulation of stress factors that can lead

to a tree's death. This phenomenon increases the availability of snags, a key habitat feature for many bird species. In addition, the declining exploitation of timber in most European mountain ranges during the second half of the 20th century caused an accumulation of old, dead wood. As a result, these key structural habitat features important for birds occur nowadays almost everywhere in European subalpine forests. However, two grouse species that favour open stands seem to suffer a lot from a general increase in the standing stock following the progressive abandonment of timber exploitation. They have undergone a major range shrinkage in recent decades: both black grouse and capercaillie respond negatively to the closure of the forest canopy (Suchant & Braunisch 2004; Graf *et al.* 2007; Patthey *et al.* 2008).

There is no peer-reviewed literature about the seasonal variation of bird community composition in subalpine forests. Only qualitative information from citizen science platforms is available. The most widespread of these platforms in central and southern Europe is currently the 'www.ornitho.xx' family, where bird observation data, provided by the public, is validated by experts, and compilations of data are made publicly available. Generally, bird-species richness and abundance seem to be much lower there in winter than during the breeding season, probably due to a shortage of their principal food sources. Most insectivorous species, for instance from the genera *Anthus*, *Sylvia* and *Phylloscopus*, are migratory and thus absent from subalpine environments during the cold season. Even the majority of granivorous passerines, such as the siskin *Carduelis spinus*, citril finch or bullfinch *Pyrrhula pyrrhula*, leave subalpine forests in winter, moving to lower elevations or warmer latitudes. Those granivorous bird species that forage mostly on the ground can no longer access seeds when snow cover is both deep and persistent. Moreover, the amplitude of their winter dispersal and spatial movements varies from year to year due to fluctuating snow conditions. Thrushes adopt a similar seasonal spatial pattern, being short-distance migrants or simply altitudinal transhumants. Among seed-eaters, nutcrackers *Nucifraga caryocatactes* are a noticeable exception: they feed on tree seeds that are stored in ground caches at relatively high altitude, even if the food has been collected at lower elevation (e.g., hazel *Corylus avellana* nuts), which enables them to stay year-round in upper subalpine forests. The crossbill *Loxia curvirostra* is another year-round inhabitant of subalpine forests, due to its food specialisation on spruce, fir and larch seeds. Its local density varies a lot in response to the highly fluctuating yearly masting patterns of its favourite resource trees.

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Only very few bird species of subalpine forests can be considered as sedentary. This concerns, for instance, the three-toed woodpecker, sightings of which are extremely rare in the lowlands of western and central Europe. Goldcrest *Regulus regulus*, treecreeper *Certhia familiaris*, nuthatch *Sitta europaea* and three species of tits (willow, crested and coal tit) do show some altitudinal movements, as they show up in the lowlands in winter. Still, regular observations show that quite a few individuals seem to stay in their high-altitude habitats in winter. These birds adopt specific behaviours that allow them to survive the low ambient temperatures and extreme food scarcity that characterise upland winters (Thaler-Kottek 1986). Among them are food hoarding, social aggregations at night roosts and a general reduction of activity, which all serve to save energy. Very little is known about seasonal movements of predatory birds such as goshawk *Accipiter gentilis*, sparrowhawk *Accipiter nisus*, pygmy owl and Tengmalm's owl. Yet, observations suggest that they might also move to lower-elevation forests in winter. Finally, all central European grouse species except rock ptarmigan *Lagopus muta* are regularly observed in subalpine forests and treeline ecotonal woody formations all year round. They, too, have evolved specific physiological and behavioural adaptations to overcome the harsh winter conditions. For example, black grouse, hazel grouse and sometimes also capercaillie spend hours in self-burrowed 'igloos' in the snow, which is an efficient energy-saving strategy (Marti & Bossert 1985; Arlettaz *et al.* 2015).

Subalpine forests do not seem to play a major role as wintering grounds for northern migratory birds. Typical migrants from northern and north-east Europe that overwinter at lower latitudes in central Europe, such as waxwing *Bombycilla garrulus* and brambling *Fringilla montifringilla*, actually prefer to forage in deciduous and mixed forests at lower altitudes. During autumn and spring migrations, however, subalpine forests can provide good stopover sites for birds in transit.

7.2.3 Conservation Issues

In general, the current conservation status of birds in central European subalpine forests is favourable. According to BirdLife International (2015) and the IUCN Red List criteria, all species listed in Table 7.1 are considered 'least concern' at the pan-European scale. Some of them, however, have been classified as 'species of European conservation concern' (SPEC) by Burfield and van Bommel (2004), or they have been included in Annex I of the Birds Directive of the European Union (Directive 2009/147/EC of the European Parliament and the Council).

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This reflects the fact that the current conservation status of a certain species can be much less favourable on a regional than the pan-European level. This is well illustrated by the capercaillie. It is classified as ‘least concern’ and ‘non-SPEC’ in the European Red List of birds, although it is included in Annex I of the EU Birds Directive. However, in the national Red Lists of Switzerland and France, for example, the capercaillie is classified as ‘endangered’ and ‘vulnerable’, respectively (Keller *et al.* 2010; UICN France *et al.* 2011), which has triggered intense conservation action in both countries (Mollet *et al.* 2008; Viry & Helderlé 2012).

Human land-use changes today represent the main threat for the avifauna of European subalpine forests, although climate change might represent an even greater challenge in the future (e.g., Braunisch *et al.* 2014). In contrast, there is currently no evidence that hunting, poaching, environmental pollution or diseases can represent any serious threat. The present situation differs greatly from historical times, when, for example, nutcrackers were persecuted as pests. Regional forest authorities, at least in Switzerland and Austria, used to pay a bounty for every killed nutcracker. Ironically, they recognised that this corvid massively exploits the cones of stone pines but misinterpreted the mechanism at play: actually, the winter caches of nutcrackers are often left behind unexploited, which represents the main mode of propagation of those rather heavy seeds (Mattes 1982; Tomback *et al.* 1993; Fig. 7.5). Today



Figure 7.5 Swiss stone pine (*Pinus cembra*) rejuvenation above the current timberline at 2,280 m above sea level in Val d’Anniviers, Valais, Switzerland. Birds, notably nutcrackers *Nucifraga caryocatactes*, collect the heavy seeds in the adult trees below and sometimes carry them to the upper slopes for hoarding. Non-harvested seeds germinate and grow. Photo: P. Mollet.

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the species is protected in most areas and is thriving in subalpine forests in the Alps and Carpathians.

The two forms of land-use change which have most dramatically affected subalpine species in recent times are the abandonment of traditional silvi-agricultural practices and the sprawl of recreation activities, especially snow sports (Thiel *et al.* 2011; Arlettaz *et al.* 2013). Zbinden & Salvioni (2003), for instance, have documented the reduced reproductive success and long-term demographic decline of black grouse in the southernmost Swiss Alps (Ticino) after traditional grazing practices had ceased, which irremediably leads to the encroachment of semi-open treeline habitats by woody plants. Patthey *et al.* (2012) have shown that both vertical and horizontal structural heterogeneity in all vegetation layers within the treeline matrix (from grasslands through shrubs to trees) were the best predictors of the occurrence of both sexes in the black grouse. Chick-rearing black grouse hens, in particular, show a marked preference for the most heterogeneous habitat configuration. This habitat selection pattern is probably a result of a trade-off between food availability (invertebrates are crucial for chick growth, and these abound in grasslands) and shelter from predators, which is provided by shrubs and under low-branched trees (Signorell *et al.* 2010). Current action plans for restoring black grouse breeding habitat via management interventions, notably in the shrub layer and dense conifer stands, will probably benefit other bird species typical of very open forests, such as tree pipit and lesser whitethroat.

The sprawl of winter tourism, from the construction of ski infrastructure to the practice of snow sports (back-country skiing, snowboarding and snow-shoeing) outside marked runs and trails, is considered to represent a new serious threat for subalpine wildlife (Arlettaz *et al.* 2007). Capercaillie and black grouse respond negatively to the regular presence of humans on their wintering grounds (Thiel *et al.* 2008; Braunisch *et al.* 2011). Due to their rather long flushing distances, they will eventually abandon otherwise suitable habitats if human pressure is too high (Thiel *et al.* 2007; Braunisch *et al.* 2011). Furthermore, disturbance by snow sport free-riders evokes endocrinological stress in capercaillie (Thiel *et al.* 2011) and black grouse (Arlettaz *et al.* 2007), which potentially affects population dynamics (Patthey *et al.* 2008). Specific wildlife winter refuges are currently deployed in the European Alps, with the objective of mitigating the impact of snow sports on alpine mammals and birds (Braunisch *et al.* 2011; Arlettaz *et al.* 2013).

Due to the rough terrain and limited accessibility of most subalpine woodland, forest exploitation is not economically viable in many areas. As a consequence, the pressure on subalpine forest ecosystems is much lower than on montane or lowland forests. Still, this may change with an increasing demand for timber, e.g., as a source of renewable energy. Recent evidence suggests that in the Carpathians, notably in Slovakia and Romania, forest loss, nowadays no longer occurring in other European subalpine forests, has become a serious threat for a majority of forest-dwelling wildlife (Mikoláš *et al.* 2015). Large areas of forest are being clearcut by companies that bought the rights to harvest timber. As a result, emblematic species such as capercaillie are becoming increasingly rare in these regions (Mikoláš *et al.* 2017).

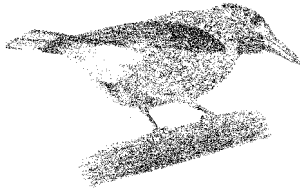
Climate warming is much more pronounced in high mountainous environments than in lowland areas (Rebetez & Reinhard 2007). Faced with this, species have no other choice than to ‘move, adapt or die’. Maggini *et al.* (2011) used data from the Swiss national common breeding bird survey to model elevational distributions of 95 bird species for two periods, 1999–2002 and 2004–2007. They found significant upward shifts for 33 out of the 95 species, among them bullfinch and ring ouzel, two typical species of subalpine forests and treeline ecosystems, respectively. These upward altitudinal shifts could eventually lead to a decrease in potential habitat and thus population size, simply because at higher altitudes the potential distribution area becomes smaller (habitat squeezing). These projections must be treated with caution, however. In effect, variable selection remains a great source of uncertainty for future range predictions in species distribution models (Braunisch *et al.* 2013), which even exceeds the variances introduced by different IPCC scenarios or circulation models (Thuiller 2004; Beaumont *et al.* 2007). In addition, most habitat suitability and distribution models are constructed from publicly available geodata that rarely include information about crucial species-specific ecological resources (e.g., the occurrence of an essential group of invertebrates for an insectivorous bird species). As a result, the variables used most of the time represent only rather crude proxies of actual species-specific ecological requirements. The good news is that predicted decreases in the habitat suitability and spatial range of emblematic, cold-adapted species such as pygmy owl, hazel grouse, capercaillie and three-toed woodpecker could, at least partially, be compensated by adaptive forest management enhancing the availability and quality of key species-specific structural elements (Braunisch *et al.* 2014). On the other hand, adaptive forestry practices implemented to cope with the

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economic risks of climate change, such as shortened harvesting periods or changes in the tree species portfolio, may represent an additional threat. The question of whether, and to what extent, climate warming will impact subalpine forest birds, and how this factor interacts with – or is even amplified by – other forms of global change (e.g., atmospheric nitrogen deposition, abandonment of pastoral systems, changes in forest exploitation) thus remain to be explored.

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