28 Frost Hollows as Interesting Areas of Geo- and Biodiversity in the Alps

Domen Svetlin, Matej Ogrin, and Janez Kermavnar

Abstract

Frost hollows are areas where cold air pools frequently form due to relief, resulting in specific microclimatic conditions. The different microclimate also manifests itself in specific ecological conditions where only adapted plant communities develop. These unique areas are of high conservation importance as they can provide suitable habitats for cold-adapted plant species that are not found in the surrounding landscape. Such microrefugia are known to maintain relict populations of some endemic species. It can be concluded that frost hollows are special areas in terms of both geodiversity and biodiversity. The chapter discusses the climatological and vegetation characteristics of frost hollows from the Slovenian alpine areas.

Keywords

Mountain climate · Topoclimate · Temperature inversion · Vegetation inversion · Cold air pools · Mountain species Adaptation

28.1 Introduction

Alpine frost hollows are climate-specific areas and represent an interesting area of bio- and geodiversity. Varying temperature conditions influence many physical processes, such as pedogenesis, decomposition of organic matter, soil moisture conditions, corrosion and mechanical weathering of rocks, thickness and duration of snow cover, and the like. In frost hollows with a persistent and pronounced temperature inversion, vegetation inversion also occurs, which is a good example of the influence of geodiversity on biodiversity. Morphologically, frost hollows are concave relief forms, they can also be called relief depressions which enable the basic condition of the frost hollow, i.e., the formation temperature inversion and cold air pools in the evening and at night.

The definition of a frost hollow was initially established as a depressional karst form, e.g., dolines or collapse dolines, in which a temperature inversion and a vegetation inversion occur. Martinčič (1975, 1977) defines a frost hollow as a special habitat that differs from its immediate

D. Svetlin
Envirodual d.o.o., Slovenske Konjice, Slovenia
e-mail: domen.svetlin@envirodual.com

M. Ogrin (✉)
Department of Geography, Faculty of Arts, University of Ljubljana , Ljubljana, Slovenia
e-mail: matej.ogrin@ff.uni-lj.si

J. Kermavnar
Department of Forest Ecology, Slovenian Forestry Institute, Ljubljana, Slovenia
e-mail: janez.kermavnar@gozdis.si

M. Zorn et al. (eds.), *Discourses on Mountains of Montenegro and Slovenia*,
Historical Geography and Geosciences, https://doi.org/10.1007/978-3-031-99017-5_28

surroundings in botanical, zoological, and climatological terms. These definitions point to the influence of the frost hollow on biodiversity, more specifically on vegetation. Later, when research in frost hollows focused on climatological and meteorological processes, other definitions emerged, such as that the frost hollow is an area where on clear and windless nights the temperature falls much lower than in the surrounding area at a similar altitude (Trošt 2008).

Undoubtedly, frost hollows are also special areas of geodiversity. At this point, it should be emphasized that the concept of geodiversity is treated holistically, i.e., as the diversity of abiotic nature and not only as the diversity of geological or geomorphological features of space. Although geodiversity is also commonly defined as diversity of abiotic nature (Prosser 2002; Gray 2013), the term geodiversity is now mostly used in the context of geological and geomorphological, and sometimes pedological, interpretations (e.g., Sharples 1993, 2002; Kiernan 1994, 1996, 1997; Dixon 1995; Eberhard 1997; Stanley 2000; Stepišnik and Repe 2015; Stepišnik and Trenchovska 2016; Stepišnik et al. 2017). We are not aware of research that would also address other abiotic phenomena in the context of geodiversity, e.g., in the hydrosphere or atmosphere.

In this paper we focus on the phenomenon of frost hollows as important areas of biodiversity and geodiversity of alpine areas in Slovenia, where the abiotic part of the natural environment is understood more broadly than only in geological and geomorphological terms and includes atmospheric phenomena and processes.

28.2 Frost Hollow as a Climatological and Geomorphological Phenomenon

The basic meteorological phenomenon that defines a frost hollow is temperature inversion. Under certain atmospheric and surface conditions, the air temperature in the near-surface layer of the frost hollow is significantly lower than in the higher layers. Temperature inversion results from the negative energy balance of the surface when it emits more energy in the evening and at night than it receives and therefore cools down. (Fig. 28.1). The surface cools the air directly above the ground. If this process takes place on the slopes, the cooled air directly above the slopes begins to flow toward the bottom of the frost hollow, and in its place less cold air flows from areas farther from the slopes. Thus, during the night, cold air flows to the bottom of the frost hollow. When the cold air reaches the bottom of the frost hollow, it continues to cool at the bottom. At the same time, cooled air flows in from the slopes, which is warmer due to the shorter cooling time and accumulates above the "older" and colder air at the bottom of the frost hollow. Thus, a cold air pool is formed during the night, reaching to the lowest point of the top of the frost hollow (Fig. 28.2). The cold air pool persists until it is dissipated by solar radiation (thermal dissipation) or the intrusion of wind turbulence (dynamic dissipation). In summer, a cold air pool can dissipate daily; in winter, it can persist for days or even weeks.

At frost hollows in karst areas, a cold air pool can also form when air escapes from the karst bedrock (Mihevc 2021), but this cooling mechanism is possible only when the ground is not covered with snow and when the karst bedrock is colder than the air in the frost hollows. At elevation of Komna (app. 1,350–1,700 m) frost hollows, this is the case during the day from June to November. Thus, this mechanism cannot contribute to extreme winter lows.

28.3 Conditions for Low Temperatures in Frost Hollows

28.3.1 Meteorological Conditions

Temperature of Air Mass

A lower initial air temperature usually means that a lower minimum temperature will be reached. The intensity of longwave radiation from the atmosphere also depends on air temperature (Ortar 2011). Low initial air temperatures

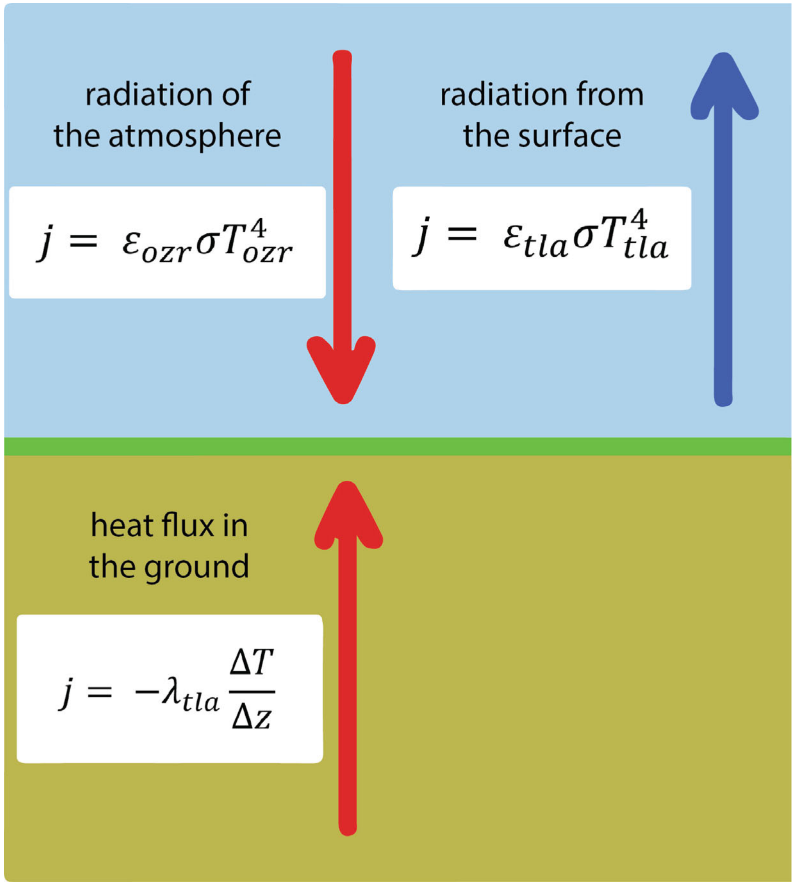

Fig. 28.1 The prerequisite for the occurrence of a radiative temperature inversion is a negative surface heat balance. The losses due to longwave radiation from the ground must be greater than the heat input from the ground and the heat input from the atmosphere. (Figure by Domen Svetlin)

in the free atmosphere in Slovenia are associated with advection of polar continental air masses from the north, northeast, or east; at the same time a blockade of the general western air circulation must be established. The pronounced area of high pressure over Scandinavia and northwestern Russia in winter often allows the advection of cold air from the northeast or east via Eastern Europe to the Central Europe, the Alps, and Balkan Peninsula. Traditionally, episodes of such advection are also associated with the Siberian anticyclone, whose influence on the weather in the Alps has been very rare in recent decades.

Wind

As the wind occurs at ground level, the layer of cooled air mixes with the warmer air higher up due to turbulence, so the formation of ground temperature inversion is difficult or completely impossible with stronger winds. If the general winds in the area of the frost hollow are relatively weak, a cold air pool can still form and continue to cool. If a ground layer of cold air has formed, it is more difficult for the overlying winds to penetrate the depressions with cooled air due to static stability. In general, shallower depressions are more prone to turbulent mixing than deeper depressions, which are more closed and where the inversion layer may be thicker. Particularly favorable conditions for radiative cooling are provided by a pronounced area of high pressure over Central Europe with weak winds, which expands and strengthens after the passage of the cold front (Whiteman et al. 2004; Ogrin et al. 2006; Trošt 2008).

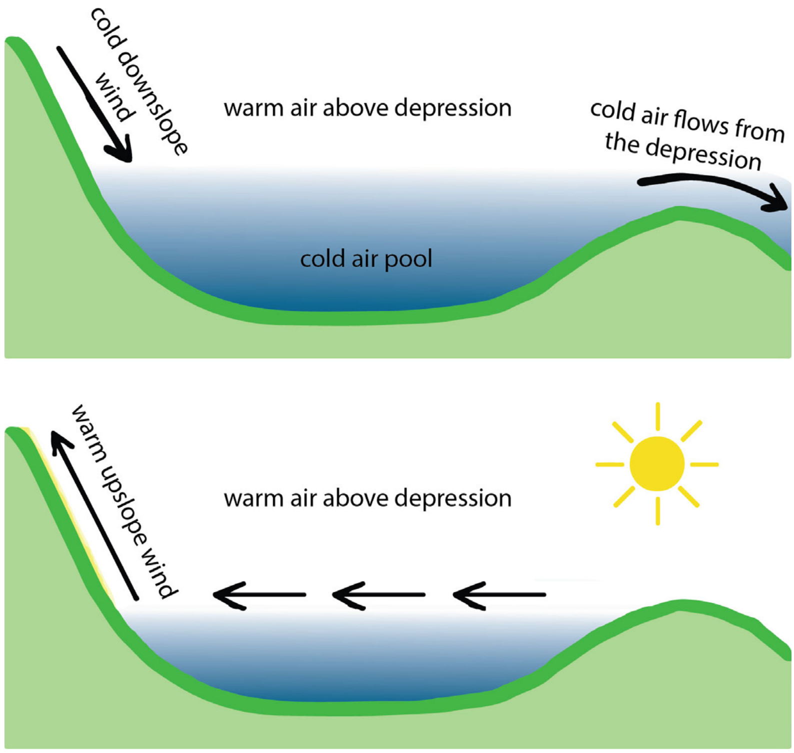

Fig. 28.2 Nocturnal formation (above) and late morning dissipation (below) of the cold air pool in the frost hollow. (Figure by Ana Seifert, authors archive)

Air Humidity

Of all the greenhouse gases, water vapor has the most important effect in emitting radiant energy from the atmosphere. The drier the air, the lower its emissivity. The saturation vapor pressure of water vapor, which limits the amount of water vapor in the atmosphere, decreases with decreasing temperature and increasing altitude. Roughly speaking, the amount of water vapor in the atmosphere decreases with altitude, so the emissivity of the atmosphere also decreases (Staley and Jurica 1972; Henderson 1994). Until cloud droplets or ice crystals form, increased relative humidity in the higher layers of the troposphere has no significant effect on the overall atmospheric emissivity (Ortar 2011).

28.3.2 Altitude

As altitude increases, the atmosphere becomes rarer and contains less and less water vapor and other greenhouse gases. The effect of atmospheric radiation is therefore less the higher the frost hollows. Higher altitude generally means lower temperatures at the onset of cooling, since temperature generally decreases with altitude. Thus, under favorable other conditions, the decrease in temperature and humidity with elevation allows higher elevation frost hollows to cool more than those at lower elevations (Ogrin et al. 2006). Wind speed usually increases with the altitude which is less favorable from the point of view of pronounced temperature changes, especially for shallower frost hollows. Thick snow cover reduces ground roughness, which reduces friction with the ground and increases wind speed at the ground (Vrhovec et al. 2006).

28.3.3 Topography

Due to complex topographic influences, such as colder downslope wind, reduced sky view factor, altered wind circulation and turbulence, heat storage in sunny slopes, and reduced insulation time, in mountain relief the dynamics of formation, maintenance, and dissipation of temperature inversion are different from those in lowlands. In the evening, longwave radiation from the surface causes a layer of cold air to form just above the surface, and density differences lead to the movement of cooled air down the slopes to lower areas. In its place comes warmer air from the higher areas, which cools above the ground and flows down the slope. This creates a downslope wind, also known as a katabatic wind. Cold air can flow down the slope, but it can't flow out of the frost hollows in a calm atmosphere, so it stays in them and builds up. This is the main reason for the formation of cold air pools which are filled with cooled air by slope winds. During radiant weather at night and in the morning, temperatures in concave relief are always lower than in the surrounding area, and inversions are more pronounced than in valleys, basins, and plains (Geiger 1966).

The concave shape of dolines, karst poljes, and other karst depressions protects the air at the bottom inside the depression from mixing with the surrounding air once a stable inversion layer has formed there. Thus, the layer of cooled air formed early in the night can more easily resist the turbulence at the top of the cold air pool that forms at the boundary between higher air currents due to shear, even if it is weak. As the temperature difference between the air at the bottom and the air at the upper edge of the depression increases, the direct downward flow of air is limited due to the static stability of the inversion. Since air temperatures are lowest at the bottom of the depression, the air there is almost completely isolated from the higher, warmer layers. Weak crosswinds can penetrate the higher parts of the basin, but they cannot directly mix the air at the bottom (Whiteman et al. 2004).

Another consequence of the concave relief of the frost hollows is the reduced proportion of visible sky. Because of the surrounding slopes, less sky is visible from the bottom of the frost hollow than from a flat or convex surface. This means that more longwave radiation from the slopes is also directed downward to the bottom of the frost hollow, reducing the total emitted longwave radiation. The downward longwave radiation and upward flux of perceived heat from deeper ground layers are the only processes that counteract radiative surface cooling. The surface temperature approaches the equilibrium temperature asymptotically during the night. As it approaches the equilibrium value, the loss of net longwave surface radiation (radiation balance) is nearly offset by the upward heat flux from the ground, so that further surface cooling is very small (Whiteman et al. 2004). The more open and shallow the frost hollow, the greater the proportion of visible sky and the more undisturbed the heat can radiate toward the sky. Shallower frost hollows, on the other hand, are more exposed to turbulence and wind effects, which reduces the number of cases of undisturbed cooling (Ogrin et al. 2006).

28.3.4 Surface and Vegetation

Lower thermal conductivity of soil means less emission of longwave radiation to the atmosphere. Higher thermal conductivity of rocky surface or higher thermal capacity of moist and grassy soils contributes to slower cooling of air and higher minimum temperatures reached than if the ground were covered with a blanket of snow. Events with extreme cooling in frost hollows were always associated with the presence of fresh snow cover (Zängl 2005).

In the Grünloch (Austria) frost hollow, the measured temperature differences between the bottom of the hollow and the edge of the hollow were between 25 and 30 K when fresh snow cover was present, and between 10 and 15 K without snow cover (Sauberer and Dirmhirn 1954, 1956). Fresh snow contains about 50 to 95% of air, which rests between the ice crystals and prevents heat transfer from the ground. Thus, when cooled by radiation, snow acts as an excellent insulator and prevents the flow of heat from the ground to the atmosphere, which would otherwise counteract the effect of radiative heat loss from the surface. The ground remains warmer than it would be without snow cover, and the air above the snow can cool more (Ogrin et al. 2006). In hollows covered with shrubs or forests, the temperatures do not drop as low as in those without higher vegetation cover. Trees, especially compared to snow cover, have a much lower albedo, so they absorb more radiation during the day and then emit it during cooling, while at the same time providing a barrier to longwave radiation from the ground by partially obscuring the sky. The higher the tree density on the frost hollow surface, the higher the longwave radiation from tree trunks and canopies and the coverage of the sky, and the lower the radiative losses from the surface. Deciduous tree species cover the sky less in winter than coniferous trees, so radiative cooling is even more inhibited in a coniferous forest than in a deciduous forest. The emissivity of tree canopies is high, ranging from 0.97 to 0.99 (DeWalle and Rango 2008).

28.4 Temperature Conditions in Frost Hollow Luknja on Komna Plateau as a Distinct Representative of an Alpine Frost Hollow

As an example of a distinct frost hollow in Slovenian Alps, we present measurements from the Luknja frost hollow at Komna Plateau, where we also measured temperatures outside the frost hollow (Dom na Komni measuring site) in its immediate vicinity (Fig. 28.3), allowing a direct comparison of conditions in the frost hollow and in the environment outside the hollow.

The Luknja frost hollow (Figs. 28.3, 28.4, and 28.6) is located in the central part of Spodnja Komna Plateau (Julian Alps) at an altitude of

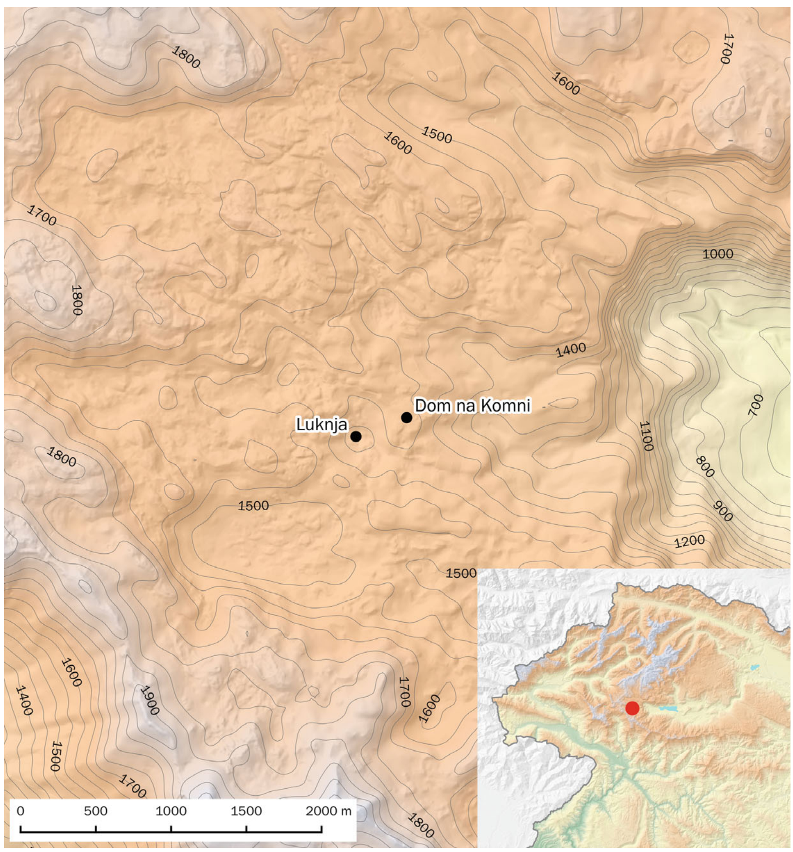

Fig. 28.3 Komna Plateau with locations of measuring sites (black dot). (Author of the map Domen Svetlin)

Fig. 28.4 The Luknja frost hollow in winter from south. (Photo by Matej Ogrin)

Fig. 28.5 Measuring site Dom na Komni outside the frost hollow. (Photo by Domen Svetlin)

1,427 to 1,483 m, about 400 m as the crow flies west to southwest of the mountain hut on Komna (*Dom na Komni*). The 56.5 m deep hollow is one of the deepest frost hollows of Komna plateau; on the bottom of the hollow there are many smaller dolines, which are only a few meters deep and wide. Most of the hollow is overgrown with dwarf pine, and only at the bottom there are some grassy clearings. The measurement site in the frost hollow was placed on a grassy area about 26 m west to northwest of the deepest point of the frost hollow at an elevation of 1,429.5 m. Measurements at the bottom of the hollow began on December 12, 2005, and initially took place in a classic radiation shield. At the beginning of July 2006, the shelter was replaced by a Stevenson screen.

The Dom na Komni monitoring site (Figs. 28.3 and 28.5) is located on a small ridge about 70 m northwest of mountain hut on Komna Plateau at an elevation of 1,521 m. At the beginning of the measurements on September 22, 2006, the measuring site, where the classical shield was used, was for some time at another microsite nearby (at a small spruce tree); on November 20, 2009, a Stevenson screen was set at the current location. Temperature measurements at this location are still ongoing. The monitoring site is primarily a reference station for temperature measurements outside the frost hollows, as its location is completely different in terms of the occurrence of ground temperature inversion, despite its proximity. The location of the measuring station on an open and slightly convex surface is closer in terms of temperature to the condition in the ground layer of the free atmosphere, as there is no accumulation of the cooled air or this effect is not so pronounced; at the same time, the wind exposure and thus the air mixing are greater.

The temperature conditions in the frost hollow differ significantly from those outside the frost hollow in some parameters (Table 28.1). Thus, of course, the greatest differences are in the absolute minimum temperatures (19.7 °C) and in the average minimum temperature (5.3 °C). The average daily temperature is also significantly lower, the difference being 2.5 °C. The average number of cool days (Tmin < 0 °C) per year is 75 days higher in the frost hollow, or negative temperatures occur on 57% of the days. There is a smaller difference in the number of icy days (Tmax < 0 °C), which is only 9 days per year, and the difference in the number of cold days (Tmin < –10 °C) increases sharply, because it is up to 54 days. In the frost hollow there are even 73 such days, i.e., every fifth day. Outside the frost hollow the temperatures never fall below –30 °C; in the frost hollow this happens on average on 3 days per year.

The differences in temperature amplitude are also interesting. The average temperature amplitude is 4.7 °C higher in the frost hollow than outside, and the absolute maximum temperature amplitude is 14.8 °C higher in the frost hollow. Temperature amplitudes above 20 °C occur 12% of the time in the frost hollow, while outside the frost hollow such days do not occur; a day with a temperature amplitude above 30 °C can also

Table 28.1 Temperature conditions in Luknja frost hollow and outside it on na measuring site Dom na Komni in period 2006–2015 (data source: Slovenian Meteorological Forum)

Parameter	Dom na Komni	Luknja
Average annual temperature (°C)	5.0	2.5
Average daily Tmax (°C)	9.3	8.7
Average daily Tmin (°C)	1.6	–3.7
Absolute Tmax (°C)	28.0	28.0
Absolute Tmin (°C)	–20.0	–39.7
Average annual number of days with Tmin < 0 °C (cool days)	135	210
Average annual number of days with Tmax < 0 °C (icy days)	40	49
Average annual number of days with Tmin < –10 °C (cold days)	19	73
Average annual number of days with Tmin < –20 °C	0	24
Average annual number of days with Tmin < –30 °C	0	3
Average annual number of days with Tmax < –10 °C	1	3
Average annual number of days with Tmax < –20 °C	0	0
Average annual number if days with Tmax ≥ 25 °C (warm days)	5	4
Average annual temperature amplitude (°C)	7.7	12.4
Absolute highest temperature amplitude (°C)	20.0	34.8
Average annual number of days with temperature amplitude < 10 °C	254	140
Average annual number of days with temperature amplitude > 20 °C	0	45
Average annual number of days with temperature amplitude > 30 °C	0	1

occur in the frost hollow, which is not the case outside. On the other hand, there is almost no difference in maximum temperature between the frost hollow and the surrounding area, which is understandable since there are no conditions for lower temperatures in the middle of the day in the frost hollow, when in most cases temperature inversion dissipates. Because the bottom of the frost hollow is lower and less ventilated (greater impact of the surface), maximum temperatures may even be higher than outside the frost hollow. The average daily maximum temperature is only 0.6 °C lower in the frost hollow, while the absolute maximum is the same at both sites. It can be concluded that the temperature conditions in the frost hollow are more extreme than in its surroundings. The difference is due to the lower minimum temperatures, while the maximum temperatures in the frost hollow are very similar to those outside.

28.5 Ecological Conditions, Flora, and Vegetation in Alpine Frost Hollows as a Result of Lower Temperatures

Specific microclimates, described in previous chapters, induce unique abiotic site conditions in which only adapted plant communities develop. Cold air accumulation has ecologically important consequences for the development of biota in such adverse habitats. Lower temperatures at the bottom of frost hollows due to cold air accumulation result in overall more stressful conditions for plant establishment, growth, and reproduction. A whole range of biological processes in the ecosystem are related to the lower temperatures, with shorter growing season being the most noticeable. Plant species therefore show rapid development during a short time window of more favorable ecological conditions. However, the main determinants of vegetation development are not only mean temperatures, but also microclimatic extremes. These act as a significant selective filter for plant species (Körner 2003). Frost events caused by cold spells, which can also occur in the summer months, have a major influence on plant survival. The harshest environmental conditions are found at the bottom of frost hollows. At the same time, concave terrain depressions are characterized by pronounced gradients in ecological factors (temperature, light, soil moisture) due to differences in local topography. The cooling effect depends mainly upon the dimension (depth, diameter) and geomorphology (shape, orientation) of depressions (Whiteman et al. 2004; Kobal et al. 2015; Čarni et al. 2022). Large-sized frost hollows generally show greater potential for persistent cold air pool compared to smaller depressions. Slope aspect and inclination are also important factors. North-facing slopes receive less solar radiation compared to south-facing slopes. Such differences impose prominent spatial partitioning of plant communities within frost hollows (Bátori et al. 2009, 2017; Čarni et al. 2022). Soil mineral nutrients, water availability, and microclimate change over short distances which translates into fine-scale mosaic of varying life conditions. Lower temperatures affect soil process. The decomposition rate of plant litter is lower at colder sites, which has important implications for organic matter formation, nutrient cycling, and nutrient availability to plant species (Aerts 2006). The formation of raw humus may contribute to the occurrence of acidophilic floral elements despite carbonate parent material. Freezing temperatures make water unavailable to plants.

Temperature inversion in frost hollows is accompanied by vegetation inversion (Fig. 28.6), where plant communities with higher thermal requirements on the edges and slopes of the hollows are gradually replaced downslope by more cold-tolerant vegetation toward the bottom (Bátori et al. 2014, 2019). Cold air pool and temperature inversion drive broad-scale patterns in vegetation and community assembly in frost hollows. The frigophilous character of vegetation weakens with increasing elevation, i.e., with distance from the bottom of the frost hollow. In the Alps, dwarf pines (*Pinus mugo*) indicate the presence of extreme conditions too unfavorable for the growth of tree species. Tree species such as European beech (*Fagus sylvatica*) are burned by late frosts, leaving only the Norway spruce

Fig. 28.6 The Luknja frost hollow is a typical alpine frost hollow. The inversion of the vegetation is remarkable: spruces (*Picea abies*), larches (*Larix decidua*), and beeches (*Fagus sylvatica*) grow at the edge; only spruces in the middle and dwarf pine (*Pinus mugo*) at the bottom. In many alpine frost hollows, the original vegetation has been removed by grazing and the vegetation inversion is formed by selective succession. (Photo by Matej Ogrin)

(*Picea abies*). Thus, bottoms of frost hollows are occupied by treeless vegetation composed predominantly by dwarf shrubs, alpine flowering plants, non-woody frigophilous scree vegetation, graminoids (grasses, sedges), and hygrophilous bryophytes. The boundaries between adjacent communities are often sharp and differ not only in terms of distinct species composition but also in contrasting plant forms and functions. Bottoms of frost hollows are extreme environments for tree growth (Dy and Payette 2007). However, treeless clearings at the bottoms of some frost hollows in the Alps or other mountainous areas are not merely a result of adverse conditions but can also be interpreted as a consequence of profound anthropogenic activities in the past (Fig. 28.7; Martinčič 1975). Woody plants generally have weaker cold tolerance than herbaceous vegetation, and their altitudinal limits are strongly controlled by cold sensitivity (D'Odorico et al. 2013). Bottoms of frost hollows are characterized by long winters in which deposited snow persists into the summer. Under these harsh conditions, the length of the growing season is short (about three to four months), but it can also be shorter depending on elevation and snowfall patterns. Such habitats provide suitable conditions for rare plants with specific developmental (phenological) adaptations. For instance, bottoms of frost hollows may be favorable for life cycle completion of alpine snow-bed clonal herb *Soldanella pusilla (Primulaceae)* due to long-lasting snowpack. In this case, the snow cover provides protection from deep soil frosts, thus protecting plant's growth and reproductive structures from freezing (Wheeler et al. 2014). Similarly, *Androsace alpina* (*Primulaceae*), a taxon endemic to the Alps, prefers scree areas, which can also be found at the bottom of frost hollows.

In terms of vegetation ecology and phytosociology, frost hollow vegetation is a classic example of azonal vegetation. This means that extreme cold significantly reduces the influence of macroclimate, so that low temperatures and associated temperature amplitudes become the limiting factor. Vegetation-microclimate feedbacks (D'Odorico et al. 2013) can be observed at the bottom of frost hollows where treeless vegetation (mostly formed by tussock grasses and cushion plants) cannot reduce net longwave radiation at clear nights, resulting in greater radiative cooling compared to higher parts of depressions where tree canopy cover induces a buffering effect and prevents additional cooling of the air. Sparse

Fig. 28.7 Medvedova konta frost hollow on the Pokljuka Plateau in Julian Alps. Although it is a pronounced frost hollow, the vegetation inversion is not formed. The clearing at the bottom of the frost hollow is of anthropogenic origin. (Photo by Uroš Stepišnik, authors archive)

forests are more susceptible to loss energy than closed-canopy stands (Martinčič 1975).

From an ecological, floristic, and vegetational perspective, cold air pool sites are interesting because they provide suitable environments for high-altitude plant species which can thus occur also at lower elevations. Botanists, phytosociologists, plant ecologists, and foresters have frequently studied this phenomenon particularly in large karst depressions of Dinaric mountains (e.g., Zupančič 1980) and less so in the Alps. Terrain depressions as characteristic topographic situation and diagnostic landforms of karst landscapes (Kobal et al. 2015) were examined in different setup contexts, respectively. Bátori et al. (2012) reported the importance of forested dolines in preserving relict, endemic, and high mountain plant species in *Fagus sylvatica* forests. Similar conclusions were made by Vilović et al. (2019).

In adverse environments with extreme site conditions and lack of disturbance-driven dynamics (Kammer and Möhl 2002), temporal community-level turnover tends to be low, but such stability is counterbalanced by high spatial asynchrony due to diverse microtopography and fine-scale changes in environmental conditions. In general, frost hollows represent one of the most stressful habitats due to cold conditions, where only cold-adapted plant species can survive. Communities are formed by plants with specific functional traits that reflect their adaptations to the harsh abiotic environment and ultimately capture the allocation trade-offs between coping with environmental stress and competitive ability (Körner 2016). Plants growing at high altitudes and frost hollows are considered typical stress-tolerators with conservative strategies (e.g., small stature, low specific leaf area, and high leaf dry matter content). These life history traits imply their intolerance to biotic competition. Owing to stressful conditions, these alpine plant communities tend to be relatively species-poor, but at the same time include a large number of unique species with narrow ecological niches (Good et al. 2019). Community species richness within the alpine life zone is generally controlled by stress intensity (Kammer and Möhl 2002).

Plant species in alpine habitats are exposed to several limiting constraints: low mean temperatures, thermal extremes, short growing season, scarcity of soil, low nutrient levels, strong daily thermal amplitudes, and related ecosystem processes (e.g., slow decomposition of organic matter). Plants of extreme environments have evolved numerous adaptations and mechanisms in response to these selective pressures that enable their survival (Sakai and Larcher 1987; Lütz 2012). Adaptations to challenging physical environments are manifold and can be detected on morphological, anatomical, phenological, and reproductive levels (Billings 1974; Körner et al. 1989). Life cycles of alpine plants are threatened by the high uncertainty whether flowering and fruiting, germination, and establishment can be successfully completed.

There is a relatively high degree of similarity between the vegetation of high alpine mountains and the most stressful parts of frost hollows, i.e., bottoms. However, important differences in physical characteristics between the alpine environment and the ecological conditions found in frost hollows suggest that these two habitats cannot simply be considered equivalent. Because of the concave terrain, bottoms of the frost hollows are characterized by less windy and more humid conditions in contrast to alpine slopes and especially ridges (strong winds, lower humidity, higher solar radiation). Nevertheless, some common patterns are expressed, such as the high proportion of long-lived species that rely on vegetative reproduction (via rhizomes, stolons, or bulbils) for population dynamics. Clonality and lateral spread seem to occur more frequently in cold environments compared to other, less stressful occasions (Klimešová and Doležal 2011). Relatively few life forms are present in alpine vegetation: evergreen or deciduous prostrate shrubs, short-stemmed herbaceous perennials, cushion plants, rosette plants, lichens, and mosses. Succulent plants with fleshy storage organs indicate water-limiting conditions. Annual plants are very rare because their life cycle depends on flowering and fruiting (Larcher et al. 2010). The vegetational dimension of frost hollows, bearing some botanical and floristic peculiarities, should be described from multiple (i.e., taxonomic, ecological and functional) aspects (Good et al. 2019). Lim et al. (2017) showed a shift in ecological strategies in frost hollows. Shrubs that are shorter and have smaller leaves may be better at avoiding the risk of frost damage. Their study shows how fine-scale turnover in shrub species composition around frost hollows is related to plant functional traits.

Mountain habitats play an important role from the point of view of biodiversity and its protection, as they have a unique flora and harbor relict vascular plant and bryophyte species. Alpine vegetation is highly susceptible to climate warming and drying (Theurillat and Guisan 2001). Populations of cold-adapted species confined to alpine habitats and frost hollows are highly vulnerable to climate change, while their habitats tend to shrink (Plasse and Payette 2015). Frost hollows are of high conservation importance as they can provide suitable habitats for cold-adapted plant species that are not found in the surrounding landscape (Bátori et al. 2012, 2014, 2017). These unique areas have the potential to act as refugia in times of global change. Such microrefugia are known to maintain relict populations, and many endemic taxa of European conservation concern can be found in these vulnerable systems. The relatively high degree of specialization and naturalness (i.e., preserved species composition due to lower anthropogenic impacts in the past) of such areas should further facilitate our conservation efforts. The climate-induced decrease of snow cover often leads to frost damage to vegetation, which creates gaps suitable for the establishment of new colonizing species. One of the species groups that benefits from warming is the more thermophilic tall herbs, which are more common in the subalpine zone but have recently been actively spreading (Grabherr et al. 2010). However, in mountainous regions, topological differences at the microscale can strongly influence microclimate and counteract the average effects of climate warming (Lampei et al. 2019). Decoupling local microclimate from regional macroclimatic conditions plays an important role in maintaining certain plant communities in concave landforms (Lenoir et al. 2017).

28.6 Conclusions

Alpine frost hollows are especially common in alpine karst areas, although they occur in other areas as well. They are among the coldest areas in the Alps and in Europe, and the temperature at the bottom may fall below –50 °C (Trošt 2008). Specific relief conditions influence the occurrence of a specific microclimate and specific soil conditions, which often leads to the occurrence of vegetation inversion. From the point of view of climatic conditions, frost hollows are extreme environments, which is reflected mainly in significantly lower minimum temperatures, while the maximum temperatures do not differ significantly from the ambient temperature. Only cold-adapted plant communities are able to thrive in harsh conditions, with specific plant life-history strategies and functional traits reflecting their adaptations to stressful environments. Alpine frost hollows are also home to many relict and endemic species with narrow ecological niches. These additionally increase the overall biodiversity value of such unique alpine habitats.

Undoubtedly, frost hollows are climatological, vegetational, and geomorphological phenomena that contribute to both biotic and abiotic diversity. Geomorphological features (such as concavity) enable the maintenance of a cold air pool that is long-lasting in some frost hollows and short-lived in others. The longer a cold air pool is present, the more likely it is to form specific soil conditions and vegetation inversion. Unlike geomorphological forms, which are permanent, and vegetation inversion, which is also a long-term phenomenon, the climatological phenomenon lasts much shorter. In most frost hollows, the cold air pool dissipates daily in the warm half of the year, and in winter usually only in the advective type of weather. From a climatological point of view, frost hollows can therefore be considered as phenomena rather than forms, representing an element of geodiversity, but in a different context from geological, geomorphological, and vegetation forms. Something similar can be observed with some hydrological forms, which are also not permanent. Such examples are torrents, intermittent lakes, and high tides, which, despite the limited time of their occurrence, make an important contribution to geo- and biodiversity.

Acknowledgements The authors thank Iztok Sinjur, Gregor Vertačnik, and other members of Slovenian Meteorological Forum for their help with the measurements on Komna Plateau.

References

Aerts R (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. J Ecol 94(4):713–724. https://doi.org/10.1111/j.1365-2745.2006.01142.x

Bátori Z, Csiky J, Erdős L, Morschhauser T, Török P, Körmöczi L (2009) Vegetation of the dolines in Mecsek mountains (South Hungary) in relation to the local plant communities. Acta Carsologica 38(2–3):237–252. https://doi.org/10.3986/ac.v38i2-3.125

Bátori Z, Körmöczi L, Erdős L, Zalatnai M, Csiky J (2012) Importance of karst sinkholes in preserving relict, mountain, and wet-woodland plant species under sub-Mediterranean climate: a case study from southern Hungary. J Cave Karst Stud 74(1):127–134. https://doi.org/10.4311/2011LSC0216

Bátori Z, Csiky J, Farkas T, Vojtkó AE, Erdős L, Kovács D, Wirth T, Körmöczi L, Vojtkó A (2014) The conservation value of karst dolines for vascular plants in woodland habitats of Hungary: refugia and climate change. Int J Speleol 43(1):15–26

Bátori Z, Vojtkó A, Farkas T, Szabó A, Havadtői K, Vojtkó AE, Tölgyesi C, Cseh V, Erdős L, Maák IE, Keppel G (2017) Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. Ann Bot 119(2):301–309. https://doi.org/10.1093/aob/mcw233

Bátori Z, Vojtkó A, Maák IE, Lőrinczi G, Farkas T, Kántor N, Tanács E, Kiss PJ, Juhász O, Módra G, Tölgyesi C, Erdős L, Aguilon DJ, Keppel G (2019) Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. Scientific Reports 9. https://doi.org/10.1038/s41598-019-43603-x

Billings WD (1974) Adaptations and origins of alpine plants. Arct Alp Res 6(2):129–142. https://doi.org/10.2307/1550081

Čarni A, Čonč Š, Breg Valjavec M (2022) Landform-vegetation units in karstic depressions (dolines) evaluated by indicator plant species and Ellenberg indicator values. Ecological Indicators 135. https://doi.org/10.1016/j.ecolind.2022.108572

D'Odorico P, He Y, Collins S, De Wekker SFJ, Engel V, Fuentes JD (2013) Vegetation-microclimate feedbacks in woodland-grassland ecotones. Glob Ecol Biogeogr 22(4):364–379. https://doi.org/10.1111/geb.12000

DeWalle DR, Rango A (2008) Principles of snow hydrology. Cambridge University Press, Cambridge

Dixon G (1995) Aspects of geoconservation in Tasmania: a preliminary review of significant earth features. Parks and Wildlife Service, Hobart

Dy G, Payette S (2007) Frost hollows of the boreal forest as extreme environments for black spruce tree growth. Can J for Res 37(2):492–504. https://doi.org/10.1139/X06-235

Eberhard R (ed) (1997) Pattern and process: towards a regional approach to national estate assessment of geodiversity. Australian Heritage Commission, Canberra

Geiger R (1966) The climate near the ground. Harvard University Press, Cambridge

Good M, Morgan JW, Venn S, Green P (2019) Timing of snowmelt affect species composition via plant strategy filtering. Basic Appl Ecol 35:54–62. https://doi.org/10.1016/j.baae.2019.01.004

Grabherr G, Gottfried M, Pauli H (2010) Climate change impacts in alpine environments. Geogr Compass 4(8):1133–1153. https://doi.org/10.1111/j.1749-8198.2010.00356.x

Gray M (2013) Geodiversity: valuing and conserving abiotic nature. Wiley, Chichester

Henderson JR (1994) Remote measurement of ground temperature and emissivity. In: Proceedings: international symposium on optics, imaging, and instrumentation. San Diego. https://doi.org/10.1117/12.188681

Kammer PM, Möhl A (2002) Factors controlling species richness in alpine plant communities: an assessment of the importance of stress and disturbance. Arct Antarct Alp Res 34(4):398–407. https://doi.org/10.1080/15230430.2002.12003510

Kiernan K (1994) The geoconservation significance of lake pedder and its contribution to geodiversity. Unpublished Report to the Lake Pedder Study Group. University of Tasmania, Hobart

Kiernan K (1996) The conservation of glacial landforms. Forest Practices Unit, Hobart

Kiernan K (1997) The conservation of landforms of coastal origin. Forest Practices Board, Hobart

Klimešová J, Doležal J (2011) Are clonal plants more frequent in cold environments than elsewhere? Plant Ecolog Divers 4(4):373–378. https://doi.org/10.1080/17550874.2011.586734

Kobal M, Bertoncelj I, Pirotti F, Dakskobler I, Kutnar L (2015) Using lidar data to analyse sinkhole characteristics relevant for understory vegetation under forest cover–case study of a high karst area in the Dinaric mountains. PLoS ONE 10(3). https://doi.org/10.1371/journal.pone.0122070

Körner C (2003) Alpine plant life—functional plant ecology of high mountain ecosystems. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-18970-8

Körner C, Neumayer M, Pelaez Menendez-Riedl S, Smeets-Scheel A (1989) Functional morphology of mountain plants. Flora 182(5–6):353–383. https://doi.org/10.1016/S0367-2530(17)30426-7

Körner C (2016) Plant adaptation to cold climates. F1000Res 5:2769–2774. https://doi.org/10.12688/f1000research.9107.1

Lampei C, Wunder J, Wilhalm T, Schmid KJ (2019) Microclimate predicts frost hardiness of alpine *Arabidopsis thaliana* populations better than elevation. Ecol Evol 9(23):13017–13029. https://doi.org/10.1002/ece3.5659

Larcher W, Kainmüller C, Wagner J (2010) Survival types of high mountain plants under extreme temperatures. Flora 205(1):3–18. https://doi.org/10.1016/j.flora.2008.12.005

Lenoir J, Hattab T, Pierre G (2017) Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography 40(2):253–266. https://doi.org/10.1111/ecog.02788

Lim FKS, Pollock LJ, Vesk PA (2017) The role of plant functional traits in shrub distribution around alpine frost hollows. J Veg Sci 28(3):585–594. https://doi.org/10.1111/jvs.12517

Lütz C (2012) Plants in alpine regions—cell physiology of adaptation and survival strategies. Springer, Wien. https://doi.org/10.1007/978-3-7091-0136-0

Martinčič A (1975) Vpliv človeka na nastanek nekaterih mrazišč v Trnovskem gozdu [Human impact on the formation of some frost hollows in the Trnovski gozd plateau]. Razprave: posebna številka. Simpozij: meteorologija - gospodarstvo, vol 1. Društvo meteorologov Slovenije, Ljubljana, pp 35–43

Martinčič A (1977) Prispevek k poznavanju ekologije mrazišč v Sloveniji: botanično ekološka skica [Contribution to the knowledge of the ecology of frost hollows in Slovenia: a botanical-ecological sketch]. Razprave IV Razreda SAZU 20(5):227–317

Mihevc A (2021) Ice in caves and its effect on thermal inversion and permafrost in the case of the Velika ledena jama v Paradani, Smrekova draga and neighbouring dolines. Acta Carsologica 50(2–3):241–251. https://doi.org/10.3986/ac.v50i2-3.10495

Ogrin M, Sinjur I, Ogrin D (2006) Minimalne temperature v slovenskih mraziščih pozimi 2005/2006 [Minimum tempertures in Slovenian frost hollows in winter 2005/2006]. Geografski Obzornik 53(2):4–12

Ortar J (2011) Tipizacija in regionalizacija Slovenskih mrazišč [Typification and regionalisation of frost hollows in Slovenia]. BSc Thesis, University of Ljubljana, Ljubljana

Plasse C, Payette S (2015) Frost hollows of the boreal forest: a spatiotemporal perspective. J Ecol 103(3):669–678. https://doi.org/10.1111/1365-2745.12399

Prosser C (2002) Terms of endearment. Earth Herit 17:12–13

Sakai A, Larcher W (1987) Frost survival of plants—responses adaptation to freezing stress. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-71745-1

Sauberer F, Dirmhirn I (1954) Über die Entstehung der extremen Temperaturminima in der Doline Gstettner-Alm. Archiv Für Meteorologie, Geophysik und Bioklimatologie B5:307–326. https://doi.org/10.1007/BF02242757

Sauberer F, Dirmhirn I (1956) Weitere Untersuchungen über die kaltluftansammungen in der Doline Gstettner-Alm bei Lunz im Niederösterreich. Wetter Leben 8:187–196

Sharples C (1993) A methodology for the identification of significant landforms and geological sites for geoconservation purposes. Forestry Commission Tasmania, Hobart

Sharples C (2002) Concepts and principles of geoconservation. Tasmanian Parks and Wildlife Service, Hobart

Staley DO, Jurica GM (1972) Effective atmospheric emissivity under clear skies. J Appl Meteorol Climatol 11(2):349–356. https://doi.org/10.1175/1520-0450(1972)011%3c0349:EAEUCS%3e2.0.CO;2

Stanley M (2000) Geodiversity. Earth heritage 14:15–18

Stepišnik U, Repe B (2015) Identifikacija vročih točk geodiverzitete na primeru krajinskega parka Rakov Škocjan [Identification of geodiversity hotspots on example of the Rakov Škocjan landscape park]. Dela 44:45–62. https://doi.org/10.4312/dela.44.45-62

Stepišnik U, Trenchovska A (2016) A proposal of quantitative geodiversity evaluation model in the example of Upper Pivka Karst, Slovenia. Dela 46:53–65. https://doi.org/10.4312/dela.46.2.41-65

Stepišnik U, Ilc Klun M, Repe B (2017) Vrednotenje izobraževalnega potenciala geodiverzitete na primeru Cerkniškega polja [Assessment of educational potential of geodiversity on example of Cerknica polje, Slovenia]. Dela 47:5–21. https://doi.org/10.4312/dela.47.1.5-39

Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. Clim Chang 50:77–109. https://doi.org/10.1023/A:1010632015572

Trošt A (2008) Mrazišča na Komni [Frost hollows in Komna Plateau]. BSc Thesis, University of Ljubljana, Ljubljana

Vilović T, Buzjak S, Buzjak M (2019) Floristic and microclimatic features of the Sovljak doline (Mt. Velika Kapela, Croatia). Šumarski List 143(1–2):35–43. https://doi.org/10.31298/sl.143.1-2.4

Vrhovec T, Kastelec D, Petkovšek Z (2006) Vreme in podnebje v gorah [Weather and climate in the mountains]. Tehniška založba Slovenije, Ljubljana

Wheeler JA, Hoch G, Cortés AJ, Sedlacek J, Wipf S, Rixen C (2014) Increased spring freezing vulnerability for alpine shrubs under early snowmelt. Oecologia 175:219–229. https://doi.org/10.1007/s00442-013-2872-8

Whiteman CD, Haiden T, Pospichal B, Eisenbach S, Steinacker R (2004) Minimum temperatures, diurnal temperature ranges, and temperature inversions in limestone sinkholes of different sizes and shapes. J Appl Meteorol 43(8):1224–1236. https://doi.org/10.1175/1520-0450(2004)043%3c1224:MTDTRA%3e2.0.CO;2

Zängl G (2005) Formation of extreme cold-air pools in elevated sinkholes: an idealized numerical porocess study. Mon Weather Rev 133(4):925–941. https://doi.org/10.1175/MWR2895.1

Zupančič M (1980) Smrekovi gozdovi v mraziščih Dinarskega gorstva Slovenije [Spruce forests in the frost hollows of the Dinaric Alps of Slovenia]. Dela IV Razreda SAZU, vol 24. SAZU, Ljubljana