DIPLOMARBEIT / DIPLOMA THESIS

Titel der Diplomarbeit / Title of the Diploma Thesis

„Changes in bird assemblages along an elevational gradient in the Eastern Alps (National Park Gesäuse) between 2006 and 2016“

verfasst von / submitted by

Caroline Verena Fraundorfer

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Magistra der Naturwissenschaften (Mag.rer.nat.)

Wien, 2020 / Vienna, 2020

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 190 333 445
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Lehramtsstudium UF Deutsch UF Biologie und Umweltkunde
Betreut von / Supervisor:	Dipl.-Biol. Dr. Christian Schulze

This study was conducted in collaboration with the Nationalpark Gesäuse GmbH which supported me financially and logistically.

Acknowledgements

I would first want to thank my supervisor Dr. Christian Schulze who supported me during my working process with professional advice and feedback. He consistently allowed this paper to be my own work, but steered me in the right direction whenever he thought I needed it. I am also grateful to all the people working and living in and for the National Park Gesäuse, who offered shelter, meals and company during my fieldwork. A special gratitude goes to my parents, who enabled me to study at the University of Vienna and provided continuous encouragement. Last but not least I want to thank my friends, other family members and fellow students who offered moral and emotional support throughout my studies. Thank you.

Abstract

As climate change moves on, especially mountain ranges are expected to be under high pressure as they cover a wide temperature gradient within a small spatial scale. This study examines changes in the distribution of bird species along an elevational gradient in the National Park Gesäuse (Eastern Alps) between 2006 and 2016. It aims to investigate the changes (1) in the elevational distribution of species richness, (2) in species' elevational niches and (3) in the composition of species assemblages along an elevational gradient. The bird survey was conducted as point-counts along three line transects covering an elevational gradient of 1520 m. Due to climate change, an upward shift of bird species along with changes in species assemblages was expected. Statistical analyses show that no shifts of species' elevational niches are observable. However, there are differences on the level of bird species assemblages indicating that the bird community has changed more at higher elevations around and above the timberline. The results also show an increasing species richness above 1400 m while there are losses at lower elevations producing a pattern of low-elevation plateau with a mid-elevation peak along the elevational gradient. These findings imply that climate change is affecting higher elevations more than lower ones, causing more changes around and above the timberline. Additionally, the comparison of the data from 2006 and 2016 also shows a homogenization of bird species assemblages up to an elevation of 1750 m and decreasing species richness in lower elevations. These phenomena are probably linked. Taking all these results into consideration, it becomes visible that climate change does have an effect on the bird species assemblages within the National Park Gesäuse and that higher elevations at the timberline and above will probably be undergoing the most severe changes in the near future.

Keywords: avifaunal changes, climate change, elevational niches, species composition, species richness, The Alps

Zusammenfassung

Mit dem fortschreitenden Klimawandel geraten besonders Gebirgsregionen unter Druck, weil sie einen hohen Temperaturgradienten auf kleinem Raum abdecken. Diese Studie untersucht die Veränderungen der Verteilung von Vogelarten entlang eines Höhengradienten im Nationalpark Gesäuse (Ostalpen) zwischen 2006 und 2016. Sie hat zum Ziel, die Veränderung (1) der Verteilung des Artenreichtums, (2) der Höhennischen der Arten sowie (3) der Artenzusammensetzung der Avifauna entlang eines Höhengradienten zu untersuchen. Die Datenaufnahme wurde in Form von Punkt-Stopp-Zählungen entlang von drei Linientransekten durchgeführt, die einen Höhengradienten von 1520 m abdecken. Aufgrund des Klimawandels

wurden Verschiebungen der Höhennischen nach oben sowie damit einhergehende Veränderungen in der Zusammensetzung der Vogelgemeinschaft erwartet. Die statistischen Auswertungen zeigen, dass keine Verschiebung der Höhennischen der Arten beobachtbar ist. Hingegen gibt es Veränderungen in der Artenzusammensetzung der Vogelgemeinschaft, vor allem in höheren Lagen in der Region an und über der Baumgrenze. Die Ergebnisse zeigen außerdem einen Anstieg des Artenreichtums oberhalb von 1400 m, während sich der Artenreichtum in tieferen Lagen verringert hat. Dies führt zu einem Plateau an Diversität in niedrigeren Höhen mit dem höchsten Artenreichtum in mittleren Lagen. Diese Ergebnisse weisen darauf hin, dass der Klimawandel höhere Lagen stärker als niedrigere betrifft und daher stärkere Veränderungen um und über der Baumgrenze bedingt. Außerdem zeigt ein Vergleich der Daten von 2006 und 2016 eine Homogenisierung in der Zusammensetzung der Artengemeinschaften bis zu einer Höhe von 1750 m und einen Verlust an Artenreichtum in niedrigeren Lagen. Diese beiden Phänomene hängen wahrscheinlich zusammen. In Anbetracht dieser Erkenntnisse zeigt sich, dass der Klimawandel Auswirkungen auf die Zusammensetzung der Vogelgemeinschaft im Nationalpark Gesäuse hat. Die tiefgreifendsten Veränderungen in naher Zukunft werden wahrscheinlich in höheren Lagen um die und über der Baumgrenze auftreten.

Table of Contents

Introduction

It is well known that climate is one of the most important factors determining the distribution of species worldwide. Current global warming and climate changes have already had measureable effects on the distribution and abundance of species and will have an even more powerful impact in the future (Chen et al. 2011, Gillings et al. 2015, Stephens et al. 2016). As temperature is not only highly correlated with latitude but also with elevation, mountain ranges are under high pressure because there are pronounced differences in temperature on a small spatial scale (Flousek et al. 2015). It is important to understand, how severe and how rapid changes in species richness distribution are in order to identify possible measurements for species conservation (e.g. Chamberlain et al. 2016). Studies on species distribution in mountain regions worldwide may also contribute data to develop models which aim to predict the future impacts of climate change on the global distribution of species richness (McCain 2009).

There is an extensive record of bird species richness along elevational gradients in different climatic regions, but long-term studies are scarce (Saracco et al. 2019; Flousek et al. 2015; Reif & Flousek 2012). The study at hand quantifies changes in bird species distribution along an elevational gradient in the eastern Alps over a time span of ten years. Therefore, a bird survey conducted across an elevational gradient in 2006 (Klosius 2008) was repeated in 2016. The questions addressed in this study were the following:

(1) *Did bird species richness change along the elevational gradient between 2006 and 2016?* Due to global warming, temperatures are rising and species are expected to follow their climatic optima, forcing species living in mountain habitats to shift towards the mountain tops. Therefore, an upward shift of bird species is expected as it was proven for other mountain ranges in temperate climatic regions (Flousek et al. 2015; Reif & Flousek 2012). In the study of Klosius (2008), the species richness pattern along the elevational gradient showed a plateau from the valley floor up to about 1200 m a.s.l. and then a decrease towards the mountain top or summit, respectively. If there was an upward shift of species, the plateau in species richness is expected to reach up further in 2016. These assumptions can be formulated as *hypothesis 1:* There is a general upward shift of bird species which leads to a plateau of high bird species richness from the valley floor up to an elevation higher than 1200 m followed by a decreasing pattern towards the mountain tops.

(2) *Did species' elevational niches change between 2006 and 2016?*

If there was an upward shift of species due to global warming, this should also affect species' elevational niches and raise the mean elevation of the niches. Species breeding at lower elevations might profit from warmer climate and thus broaden their elevational niche by extending the niche's upper boundary. High alpine species are estimated to keep or even narrow their elevational niche as they cannot shift upwards and will probably move the niche's lower boundary upwards in the long-term, when the timberline raises too (cf. Flousek et al. 2015; Reif & Flousek 2012). Since a time span of ten years is too short for observable changes in vegetation structure on a big scale, effects are probably higher on low-altitude species. These expectations can be formulated as *hypothesis 2:* The width of elevational niches increases and their midpoint raises. There is a stronger effect on the upper boundary of the niches than on the lower boundary.

(3) *Did bird species assemblages change along the elevational gradient between 2006 and 2016?*

If there was a general upward shift of species as proposed in hypothesis 1, this would not affect all species equally. Those species already living at high elevations are not able to move upwards to the same extent than species in lower elevations, because they cannot move upwards beyond the mountain top. Therefore, changes in species assemblages should be higher at higher elevations, especially around and beyond the timberline. This is formulated in *hypothesis 3:* Changes in species assemblages between 2006 and 2016 are stronger in higher elevations than in lower ones. As bird species are also dependent on the vegetation structure for suitable nesting sites and food resources, census points were also assigned to habitat types to see if there was an interrelation between particular habitat types and to which extent species assemblages have changed.

Methods

Study Area

The study was conducted in the National Park Gesäuse, which is located in Styria, a province of Austria. The national park was founded on October 26, 2002 and covers an area of about 120 km^2. It mainly consists of two massifs, the Buchstein massif and the Hochtor massif, which are geologically part of the Northern Limestone Alps (Nationalpark Gesäuse 2019). Characteristic of the landscape of the National Park Gesäuse are massifs with steep slopes divided by deep valleys. The massifs mainly (>90%) consist of carbonate rock, namely dolomite and limestone, which often form rifts filled with rock waste, and steep slopes, which lack vegetation.

Elevational differences are high, with a maximum amplitude of 1792 m reaching from the valley floor in Gstatterboden (587 m) up to the peak of the Hochtor (2370 m). The study area for this survey is located on the southern slopes of the Buchstein massif, north of the Enns river (Remich 2001: 15-18).

The climate is a Central European temperate climate with oceanic influence. The Gesäuse is part of the northern stacking area, where winds from the northwest bring damp air from the Atlantic Ocean and cause frequent and sometimes long periods of precipitation. Typically for the Gesäuse are long periods of rain rather than short precipitation events like thunderstorms. The precipitation per year varies between 1200 mm in the valley and >2500 mm on the mountain peaks with most rainfall during summer and a second, smaller precipitation maximum in winter, causing lots of snow. In general, precipitation increases with increasing elevation, but due to local differences in topography this is not valid for every part of the national park. Therefore, the precipitation on the Buchstein massif is higher than on the Hochtor massif, which is located south of the Buchstein massif (Nationalpark Gesäuse 2019; Remich 2001: 20).

The land cover of the National Park Gesäuse is predominantly woodland (49%), followed by rock/rock waste (23%), scrub land/dwarf pine (16%) and pastures/alpine meadows (11%). The remaining < 2 % are made up of water bodies and infrastructure (Zimmermann & Kreiner 2012: 103). Below the vegetation-free peaks of the Großer Buchstein and the Tamischbachturm, there is an extensive belt of alpine meadows and dwarf pine areas. On the southern slopes this is either adjoined by subalpine beech-forests or natural spruce-forests. In the montane zone, due to former forestry measures, large parts of the natural beech-forests and spruce-fir-beech-forests were replaced by spruce-forests. These natural forests should make up twice the area they are currently covering in the National Park (Zimmermann & Kreiner 2012: 99; 103; Zimmermann 2017). Due to extreme reliefs, it is difficult to delimit vegetation zones as they are largely dependent on exposition and slope. For the southern slopes of the Großer Buchstein (GB) and the Tamischbachturm (T) the upper limit of beeches is around 1500 m a.s.l. (Zimmermann & Kreiner 2012: 94), while the timber line is situated at around 1550 m (GB) and 1650 m (T) respectively. The dwarf pine belt reaches up to an elevation of about 1850 (GB) or even 1950 m (T) (Zimmermann 2017).

Bird Survey

The method used for the bird survey was identical with the one used by Klosius (2008). For data collection, a total of 87 census points along three hiking trails on the southern slope of the Buchstein massif were visited. One trail leads from Hieflau to the peak of the Tamischbachturm (southeastern trail), one from Gstatterboden to the same peak (southwestern trail) and the third one from Gstatterboden to the Großer Buchstein. The lowest census points were located at 518 and 606 m a.s.l. at Hieflau and Gstatterboden, respectively; highest census points were at 1944 (GB) and 2038 m a.s.l. (T). Hence, the examined elevational gradient covered an elevational range of 1520m. As this study was designed as a comparative long-term study, the GPS-marked census points were taken from Klosius (2008). Some parts of the originally used hiking trails and other small trails were slightly relocated or even abandoned, which made it difficult to access some of the census points. In these cases, an accessible place closest to the original census point was chosen, usually being located within a radius of 20 m around the original census point from the year 2006. For more information on the selection of census points see Klosius (2008).

The point counts took place between April 4th and July 22nd in 2016 (vs. April 3rd - July 25th in 2006). Every census point was visited three times between sunrise and 4 hours after sunrise for a survey duration of 10 minutes. During each point count all birds noted acoustically or visually were recorded. It was additionally written down whether the birds were singing or calling and whether they were recorded within or outside a 50 m radius around the census point. There was a minimum time span of two weeks between each survey at the same census points. Due to bad weather conditions in June with ongoing rain and storms, the third survey for all points above 1500 m a.s.l. took place in July. Unknown bird voices were compared with the tape-recordings of Roché (2000) and, if necessary, recorded with an Olympus digital voice recorder VN-3100PC for later identification. Due to missing precision in the description of collected data, most of the census points between 500 and 1000 m were visited four times in 2006. This leads to slightly overestimated species numbers in the bottom third of the surveyed elevational gradient.

Statistical Analyses

If not mentioned otherwise, only birds found within a 50 m radius were taken into account for the statistical analyses. Birds which were flying above the census point without interacting with any structures or vegetation within the 50 m radius during the point counts were not considered any further, as they did not utilize any habitat structure related to the census point or its close vicinity.

To compare the total bird species richness in our study area between both survey periods, species accumulation curves based on species lists per census points as sampling units were calculated with *EstimateS* (version 9.1).

Spearman's rank correlations were calculated to test for relationships between changes in species richness and elevation with the software PAST (version 3.25). This was done on the spatial level of census points and 100 m elevation belts both for 2006 and 2016 individually and for the difference in species numbers between both survey years.

To check for shifts in the elevational niches of species, four elevational niche parameters were used: (1) the upper and (2) lower limit, (3) the midpoint and (4) the width of elevational niches. Pairwise t tests calculated with IBM SPSS Statistics (version 24 for Windows) were used to test for differences in species' niche parameters between 2006 and 2016.

To detect changes in species composition between the two survey periods, similarities of species assemblages were quantified by calculating Bray-Curtis similarities with PAST (version 3.25) for each census point and survey year. The similarity relationships were visualised in a non-metric multidimensional (NMDS) ordination (calculated with Primer version 5.2.9, Clarke & Gorley 2001). When the associated stress value was <0.20, the NMDS ordination was considered to reliably visualize the similarity relationships (Clarke 1993). Bray-Curtis similarities were also calculated as pairwise comparisons between the two survey years for each census point to test if changes in species composition were related to elevation, using a Spearman rank correlation calculated with PAST (version 3.25).

Results

Total species richness: 2006 vs. 2016

Species accumulation curves for both survey years show a slightly, but not significantly lower bird species richness in 2016 compared to 2006 (Figure 1).

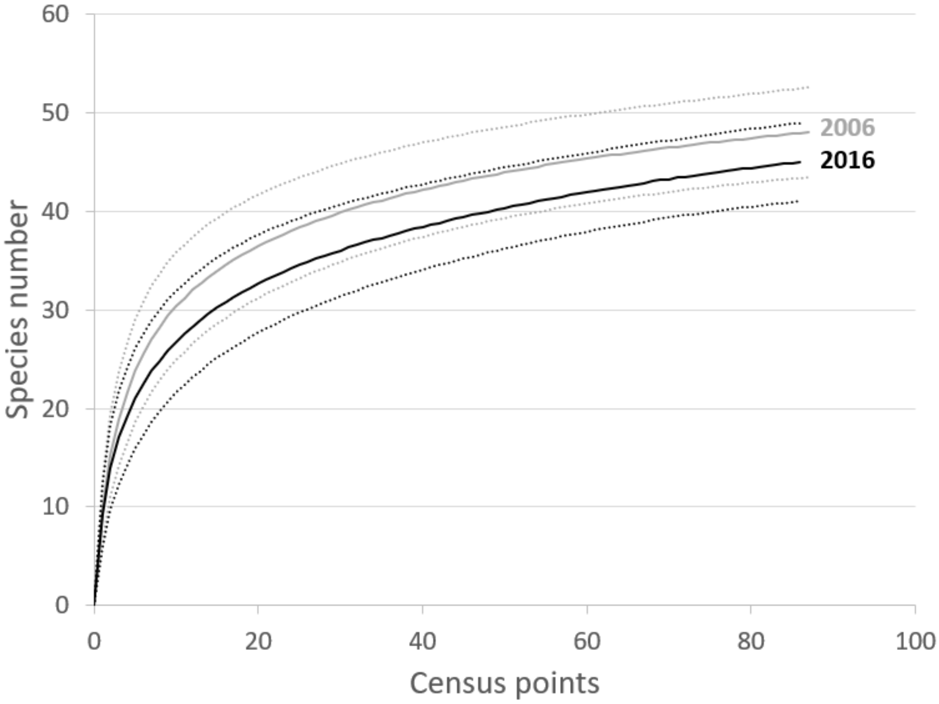


Figure 1: Species accumulation curves with 95% confidence intervals (dotted lines) for 2006 and 2016.

In 2006, a total number of 55 bird species was found, of which 48 occurred within the 50 m radius. In 2016, 54 species were found in total and 44 of them within the 50 m radius. 15 species were recorded in only one of both survey years, but all are generally rare in the study area (e.g. *Falco peregrinus*, *Tetrao urogallus*, *Tetrastes bonasia* and *Streptopelia turtur*). The only exception is *Carduelis spinus* which was recorded 70 times in 2016 within the 50 m radius but not once in 2006.

Species richness along the elevational gradient

For a direct comparison between the two survey years 2006 and 2016, species' distributions over the elevational gradient on the level of census points are plotted (Figure 2). All species ocurring in both years with a minimum number of 5 individuals in at least one of the two survey years are considered. There are a couple of species where the record was notably lower in 2016, e.g. *Anthus trivialis*, *Nucifraga caryocatactes* and *Poecile palustris*. However, there are also species with increased occurrence, such as *Dryocopus martius* and *Poecile montanus*. For *Regulus regulus* and *Pyrrhula pyrrhula*, there seems to be an upward shift of the upper border of the elevational niche, meaning they expanded their elevational niches, while *Prunella modularis* shifted its main distribution range upwards. While there seems to be no overall trend for most taxa, there was a considerable decrease in recordings for all species of *Turdus* sp.

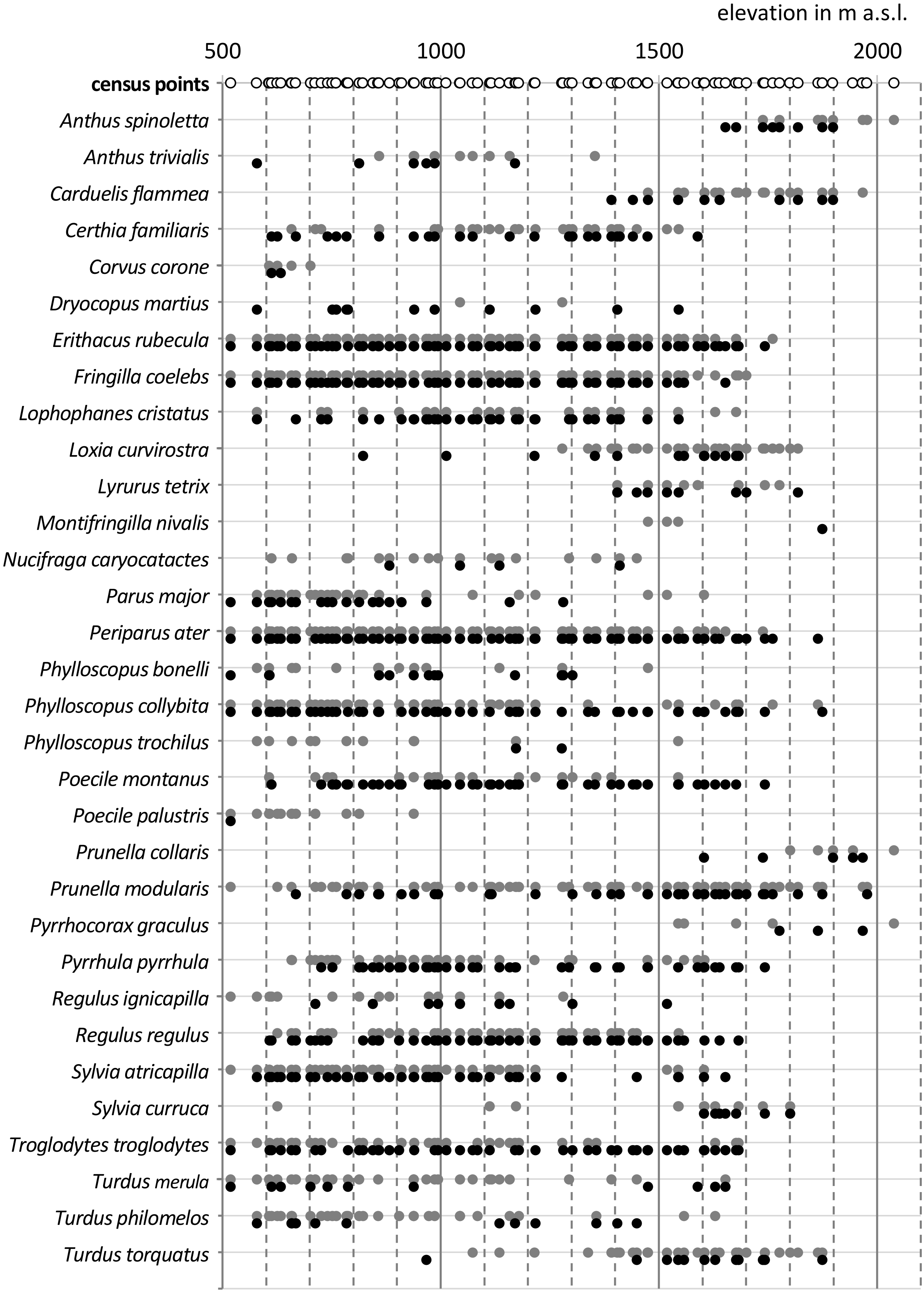


Figure 2: Distribution of species over the elevational gradient for 2006 (grey dots) and 2016 (black dots) on the level of census points; species within r=50 m, minimum number of 5 individuals in one of both survey years.

Species richness 2006 vs. 2016

In 2006, the species richness on the level of census points was more or less constant from the valley floor up to an elevation of about 1200 m and slightly decreased from there until the highest census point at the peak of Tamischbachturm. In contrast, the full trend line reflecting the data from 2016 is more hump-shaped. It has its maximum between 1000 m and 1200 m and shows a decreasing species richness both down to the valley floor and up to the highest elevation. When the survey years are compared, the species richness for points at an elevation of 1100 m or higher seems similar whilst the species richness for lower points appears to be lower in 2016 (Figure 3).

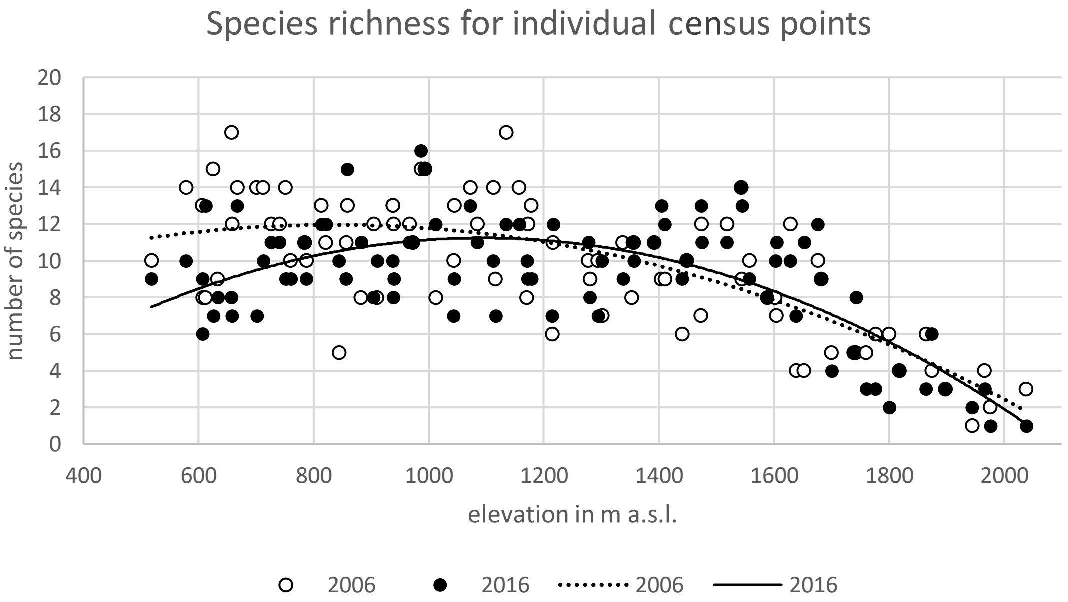


Figure 3: Species richness for the individual census points; number of species plotted against the elevation of the census points; only species within r=50 m considered; trend lines for the relationships between species richness at census points and elevation are provided seperately for both survey years (polynomous, both with R^2>0.51).

The number of species recorded within the 100 m elevation belts is shown in Figure 4. As only two census points were in the lowest belt from 500 to 600 m a.s.l., this belt was not taken into account. One census point is more than 2000 m high. As it is located at the peak of Tamischbachturm and species input from higher elevations can thus be excluded; this census point was added to the elevational belt below. For most of the belts below 1400 m a.s.l., the number of species found in 2016 was notably lower than in 2006. However, the number of species for most elevational belts above 1400 m was slightly higher in 2016.

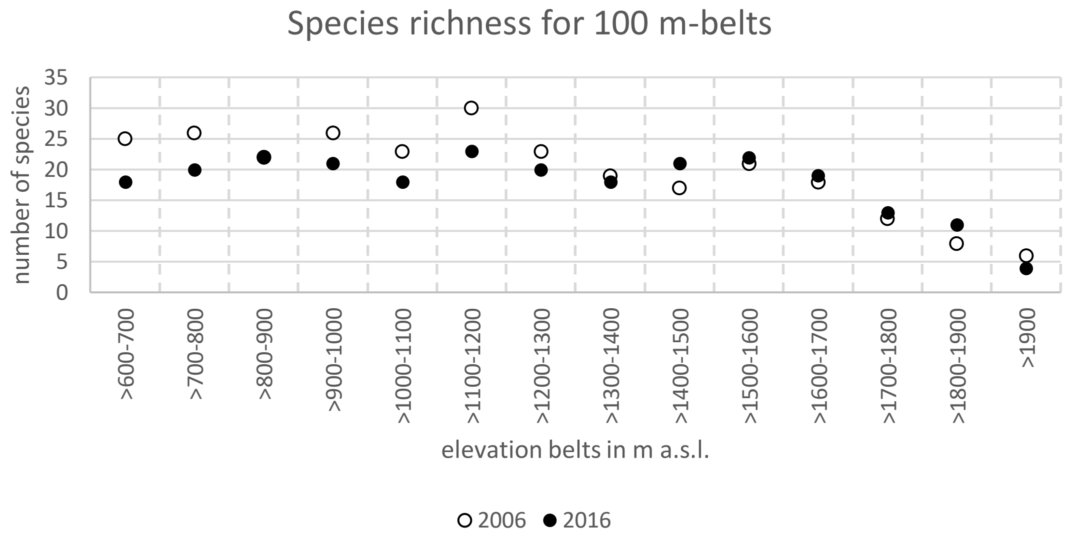


Figure 4: Species richness in 100 m elevational belts; the lowest belt (500-600 m) is not shown in the graph; only species within r=50 m considered.

Differences in species richness

The differences in the number of recorded species per census point between both survey years were significantly correlated with elevation (Spearman's rank correlation: r_s=0.2848, p=0.0075), indicating a decreasing species richness towards lower elevations and an increasing species richness towards higher elevations within the 10 years. This is particularly obvious from the valley floor till the timberline (compare Figure 5).

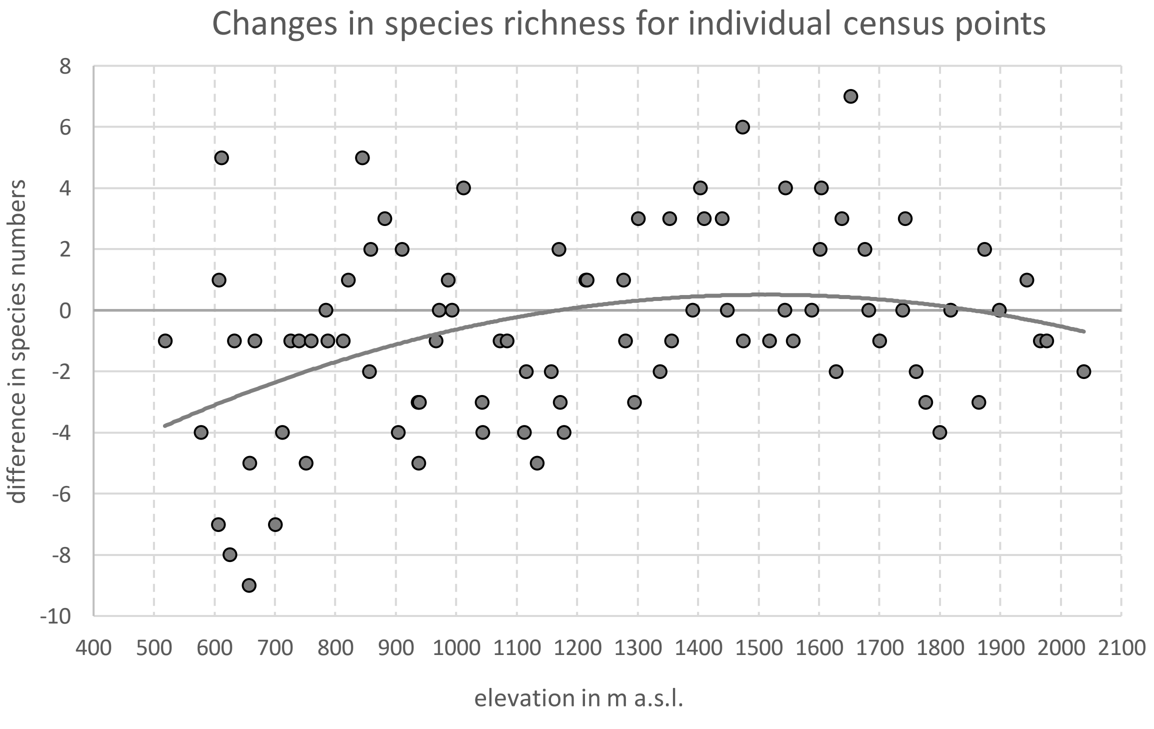


Figure 5: Changes in species richness 2006 vs. 2016 on the level of species numbers per census point; negative values denote a decrease of species found in 2016, positive values denote an increase of species.

Also for the species numbers of the 100 m elevation belts, the calculated Spearman's rank correlation indicates a positive correlation between differences in species richness and elevation (r_s=0.7013, p=0.0052). For the same reasons as before, the lowest belt from 500 to 600 m was not considered. The highest census point at the peak of Tamischbachturm, which is located over 2000 m, was integrated into the belt below (>1900 m). The remaining 14 elevational 100 m belts are shown in the graph below (Figure 6). Negative numbers on the y-axis represent a lower number of species in 2016 than in 2006, while positive numbers represent a higher one. Zero stands for an equal number of species in both survey years. The trend line for this graph is nearly linear. It indicates a decline in species richness in lower elevations until approximately 1550 m and a slight increase in species richness above.

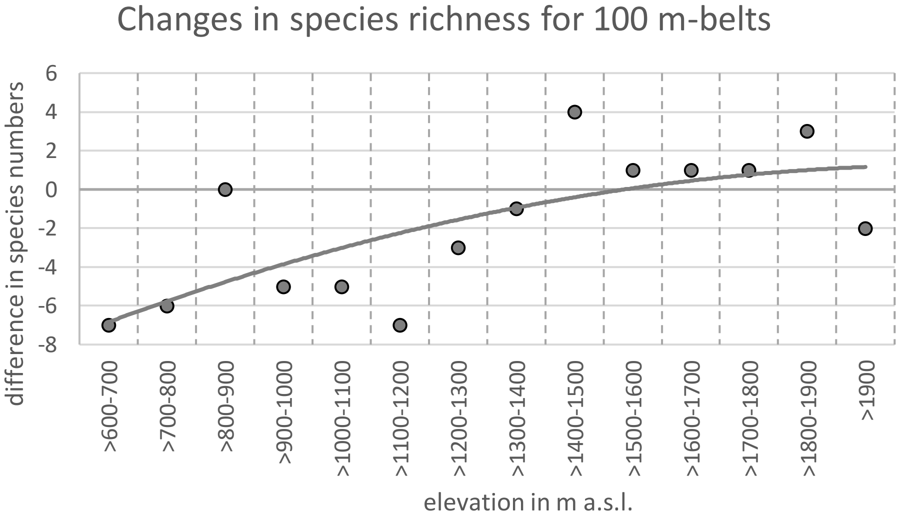


Figure 6: Changes in species richness for 100 m elevational belts 2006 vs. 2016; negative values denote a decrease of species in 2016, positive values denote an increase of species.

Shifts of elevational niches of (common) species

Based on the elevation of the census points where the species were found, the mean lower limit, upper limit, midpoint and width of the elevational niches were calculated for each survey year. Only species that occurred at a minimum of five census points were taken into account to ensure a good record of their niches, which was the case for 26 species. To test for shifts in the elevational niches, pairwise t tests were made for each of the four variables in the data of 2006 and 2016. Differences in none of the four niche parameters achieved a level of significance (Table 1).

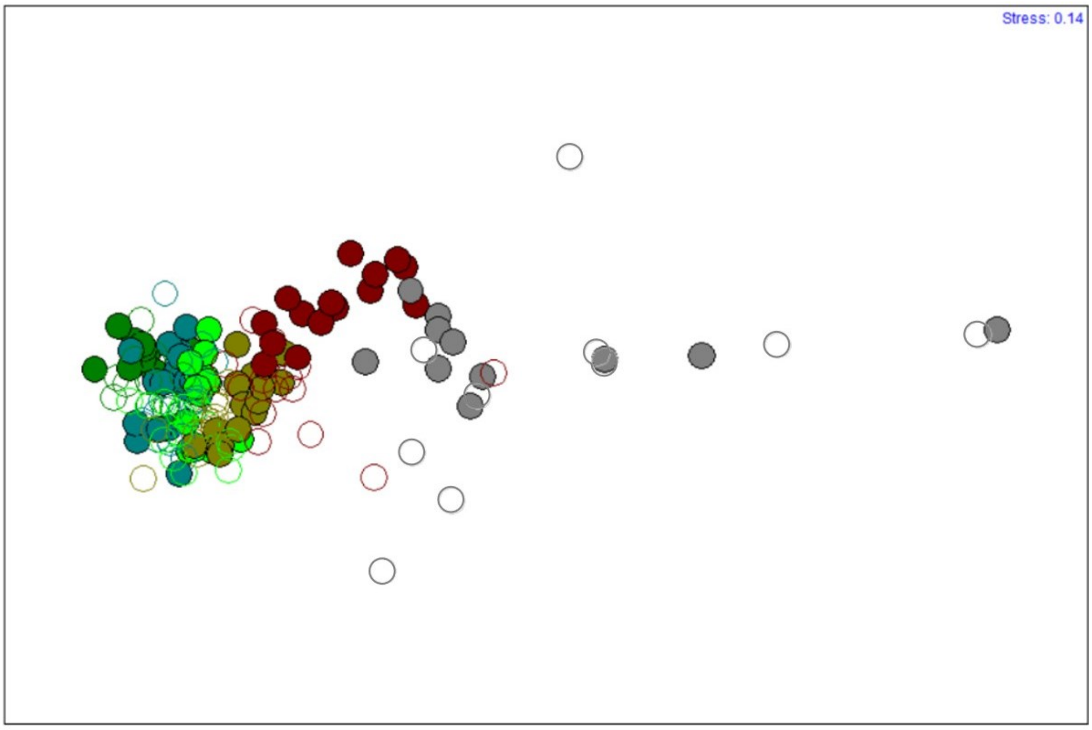
Table 1: Pairwise t tests for elevational niches 2006 vs. 2016.

Elevational niche parameter	**Mean (± SD)**		**Results of pairwise t tests**	
	2006	**2016**	***t***	***p***
lower limit of elevational range	794.5 (± 408.9)	800.0 (± 394.0)	-0.114	0.9101
upper limit of elevational range	1708.0 (± 183.1)	1677.5 (± 217.8)	1.272	0.2156
midpoint of elevational range	1251.2 (± 269.6)	1238.7 (± 267.7)	0.420	0.6781
width of elevational range	913.5 (± 333.5)	877.5 (± 344.6)	0.745	0.4637

Changes in species assemblages

To measure the differences in species assemblages between the census points and the two survey years, Bray-Curtis similarities were calculated for each census point and year. All census points with at least four recorded species in each of the two survey years were considered. The Bray-Curtis similarities are shown in the NMDS ordination plots below (Figures 7a and 7b). The census points were divided in 250 m belts to allow a better overview.

7 a)



7 b)

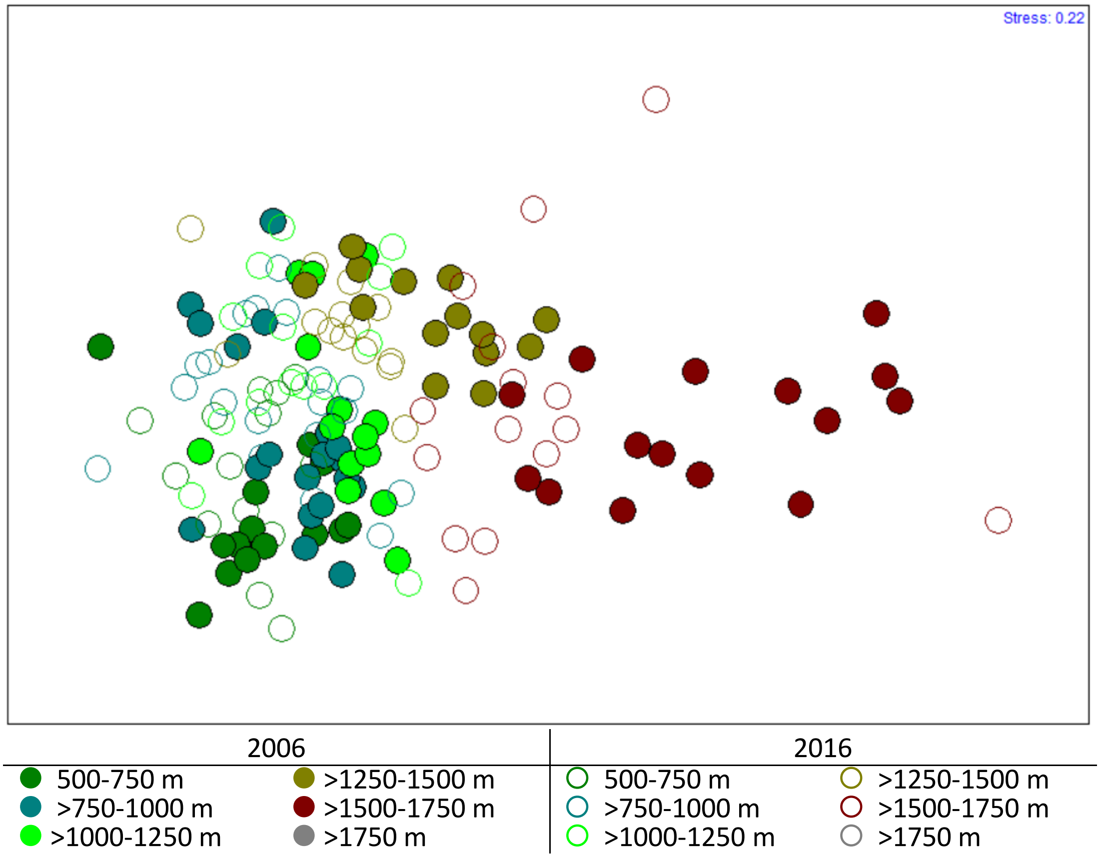


Figure 7a and 7b: Bray-Curtis similarities shown in NMDS ordination for all census points with a minimum of four individuals in both survey years; census points were divided in 250 m belts; data from 2006 marked as filled circles, data from 2016 marked as open circles. a) census points of the whole elevational gradient; stress value=0,14 b) census points up to an elevation of 1750 m for better resolution of the distance between the census points below the timberline; stress value=0,22

The Bray-Curtis similarities for each census point between the two survey years and the elevation of the points are shown in the scatter plot below (Figure 8). All census points with recordings in both years were taken into account. The Spearman's rank correlation was calculated and indicates a significant decreasing similarity of species assemblages between both survey years with increasing elevation (r_s=-0.292; p= 0.0086).

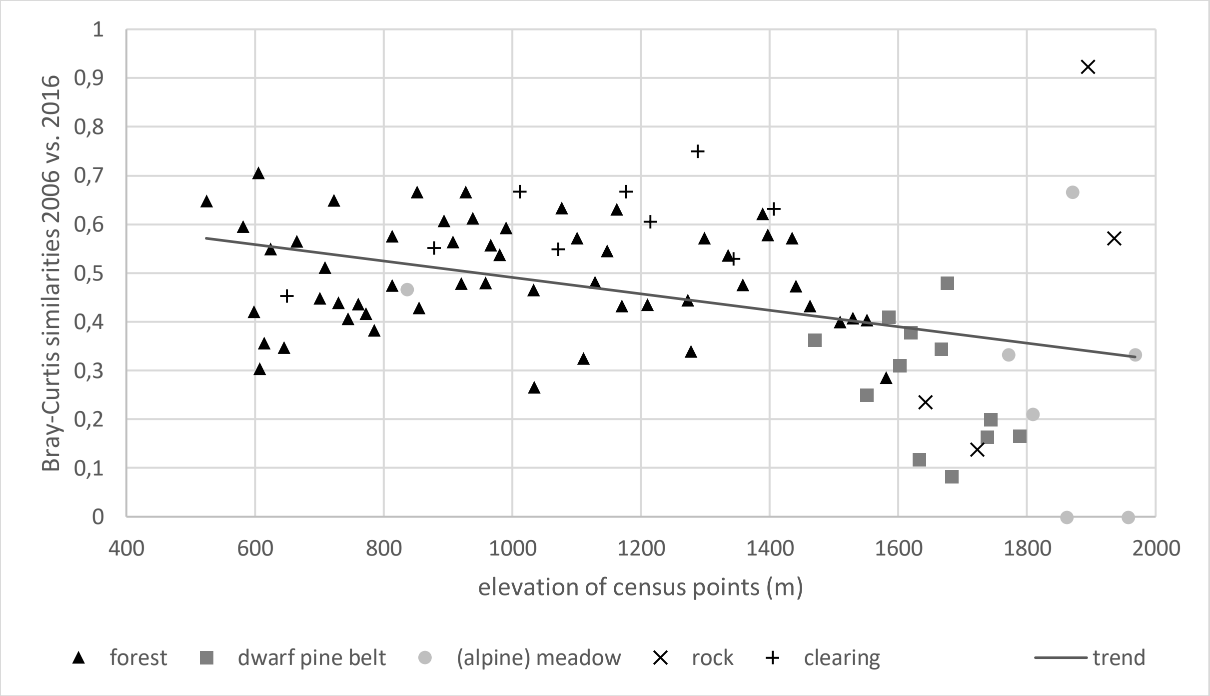


Figure 8: Relationship between changes of species composition (quantified as Bray-Curtis similarities) at census points between 2006 and 2016 and elevation; all species within r=50 m considered; affiliation of census points to different vegetation types indicated by different symbols.

Discussion

Species distribution along the elevational gradient

While this study recorded a general increase or decrease of some species, for some other species an upward shift of their elevational ranges was found. The only species with high numbers of individuals that occurred only in 2016 but not in 2006 was *Carduelis spinus*. As this species shows a strong breeding nomadism in correlation to the maturation of spruce seeds, the big difference between 2006 and 2016 can be identified as an annual variation and does most likely not represent a general trend over the ten years' time span (Schmidt et al. 2014: 176). For the taxon *Turdus* sp. there is a notable decrease of recordings for all species, yet the reasons for this remain unclear for now. There were no indications of an adverse development of the habitat structure and bird monitoring data from neighbouring regions did not show a negative trend of the populations (Teufelbauer et al. 2017). However, there is no such overall trend for other taxa common in the study area such as *Paridae* or *Phylloscopus* sp., of which both contain species with increased, decreased and stable recordings along the elevational gradient. This indicates that changes are visible – even at a short look – but they mainly occur on the species level and not on the level of higher taxa.

Changes in species richness along the elevational gradient between 2006 and 2016

As described by Klosius (2008), the species richness for 2006 shows a plateau from the valley floor up to an elevation of 1200 m and is then decreasing towards the mountain tops. In contrast, the trend line for 2016 is more hump-shaped with a maximum of species richness between 1000 and 1200 m. The species richness in 2016 is slightly higher between an elevation of 1200 and 1800 m which could reflect an upward shift of the elevational zone with the major species richness. There seems to be a loss of species richness for elevations below 1100 m in 2016 which was unexpected, as species of lower altitudes should benefit from warming climate and respond with an extended elevational niche and positive population trends (Flousek et al. 2015; Saracco et al. 2019). The two different patterns of species distribution, low-plateau and low-plateau with a mid-elevation peak, are both described as common patterns in species richness distribution along the elevational gradient (McCain 2009). Though, the reasons for a change of the observed pattern within the same survey area are yet unclear.

Potentially, methodological problems could contribute to the recorded differences to a certain extent. Lehikoinen (2013) observed advanced breeding and migrating dates due to the warming climate and illustrated that the detectability of one third of all species was highly dependent on their phenology. In mountain habitats, where the phenology also depends on the elevation as breeding starts earlier at a lower elevation, effects of species detectability (mainly singing males) could culminate over the elevational gradient and the three visits of the transects. In this case, species richness estimates would be too low in lower elevations due to earlier breeding and maybe too high in mid elevations due to a second singing period when data from 2016 are compared to 2006. However, changes in overall diversity patterns are unlikely to occur simply due to sampling (McCain 2009) and therefore other reasons are probably more influential.

Another factor that has confirmed influence on the distribution of species is the amount of precipitation (Albright et al. 2010; McCain 2009). McCain (2009) showed, that the different patterns of bird diversity along an elevational gradient correlated with the humidity of the observed mountain ranges. While humid regions displayed most diversity at low elevations, arid mountain ranges showed a maximum diversity at medium elevations (McCain 2009). Saracco et al. (2019) have shown, that bird species' breeding dates respond to snowfall as well as to spring temperatures. In 2006, there was lots of snow in the previous winter season which may have delayed the upwards movement of birds within the breeding season. This could cause more species to stay at lower elevations as the higher regions were not yet available for nesting due to the snowpack lasting late in season, while in 2016 the spring was warmer with good weather conditions for most of April and May. This observation could reflect a general trend, as spring temperatures become warmer due to climate change (Saracco et al. 2019; Flousek et al. 2015; Reif & Flousek 2012), but it could also reflect an annual variation in precipitation to some extent.

The changes in species richness between 2006 and 2016 vary strongly between the census points, although there is a general trend observable. The trend line shows a decrease in species numbers at lower elevations and a small increase of species between 1200 m and 1850 m. The changes for 100 m elevational belts across the elevational gradient draw a similar picture, but decreased species numbers here reach up to an elevation of 1400 m with again slightly decreased richness in the highest elevational belt. The increased species richness in higher elevations above 1200 and 1400 m a.s.l., respectively, could be caused by species of medium elevations moving upwards.

The assumptions made in *hypothesis 1* are therefore not fully supported by our data. In fact, there is an increase of species richness in medium to high elevations with a deferred decrease in species richness toward the mountain tops. This is probably due to an upward shift of species of lower elevations adding themselves to the avifauna of higher elevations above 1400 m which supports our hypothesis. However, there is a loss of species richness in lower elevations which was not expected. The simplistic explanation that low-altitude species, usually breeding at warmer climate, benefit from global warming is therefore not sustainable. The breeding season of bird species is not only dependent on temperature but also on the availability of food resources. There is evidence that warming climate has led to an earlier and faster development of caterpillars, which advanced the peak of available food for bird species which use them as a main food resource. This can cause mistiming between the date of hatching and the peak in food resources as proven for the great tit (Visser et al. 2006). Many bird species have reacted to the changes in food availability and advanced their breeding season, which resulted in expanded breeding seasons for some species, while other species do not benefit from warmer climate and even show shortened breeding seasons (Møller et al. 2010). This is mainly dependent on the number of clutches per year. Breeding season seems to extend for species with more broods, while single-brooded species have shortened breeding seasons (Møller et al. 2010). The number of clutches per season can also differ between populations of the same species and between years. Visser et al. (2003) has proven a decrease in second broods for great and blue tit for European populations, which also results in shortened breeding seasons and presumably in a lower reproductive success. The implications of these observed changes in phenology are not yet clear, but they will probably have an effect on the dynamics of populations and they will affect species' reproductive success differently due to its phenological plasticity and adaptive capacity (Møller et al. 2008). It is likely that those mechanisms affect different elevations unequally due to different temperatures and could therefore cause a decrease in species richness in lower elevations because of mistimed broods and fewer second clutches. Trophic mismatching impairs long-distance migratory birds most as they cannot react to local temperatures at their breeding grounds easily which leads to declining populations (Both et al. 2010; Møller et al. 2008; Flousek et al. 2015). This could be reflected by declines of *Anthus trivialis* and *Phylloscopus trochilus* in our data.

Another observed effect of warming climate is the homogenization of species assemblages. This is reflected by an increase of a few generalist species at the expense of many specialist species leading to a more similar fauna over different habitats. This was described for the avian fauna of the UK (Davey et al. 2012) and of the Czech Republic (Reif et al. 2013). Davey et al. (2012) have also shown that homogenization is linked to an increase of species richness in short-term but to a decrease in long-term, which could reflect our findings in species richness distribution along the elevational gradient if it is linked to different grades of homogenization.

Thus, we can conclude that the observed change in the pattern of species richness along the elevational gradient is probably caused by a range of factors. These include effects of climate change on various levels affecting species' breeding seasons such as the extent of snowpack, spring temperatures and availability of food.

Changes in species' elevational niches between 2006 and 2016

Paired t tests for the 26 most common bird species did not show any significant change in the species' elevational niches. An effect is neither visible on the midpoint and width of elevational niches, nor on their lower and upper boundaries. The assumptions made in *hypothesis 2* are thus not applicable on our data, but it is possible that the proposed effects on species' elevational niches may be influential in the future within the study area and the time span of ten years might have been too short to detect such effects. The findings in the distribution of species richness reveal that there are changes, but they are currently seen more on the level of bird assemblages than on the species level.

Changes of bird species assemblages between 2006 and 2016

Our data support *hypothesis 3:* "Changes in species assemblages between 2006 and 2016 are stronger in higher elevations than in lower ones." This seems to be especially true for the census points above 1500 m, which coincides with changes in habitat structure as dwarf pines and alpine meadows become the dominant structural elements for those habitats. Thus, our assumptions that changes will be stronger for elevations around and beyond the timberline, which is situated at about 1550 m a.s.l., are also confirmed. There is no observable effect on census points within small clearing sites, which were made to enhance a renaturation of tree species inventory. Additionally, the compared Bray-Curtis similarities between all census points and years revealed that census points up to an elevation of 1750 m are more similar to each other in 2016 than in 2006. This indicates a homogenization of species assemblages towards more generalist and lesser specialist bird species (cf. Davey et al. 2012; Reif et al. 2013).

Conclusions

Unlike other studies on birds conducted within the National Park Gesäuse which focused on single bird species (e.g. Wirtitsch 2016, Grünschachner-Berger & Sittenthaler 2016, Promberger 2012), the study at hand follows a community ecology approach. Hence, the changes in overall species diversity patterns and in the composition of bird species assemblages are the primary focus. The statistical analysis did not show a significant upward shift on the level of species, but changes towards more species richness in higher elevations were visible on the level of the bird community. This observation is consistent with the differences in bird species assemblages, whose composition changed most around and above the timberline. These findings stress once more the importance of ecotones for the distribution of species and emphasize that effects of climate change will probably be more severe at higher elevations as spring temperatures are rising more rapidly with elevation (Flousek et al. 2015; Chen et al. 2011). The loss in species richness in lower elevations was unexpected as species living in low to mid elevations were thought to profit from climate change (Saracco et al. 2019; Flousek et al. 2015), especially because human disturbances, which are often higher in lower elevations (McCain 2009), can be excluded as the survey area is under protection. This observation provides an informative basis for future studies conducted within the National Park to detect the mechanisms causing these bird diversity patterns below the timberline. Additionally, our analysis revealed a trend towards more homogenous bird species assemblages along the elevational gradient up to an elevation of 1750 m. This indicates that homogenization of bird species assemblages, as it was observed for other regions in Europe (Reif et al. 2013; Davey et al. 2012), is also taking place in the National Park Gesäuse.

Literature

Albright TP, Pidgeon AM, Rittenhouse CD, Clayton MK, Flather CH, Culbert PD, Wardlow BD, Radeloff VC (2010) Effects of drought on avian community structure. Global Change Biology 16:2158–2170.

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B 277:1259–1266

Carli A, Kreiner D (2009) Waldinventur Nationalpark Gesäuse 2006-2009. Im Auftrag der Nationalpark Gesäuse GmbH. 126pp (available on https://www.nationalpark.co.at/de/forschung/veroeffentlichungen)

Chamberlain D, Brambilla M, Caprio E, Pedrini P, Rolando A (2016) Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions. Oecologia 181:1139–1150

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143

Clarke KR, Gorley RN (2001) Primer v5: user manual/tutorial. Primer-E, Plymouth, UK.

Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A (2012) Rise of the generalists: evidence for climate driven homogenization in avian communities. Global Ecology and Biogeography 21:568–578

Flousek J, Telenský T, Hanzelka J, Reif J (2015) Population Trends of Central European Montane Birds Provide Evidence for Adverse Impacts of Climate Change on High-Altitude Species. PLoS ONE 10(10): e0139465

Gillings S, Balmer DE, Fuller RJ (2015) Directionality of recent bird distribution shifts and climate change in Great Britain. Global Change Biology 21:2155-2168.

Grünschachner-Berger V, Sittenthaler M (2016) Genetisches Bestandesmonitoring von Auerhühnern am Gscheidegg 2016. Weng im Gesäuse. 23 pp

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 9pp

IBM Corp. (Released 2017) IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp.

Kim J-Y, Seo C, Hong S, Lee S, Eo SH (2018) Altitudinal patterns in breeding bird species richness and density in relation to climate, habitat heterogeneity, and migration influence in a temperate montane forest (South Korea). PeerJ 6:e4857

Klosius H (2008) Species richness and composition of bird assemblages along an elevational gradient in the Eastern Alps (National Park Gesäuse, Austria). Diplomarbeit, Universität Wien.

Lehikoinen A (2013) Climate change, phenology and species detectability in a monitoring scheme. The Society of Population Ecology 55:315–323

McCain CM (2009) Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346-360

Møller AP, Flensted-Jensen E, Klarborg K, Mardal W, Nielsen JT (2010) Climate change affects the duration of the reproductive season in birds. Journal of Animal Ecology 79 (4):777-784

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. PNAS 105 (42):16195–16200

Nationalpark Gesäuse (2019) Geologie des Gesäuses. https://www.nationalpark.co.at/de/naturraum/52-naturraum/1745-zur-geologie-und-geomorphologie-des-gesäuses. Last access: 22 October 2019.

Promberger M (2012) The conservation status of capercaillie and black grouse in the South-eastern Alps: an assessment on the level of hunting districts. Masterarbeit, Universität Wien. 25 pp

Reif J & Flousek J (2012) The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. Oikos 121: 1053–1060.

Reif J, Prylová K, Šizling AL, Vermouzek Z, Štastný K, Bejček V (2013) Changes in bird community composition in the Czech Republic from 1982 to 2004: increasing biotic homogenization, impacts of warming climate, but no trend in species richness. Journal of Ornithology 154:359–370

Remich B (2001) Geomorphologische Grundlagenerhebung und Bewertung im Projektgebiet Nationalpark Gesäuse. Diplomarbeit, Karl-Franzens-Universität Graz. 83pp

Roché JC (2000) Die Vogelstimmen Europas auf 4 CDs. Franckh-Kosmos Verlag. Stuttgart.

Saracco JF, Siegel RB, Helton L, Stock SL, DeSante DF (2019) Phenology and productivity in a montane bird assemblage: Trends and responses to elevation and climate variation. Global Change Biology 25:985–996.

Schmidt M, Vogl W, Winkler HC (2014) Grundlagen zur Erforschung des Vogelzuggeschehens in Österreich. Teil I – Allgemeine Ergebnisse und Artauswertungen. Endbericht des Projekts 100103 der Bund/Bundesländer-Kooperation (BBK), Wien. 204 pp.

Stephens PA, Mason, LR, Green RE, Gregory RD, Sauer JR, Alison J ... & Chodkiewicz T (2016) Consistent response of bird populations to climate change on two continents. Science 352(6281):84-87.

Teufelbauer N, Seaman BS, & Dvorak M (2017) Bestandsentwicklungen häufiger österreichischer Brutvögel im Zeitraum 1998-2016 – Ergebnisse des Brutvogel-Monitoring. Egretta 55: 43-76.

Visser EM, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172

Visser ME, Adriaensen F, van Balen JH, Blondel J, Dhondt AA, van Dongen S, du Feu C, Ivankina EV, Kerimov AB, de Laet J, Matthysen E, McCleery R, Orell M, Thomson DL (2003) Variable responses to large-scale climate change in European *Parus* populations. Proceedings of the Royal Society London B 270:367–372

Wirtitsch M (2016) Monitoring ausgewählter Wald-Brutvogelarten im Nationalpark Gesäuse 2016. Kartierung 2015/2016. Im Auftrag der Nationalpark Gesäuse GmbH, Graz. 28 pp

Zimmermann T (2017) Karte der FFH-Lebensraumtypen im Natura-2000-Gebiet Ennstaler Alpen/Gesäuse und Nationalpark Gesäuse. Im Auftrag der Nationalpark Gesäuse GmbH. (unpublished)

Zimmermann T (2018) Waldinventur Nationalpark Gesäuse. Auswertung des 1. Wiederholungsdurchgangs 2016/17. Im Auftrag der Nationalpark Gesäuse GmbH. 211pp (unpublished)

Zimmermann T, Kreiner D (2012) Luftbildbasierte Modellierung der aktuellen Waldvegetation für das Natura-2000-Gebiet Ennstaler Alpen & Nationalpark Gesäuse (Nördliche

Kalkalpen, Steiermark). Mitteilungen des naturwissenschaftlichen Vereines für Steiermark 142:89–106