

## Habitat requirements of the pulmonate land snails *Trochulus oreinos oreinos* and *Cylindrus obtusus* endemic to the Northern Calcareous Alps, Austria

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### Abstract

The habitat needs and potential threats to *Trochulus oreinos oreinos* (Wagner 1915) and *Cylindrus obtusus* (Draparnaud 1805) were assessed by comparing vegetation maps and our own records. We selected four sites from which we had adequate samples and for which exact vegetation maps were available: the mountains Hochschwab, Schneealpe, Rax and Schneeberg. Both taxa prefer open dry alpine grassland with diggable soil and/or stones. *T. oreinos oreinos* is restricted to subalpine and alpine boulder societies and *Caricetum firmae*. While *C. obtusus* dwells on several communities of plants, it seems to be bound to unconsolidated stony ground. As both taxa prefer naturally forest-free areas, they are not affected by structural changes of the habitat, such as reforestation caused by the abandonment of grazing and the shift of vegetation zones. But it has to be considered that *T. oreinos oreinos* and *C. obtusus* are limited by microclimatic factors, as they prefer cooler habitats. The mountains Schneealpe, Rax and Schneeberg, reaching barely 2000m in height, are on the climatic limit of the species distribution. Therefore, the investigated taxa are vulnerable to the upward shift of climate zones. *T. oreinos oreinos* shows striking similarities in its habitat preference to the Swiss endemic *T. biconicus*, as both taxa prefer the same dry alpine habitats which are quite different to those of other representatives of the genus, which prefer damp habitats.

### Profile

Mountain range

Alps

Country

Austria

### Introduction

The north-eastern Calcareous Alps are a hotspot of endemic plants and animals (Rabitsch & Essl 2009). This is also the case for land snails, which have a maximum of endemics in this area. Because of their poor dispersal abilities, they are especially predestined to develop local forms in isolated areas. Two of the endemic pulmonate land snail species of the north-eastern Alps – *Trochulus oreinos* (Wagner 1915) and *Cylindrus obtusus* (Draparnaud 1805) – which are the focus of a larger project on the phylogeography of Alpine land snails – inhabit open, rocky areas from the subalpine ecotone upwards to the alpine zone (Klemm 1974; Reischütz & Reischütz 2009). *Trochulus oreinos* comprises two subspecies: *Trochulus oreinos oreinos* (Wagner 1915), subject of the present paper, distributed in the northern Calcareous Alps of Lower Austria and Styria from Schneeberg to Totes Gebirge, and *Trochulus oreinos scheerpeltzi* (Mikula 1954), restricted to the Northern Calcareous Alps of Upper Austria from Sengengebirge to Höllengebirge. *Cylindrus obtusus* is distributed in the Northern Calcareous Alps from Schneeberg in Lower Austria, across the northern parts of Styria to Mt. Dachstein in Upper Austria and carbonate sites within siliceous bedrock of the Central Alps westwards to the Glocknergruppe. Both species are restricted to higher elevations: *Trochulus oreinos* from 1400 to 2200 m (Klemm 1974; Duda et al. 2010), *Cylindrus obtusus* from 1100 to 2680 m (Klemm



Figure 1 – Alpine boulders and screes with poor vegetation are a suitable habitat for both *Trochulus oreinos* (left) and *Cylindrus obtusus* (right). © Helmut Sattmann

1974). The lower altitudinal range of the latter was already seen as atypical exception by Klemm (1974).

For both species there are only sparse documentations on their habitat needs, as is the case for many Central European land snails. In *Cylindrus obtusus*, previous investigations focused on morphology, anatomy, phylogeography and on systematics (Adensamer 1937; Freitag & Desch 1996; Shileyko et al. 1997; Edlinger 1999), but only little information is available about the ecology and biology of the species (Kühnelt 1937; Freitag & Desch 1996; Bisenberger et al. 1999). For *Trochulus oreinos*, some taxonomic appraisals have been published (Falkner 1982, Falkner 1995). A first

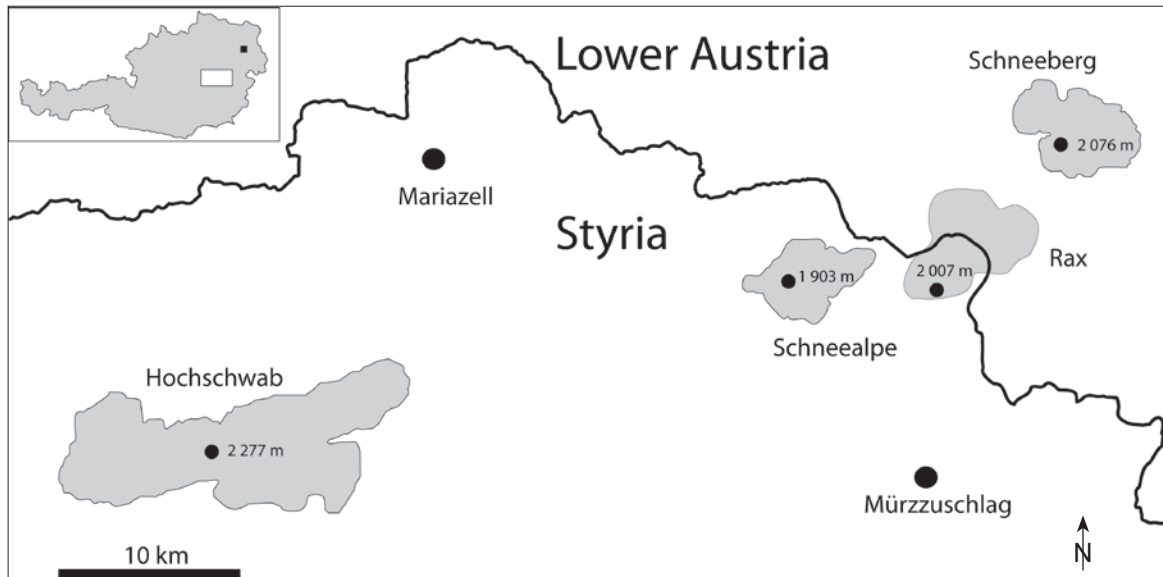


Figure 2 – Location (top left) and sketch map of study area. Elevation of the highest peaks in metres above sea level.

phylogenetic analysis, combined with more detailed morphological investigations, was performed recently (Duda et al. 2010) indicating that *T. oreinos* is an old phylogenetic lineage and presumably has a long independent history in the north-eastern Calcareous Alps. Also *C. obtusus*, which is the only representative of the genus *Cylindrus*, is considered an old endemic of this region. Yet, so far hardly any published information has been available on habitat preferences and population ecology of the two species (Reischütz & Reischütz 2009; Duda et al. 2010). From the literature it is known that both species are restricted to alpine and subalpine ecotones above 1400 m and occur predominantly near calcareous gravel (Klemm 1974; Duda et al. 2010). As both species are endemics of the Eastern Alps with quite restricted distribution – concerning their ranges as well as their altitudinal distribution – their habitat requirements are of special interest, also in the light of human habitat destruction and climate change.

In the course of collecting trips in the years 2006–2009, we gathered a high number of specimens of these taxa throughout the Austrian Eastern Alps. As a result, detailed data on their occurrences are now available for further interpretations. In the present paper, we combine our data with published vegetation maps (and general climatic assessments) to address questions of ecological requirements and possible threats.

For our investigations we selected mountain ranges of the north-eastern margins of the distribution ranges (Hochschwab, Schneecalpe, Rax and Schneeberg), because these regions are well surveyed in terms of vegetation mapping (Figure 2). The selected areas represent potential glacial refugia and thus allow interpretations concerning the Pleistocene history of the species. These northern margins of the north-eastern Calcareous Alps have been the focus of several research projects intended to determine potential glacial refugia (e.g. Tribsch 2004; Schönswetter et al. 2005), as several parts of it remained ice-free during the last

glaciations (Van Husen 1997). Thus, they might play an important role for endemism.

We assumed that the proportion of primarily (post-glacially) non-forested habitats compared to areas deforested by human activities like pasturing might be the most crucial factor and addressed the following questions: 1) How can the preferred habitat of *C. obtusus* and *T. oreinos* be characterized? 2) Do the species also occur at locations that are influenced by anthropogenic activities, like man-made mountain pastures on forest and krummholz sites or are they restricted to primarily forest-free sites? 3) Are they afflicted by recent changes of alpine agriculture? 4) Are the habitats and studied populations affected by climatic changes? The latter question is of particular interest as the influence of global warming on high-mountain organisms is a matter of debate and was discussed in several studies and projects.

## Material and methods

### Sampling areas and vegetation maps

The mountain ranges of Hochschwab, Schneecalpe, Rax, and Schneeberg were selected, because, according to the available literature, these regions are well documented by vegetation mapping. On Rax and Schneecalpe, large parts of alpine meadows are situated below the tree line. They are the result of human agricultural activities (traditional pasture management). As the pasture activities declined during the last hundred years, intrusion of krummholz has taken place in many of these areas (Dirnböck et al. 2003). On Schneecalpe, only a few exposed peaks on the plateau and steep rock faces on the eastern slopes are thought to have been originally free of forest. Also on the Rax, large parts of the high plateau were primarily forested except for a few steep ridges and summit areas (Dullinger et al. 2001). Mt. Schneeberg as the easternmost high-alpine peak of the northern Calcareous Alps is

Table 1 – Sample sites on Schneeberg, Rax, Schneetalpe and Hochschwab. Occurrences of *C. obtusus* (C) and *T. oreinos* (T) and none of both species (–).

Abbreviations: Vegetation type: AG: alpine grassland, AS: *Alnus viridis* shrub; DF: deciduous forest; FV: free of vegetation; ME: meadow; MF: mixed forest; PM: *Pinus mugo* shrub

Landscape structure: CA: canyon / rock face; BD: bank, dam; BO: boulders; EF: edge of forest; LT: loose tree stands and shrubs; RO: rocks; SI: single stones

Plant society (based on Greimler & Dirnböck 1996): BSC: boulder and scree societies, CFE: Caricetum ferruginae, CFD: Caricetum firmae, dense, CFL: Caricetum firmae, loose, FSF: complex of Firmetum, Seslerio-Sempervivum and Festuca-Agrostis meadow, SFO: subalpine forest societies, SCS: Seslerio-Caricetum sempervirentis. Additional societies in brackets.

Mountain/Site	Taxa	Elevation (m)	Vegetation types	Landscape structures	Plant society
Schneeberg, highest peak: Klosterwappen 2076 m					
Schneeberg, Fadenwände_1393	C	1 393	AG, FV	BO, RO	BSC
Schneeberg, Schneidergraben		1 401	AG, FV	BO, RO	BSC
Schneeberg, Fadenwände_1525	–	1 525	FV, AG	RO	BSC
Schneeberg, Fadenwände_1562	C, T	1 562	FV, AG	BO, RO	BSC
Schneeberg, Fadenwände_1695	C	1 695	FV, AG	RO	BSC
Schneeberg, Kaiserstein 1	C	1 860	AG	SI, BO	CFL
Schneeberg, Waxriegel	C, T	1 873	AG	SI	CFL
Schneeberg, Ochsenboden	C	1 905	AG	SI	FSF
Schneeberg, Kaiserstein 2	C	1 910	AG	SI, BO	CFL
Schneeberg, Klosterwappen 2	C	1 994	AG	BO	FSF
Schneeberg, Klosterwappen 1	C	2 024	AG	SI, RO	CFL
Rax, highest peak: Heukuppe 2007 m					
Rax, Preiner Gscheid	–	1 249	MF	RO	SFO
Rax, Gsolhorn-Steig	–	1 422	DF	LT, RO	SFO
Rax, Göbl-Kühn-Steig	–	1 397	DF	RO	SFO
Rax, Thörlweg	C	1 592	FV, AG	BO, RO	BSC
Rax, Schlangenberg	T	1 600	AG	BO	BSC
Rax, Höllentalaussicht	C	1 620	FV, AG	BO	BSC
Rax, Praterstern	–	1 680	AG, PM	-	CFE
Rax, Jakobskogel - Große Kanzel	C	1 734	FV, AG, PM	BO	CFL
Rax, Seehütte	C	1 761	AG, PM	RO, BO	SCS
Rax, Bismarcksteig	C, T	1 787	AG	BO	BSC
Rax, Karl Ludwig-Haus	C	1 791	FV, AG	BO	CFD
Schneetalpe, highest peak: Windberg 1 903 m					
Schneetalpe, Kohlebnerstand	–	1 487	MF	EF, BD, RO	SFO
Schneetalpe, Blarergraben-Weg	C, T	1 664	AG	RO, CA	BSC
Schneetalpe, Kutatsch-Huette	–	1 673	AG, AS		SCS
Schneetalpe, Schneetalpenhaus	C, T	1 742	AG	SI, BO	BSC (SCS)
Schneetalpe, Windberg Osthang 1	C	1 810	AG	SI, RO	SCS (BSC)
Schneetalpe, Windberg West	C	1 891	FV, AG	BO	CFL
Schneetalpe, Windberg Gipfelhang	C	1 903	AG	SI, RO	SCS
Hochschwab, highest peak: Hochschwab 2 277 m					
Hochschwab, Böser Wald	–	1 076	DF, ME	EF, BO	SFO
Hochschwab, Staritzen Ostgipfel	–	1 779	AG	RO	BSC
Hochschwab, Kleiner Ebenstein	C	1 847	AG	RO	SCS
Hochschwab, Ochsenreichkar	C	1 963	AG	BO, RO	BSC
Hochschwab, Severinkogel	C, T	2 010	AG	RO	CFL
Hochschwab, Schiestlhaus	C, T	2 179	AG, PM	SI, RO	CFL

strongly afflicted by the pannonic climate of the Vienna basin. Therefore it provides warmer and dryer conditions, but to some extent Rax and Schneetalpe are also under this climatic influence (Kilian et al. 1993; Dirnböck & Greimler 1997; Dullinger et al. 2001). On Mt. Hochschwab, larger areas seem to be naturally forest-free, but it has also been influenced by human land use till today and large parts of currently open grassland would – without alpine farming – be covered by krummholz (Dirnböck et al. 1999).

The collecting trips were performed in the years 2006–2009. We sampled primarily the locations recorded in the literature (Klemm 1974) and in the collections of the Museum of Natural History Vienna. In addition, we sampled several new localities not previously recorded. For our comparisons, we included all collecting sites registered in our database ( $n = 35$ ) that are located within the regions mentioned above and are within the altitudinal distribution of the species (Klemm 1974). Elevations of the localities ranged





Figure 3 – Complex of Firmetum, Seslerio-Sempervivetum and Festuca-Arostis meadow is a result of strong structured relief and comprises elements of several communities of plants. In this habitat only *C. obtusus* is found. © Barbara Däubel

from 1 076–2 179 m (Table 1). We included also localities at which both *C. obtusus* and *T. oreinos* were lacking, although they seemed to provide potential habitats of the species.

We tried to assess the habitat requirements of both species more precisely by combining the gathered data on the occurrences of the taxa as well as local factors (coarse vegetation types and landscape structures, see below) registered during the collection trips with published vegetation maps. The vegetations maps used for characterization of the areas are published in Greimler & Dirnböck (1996), Dirnböck & Greimler (1997), Dullinger et al. (2001) and Dirnböck et al. (2003).

### Sampling

Animals were sampled manually in an area of approximately 100–300 m<sup>2</sup>. In general, two to five collectors screened the area for the occurrence of snails for 15–30 min. A limited number of these snails were collected, other taxa were either noted or reference specimens taken. Elevation, inclination, and coordinates were determined by GPS (Geo\_WGS\_84). A coarse analysis of the habitat was performed by a presence/absence list of habitat structures and vegetation types, which were noted in a case report form developed for alpine land snails in general.

### Results

The results are summarized in Table 1. Three vegetation types were found on sites with occurrence of the investigated species, i.e. free of vegetation, alpine grassland, *Pinus mugo* shrubbery. Both taxa were constantly found on alpine grassland (*T. oreinos*: 8 out of 8; *C. obtusus* 24 out of 24); *Pinus mugo* shrubbery was only found at the edge of the investigation sites. Of the

landscape structures, stony or rocky formations were most frequent, such as single stones (*T. oreinos*: 4 out of 8; *C. obtusus* 10 out of 24), boulders (*T. oreinos*: 4 out of 8; *C. obtusus* 13 out of 24) and rocks (*T. oreinos*: 3 out of 8; *C. obtusus* 13 out of 24). The frequency data of the coarse vegetation types and landscape structures showed no striking difference between the two taxa. All points with findings of one of the two species were at primarily non-forested sites above the lowest limit of the lower subalpine ecotone (1 300 m) as defined by Kilian et al. (1993). No records of either species was found on man-made subalpine and alpine pastures. Four natural non-forested communities of plants were recorded as characteristic for at least one of the species concerned. 1) The *Caricetum firmiae* is situated on exposed, carbonate sites, which are under heavy mechanical pressure and are often blown free of snow during winter season. 2) The *Seslerio-Caricetum sempervirentis* grows on former boulder areas and is characterized by loose, stony ground (Grabherr & Mucina 1993). 3) The complex of *Firmetum*, *Seslerio-Sempervivetum* and *Festuca pumila* – *Agrostis alpina* meadow (Figure 3) is a result of heavily structured relief and comprises elements of several communities of plants. 4) Alpine boulders and scree societies, as defined by Greimler & Dirnböck (1996), include areas with poor or no vegetation (see Figure 1) influenced by extreme mechanical pressure.

*Trochulus oreinos* was mostly found on alpine boulders and scree societies (5 out of 8 sample sites, most of all rock areas and boulders, but also on loose *Caricetum-firmae* (3 out of 8). Only one sample site was situated near *Seslerio-Caricetum sempervirentis* (see also Table 1). All sample sites were situated on natural forest-free parts of the mountain ranges, at altitudes from 1 562 to 2 179 m. Remarkably, half of these sites were definitely below the upper limit of the krummholz ecotone (about 1 900 m) on natural shrub- and forest-free vegetation (boulders, rocks).

*Cylindrus obtusus* in general was found more frequently than *T. oreinos* and the findings were situated on all plant communities mentioned above (Table 1). Elevations of sites ranged from 1 393 to 2 179 m. As with *T. oreinos*, about half of the sites were definitely located below the natural timberline, the others approximately at this limit or within the alpine ecotone.

### Discussion

In summary, the basic questions formulated in the introduction can be answered as follows: 1) *C. obtusus* and *T. oreinos* prefer rocky habitats from the subalpine ecotone upwards. While *T. oreinos* is restricted to *Caricetum firmiae* meadow and alpine boulder and scree societies, *C. obtusus* can inhabit several plant communities. 2) Both species are restricted to primarily forest-free sites. 3) Therefore they are not affected by the abandonment of man-made meadows, the most significant recent change within alpine agriculture. 4) As both



Figure 4 – *Trochulus oreinos oreinos* (left) and *Cylindrus obtusus* (right). © Michael Duda and Helmut Sattmann respectively

taxa are restricted to the subalpine and alpine ecotone, at least populations at the lower altitudinal distribution are potentially affected by climatic changes. Both taxa have few opportunities to enlarge their potential habitat upwards as they have already reached sites near the highest summit areas of the investigated mountain massifs. Below we discuss aspects of East-Alpine endemism on the basis of the ecology of *T. oreinos* and *C. obtusus*.

#### Vertical distribution and climatic impacts

*Trochulus oreinos* and *Cylindrus obtusus* are restricted to naturally non-forested sites, often also situated below the timberline in the subalpine ecotone. This is highlighted by the findings at Schneeralpe and Rax, where both taxa occur at the lower limit of their altitudinal and climatic distribution. Therefore, both species seem neither to be primarily affected by the end of grazing and the intrusion of shrubbery, as it is evident in many subalpine and alpine plants (Dirnböck et al. 2003), nor by an upward shift of the tree line. Also excessive land use (e.g. winter tourism) does not seem to be a major threat as the steep and rocky slopes where *C. obtusus* and *T. oreinos* live are not of major interest for human activities. The main potential threat for both taxa can be seen in the rapid warming of the climate. Although no extensive studies on climatic preferences exist for either species, their restriction to a cooler climate can be inferred from their high altitudinal distribution (Klemm 1974; Duda et al. 2010). This fact is also in accordance with the only published ecophysiological data of Kühnelt (1937), who stated that *C. obtusus* is not sensitive to low humidity, but vulnerable to high temperatures. Therefore, the lower edge of the subalpine ecotone seems to be a natural lower limit for both taxa. It thus seems like they are limited by climatic change rather than by changes in the habitat structure through reforestation.

As pointed out by Dirnböck et al. (2003) and Ohlemüller et al. (2008), the altitudinal distribution and the smaller number of colonized habitats of endemics with a limited distribution make these species especially vulnerable to climate change. Essl et al. (2009) state that although currently the endemics of high-moun-

tain areas in Austria are not threatened by extinction, this might change drastically in the future, as they have only few possibilities for moving upwards with incipient warming. This is very evident in our currently investigated area: some sites where both snail taxa occur are obviously already at the lower climatic limit of these species. This is corroborated by the fact that some populations of *C. obtusus* on lower sites in the Gesäuse area, located in northern Styria about 100 m west of Schneeberg and Rax, which Klemm listed in 1974, are now extinct (Sattmann et al. 2000). The current investigation also shows that *C. obtusus* cannot enlarge its potential habitat upwards as its highest records in the currently documented area are already near the highest summits on Schneeberg, Schneeralpe and Hochschwab (see also Table 1). Also the highest record on Rax given by Klemm (1974) is directly on its highest peak. *T. oreinos* reaches the highest summit area only on Hochschwab, but, in addition to its potential climatic restriction, it is also limited by its habitat requirements (see below “Ecological niche”). Other populations of *C. obtusus* in the western High Alps of Austria (e.g. on the Glocknergruppe at the border of Salzburg, Carinthia and Tyrol) have the potential to move upwards while, within *T. oreinos*, only populations of the western subspecies *T. o. scheerpeltzi* in the Totes Gebirge (Upper Austria) have the possibility to enlarge their habitat to higher elevations.

The suboptimal climatic conditions caused by the influence of the Pannonian climate combined with low elevation on Schneeberg and Rax are perhaps reflected in some morphological features detected in *C. obtusus*: Adensamer (1937) stated that the average shell size on these easternmost populations tends to be smaller than in western populations, a result confirmed by Edlinger (1999). Shileyko et al. (1997) pointed out that *C. obtusus* has irregular and reduced mucus glands on Schneeberg and Rax, while those from the Gesäuse area showed mucus glands of even length.

#### Ecological niche

The results show that both taxa clearly prefer sites with loose vegetation structure. Nevertheless, the community of plants itself is no prerequisite for

their occurrence but rather vegetation stands in combination with specific abiotic factors, which enable their existence.

Several authors mention that *C. obtusus* prefers “alpine black earth” and tries to avoid “red loam” (Adensamer 1937; Kühnelt 1937; Freitag & Desch 1996). The term “black earth” refers to rendzic leptosol, which is the typical soil for the *Caricetum firmae*, while “red loam” describes humic cambisol, which represents a relict soil in the investigated area. A first clue to the habitat needs lies within the structure of these soil types. Rendzic leptosols do not provide high water retention (Dirnböck & Grabherr 2000), but their loose structure enables easy digging for snails. Freitag & Desch (1996) interpreted digging by *C. obtusus* as a survival strategy during adverse climatic events (e.g. drought) besides hiding under stones and in mouse holes. Humic cambisol exhibits high water retention (Dirnböck & Grabherr 2000) but offers poor digging opportunities because of its dense structure and is therefore not suitable as habitat for *C. obtusus*. The number of findings rises above 1600 m, only two of our records of *C. obtusus* are situated below this line. This observation is similar to that of Freitag (1990), although it has to be mentioned that this author also reported findings as low as 1100 m. Yet some of those records were questioned by Frank (2006) as they could be a result of displacement of the empty shells by water or erosion. *Trochulus oreinos* seems to prefer even drier habitats than *C. obtusus*. In comparison to related forms like *T. hispidus* and *T. striolatus*, *T. oreinos* differs even more significantly as it does not prefer damp habitats (Pročków 2009). Only a few authors, like Falkner (1970) and Reischütz & Reischütz (2009), mention aspects of habitat choice. Another hairy snail, *T. biconicus* (Eder 1917), an endemic of Switzerland, shows striking parallels to *T. oreinos*, as it is restricted to the communities of plants composed of *Seslerio-Caricetum sempervirentis*, *Caricetum firmae* and alpine boulders in areas of Central Switzerland, which were potentially ice-free during Würm glaciation (Kerney et al. 1983; Baggenstos 2010). Within the investigated area, *T. oreinos* is not only restricted by climatic but also landscape-ecological factors. Only the Hochschwab massif, with its large areas of sparse vegetation on rocky ground, offers large suitable habitats for *T. oreinos*. In contrast, this species has very few opportunities to settle potential new habitats on Schneevalpe, Rax and Schneeberg in case of climate warming.

#### Patterns of endemism

According to Ohlemüller et al. (2008), areas with high climatic gradients such as mountain ranges provide long-term stability for special ecotones. Additionally, the authors mention the occurrence of rare climates as factor, which enables the radiation of endemics. In our example, this matches perfectly the distribution of *T. oreinos* and *C. obtusus*. Both dwell in ecotones which are rare amongst the Central European landscapes

because of their special abiotic factors, such as high elevation, steepness and extreme mechanical and climatic influence. The fact that some of these azonal occurrences often span wide ranges of elevations (e.g. boulders) provides the snails with the opportunity to move upwards or downwards in case of climate change. This fits well with the “climatic buffer hypothesis” of Ohlemüller et al. (2008). During the last glaciation, subalpine and alpine ecotones were situated approximately 1000 m lower than today (Rabitsch & Essl 2009). Moreover, large parts of the north-eastern Alps were not glaciated (Van Husen 1997). As shown by Rabitsch & Essl (2009), most Austrian endemics occur in high-alpine boulders and grassland. Some vascular plants like *Noccea krantzii* and *Papaver alpinum subalpinum* show similar distribution patterns and habitat preferences like *T. oreinos* and *C. obtusus*. (Schönswetter et al. 2005; Rabitsch & Essl 2009). Therefore it seems plausible that *T. oreinos* and *C. obtusus* survived the ice ages at the northern edge of the Calcareous Alps. Accordingly, both snail taxa would represent remains of the pre-Quarternary alpine fauna, as has already been suggested by Adensamer (1937) for *C. obtusus*.

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