Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
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The importance of weather for abundant saproxylic beetles- an indication of responses to climate change

Mirta Impric-Juric

Preface

This thesis was written as the completion of my master's education in general ecology at the Department of Ecology and Natural Resource Management (INA), at the Norwegian University of Life Sciences (NMBU) in Ås, Norway.

I would like to express my gratitude to my supervisors, Anne Sverdrup-Thygeson and Tone Birkemoe from NMBU, and Olav Skarpaas from NINA for their availability, communication, ideas and comments throughout the process of structuring and writing of this thesis. They have been very willing to offer their time and expertise, as well a positive outlook.

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Mirta Impric-Juric

Abstract

The effects of climate change are expected to be seen across the globe, as well as impact many different species, including saproxylic beetles. Considering their importance for both biodiversity and as providers of ecosystem services, their potential response to climate change could be crucial for the future health and functioning of their ecosystems. 14 different saproxylic beetle species were examined in two sites in southern Norway, for a period of five different years. Their abundance was analyzed in relation to microhabitat (the hollow of the trunk as opposed to the canopy of the hollow oak), average wind speed, precipitation, mean temperature, humidity and the percentage of days with precipitation. The species were also grouped into different trait-groups based on size, specialization, red list status, geographical distribution, trophic group and whether they are specialized for the hollow, and the group responses were checked against the weather variables. Significant responses were negative for increases in wind speed and percentage of days with precipitation, while the responses for temperature, precipitation and humidity were mixed. The majority of the significant responses were among the generalists and the "least concern" red-list group, while specialists and the threatened and endangered species did not appear particularly vulnerable to these weather effects. The results highlight the need to study the effects of weather on the more common species in order to understand the effects of climate change, as their responses could have great impact on communities and ecosystems.

Contents

1. Introduction

Climate change, the matter of its origin and its possible impacts, has long been the subject of a worldwide debate. The potential effects are varied, including changes in temperature, increases or decreases in precipitation, and influxes of extreme weather events. The most recent Intergovernmental panel on climate change is once again reporting an increase in temperature in both the air and bodies of water, the subsequent thawing of ice and snow, and an increase in greenhouse gasses levels (IPCC, 2013). Temperature is expected to increase throughout Europe, in both the summer and winter periods, and we can also expect to see stronger periods of intense heat (Christensen et al, 2013). Norway is no exception to this and can also be expected to experience various effects of climate change, somewhat varying in different areas of the country. Some of the expected effects include a rise in temperature by 2,3 - 4,6 °C by 2100, an increase in precipitation by 5 – 30 percent for the same period, and potential but currently inconclusive increase in wind speed (Hanssen-Bauer et al, 2009). These changes are expected to have serious impact on multiple species and ecosystems across the globe.

One of the many groups that are expected to be affected by climate change are insects. Due to the fact that they are short-lived organisms and have great variation in habitat type and population numbers, their responses are often good indicators of what is happening to an ecosystem as a consequence of climate change, and that response can be seen quicker than with longer lived organisms (Elias, 1991). An additional importance for the inclusion of insects in climate change research is the fact that this group is expected to suffer large effects from these changes, including abundance changes and habitat shifts (Elias, 1991; Bradshaw & Holzapfel, 2006), as well as changes in the timing of their life cycles.

In addition to their importance to the functioning of an ecosystem, insects are often tied to its elements through the need to follow a similar time schedule (Volney & Fleming, 2000), for example a pollinator's life stages being in sync with the flowering of a plant. Climate change has the ability to potentially disrupt this delicate synchronization, for example by altering the time of flowering due to changes in CO2 levels (Harrington, et al,1999), causing problems in ecosystems where the plants and the insects need to react in a certain time frame, dependent on each other. The impacts climate change has on plants will subsequently also impact the insects that are dependent on those plants, mostly through nutrient fluctuations (Karuppaiah & Sujayanad, 2012).

Climate change could also significantly alter the present distribution of insect species. Temperature changes can impact insects throughout their entire life cycle, influencing larval stages, dispersal, and general survival, with a higher impact being seen on species that have a narrow geographical range (Bale et al, 2002). This can be detrimental to species that are especially sensitive in certain developmental stages, or those that are narrowly specialized and depend on a small geographical area to find nutrients. Climate change is also expected to shift habitat boundaries of some insect species and cause them to make a northward shift, potentially worsening the problem of pests and invasive species (Wilson & Maclean, 2011). All of these effects are expected to have consequences for insect biodiversity across all groups, including saproxylic insects.

1.1. Saproxylic insects

Out of the many different species of insects that can inhabit a forest, a large proportion are saproxylic (Ranius, 2006). Saproxylic insects are dependent on the existence of dead/decaying wood at some part of their life cycle (Stokland et al, 2012). They hold a particular importance in an ecosystem through their role in nutrient exchange and decomposition, making them a vital consideration when discussing conservation of an area (Fayt et al, 2006). There is however still a great need for research to determine the exact contribution and magnitude of these influences (Ulyshen & Wagner, 2013). One of them is the potential increase to the productivity of a forest, mostly through contributing to a faster release of nutrients from wood in the process of decay (Takamura, 2001). Others include reducing the threat of wildfires, reducing pest problems and infestations, and the interactions with and potential higher release of carbon and methane (Ulyshen, 2013).

Saproxylic insects are also an extremely diverse group, a result of their adaptation to a wide range of potential habitat, corresponding to different tree species, various levels of wood decay and the existence of different fungi providing nutrition for the insects (Grove, 2002). Since many saproxylic insects are the most habitat dependent in their larval stage, it is that period that is the limiting factor and as such the most vulnerable to the effects of climate change (Saint-Germain et al, 2006). The abundance and diversity of saproxylic insects tends to be the highest in old-growth forests, especially if it is unmanaged (Siitonen et al, 2001).

1.2. Hollow oaks

The habitat type that is the focus of this study and the home to the selected saproxylic insect species are hollow oaks (*Quercus robur and Quercus petrea).* They form unique environments that are suitable for many different species, and often contain a large spectrum of different lichens, fungi and saproxylic invertebrates, including many that are considered threatened or endangered (Antonsson & Jansson, 2001), as well as some that are ecosystem engineers (Buse et al, 2008). This is partly due to their great age, during which the trunks of the tree develop hollows containing wood mould (Ranius & Jansson, 2002). In addition, the canopy can contain different dead branches (Sverdrup-Thygeson et al, 2010), contributing the the number of different potential microhabitats within a single hollow oak.

The biodiversity residing in the hollow oaks is dependent on many factors, on both spatial and temporal scales (Sverdrup-Thygeson et al, 2014), and requires further research in order to fully determine those impacts. Bark beetles, that are among the early colonizers, are considered to be less vulnerable with better dispersal abilities, while the later colonists that depend on fungi have lesser dispersal abilities and are considered to the the more vulnerable group (Ulyshen & Hanula, 2010). Some species that prefer the hollow oaks as their habitat have shown to be weaker dispersers, and as such more vulnerable, partly due to the long life span of these trees, that provide a temporally stable environment (Hedin et al, 2008).

1.3. Management

The availability and quantity of deadwood is also expected to be influenced by climate change, through changes in growth and decomposition rates, but also depending on the level of management in the area in question (Mazziotta et al, 2013). High levels of forest management increase the vulnerability of already threatened saproxylic insect species (Lachat & Bütler, 2009), creating an additional issue in combination with climate change. The amounts of coarse woody debris (CWD) have already been significantly reduced, which can negatively impact population numbers of various saproxylic species (Siitonen, 2001). In addition to availability, the distance between individual pieces of wood is also an important factor, relating to the potential level of dispersal of each species (Schiegg, 2001), making the highly managed areas even more unfavorable for insects that are not good dispersers. While some effects of climate change might be positive, they need to be taken with some caution, because, as studies on butterflies suggest, the negative impacts of habitat degradation have the ability to outweigh positive effects caused by, for example, increasing temperature (Warren et al, 2001).

The identification of a species at risk is an important factor in the conservation of biodiversity. Risk identification is crucial for management considerations and could enable the establishment of necessary preventive measures. These measures could potentially prevent some of the negative effects before climate change becomes too severe and the species populations are so low that they can no longer recover (Thomas et al, 2004).

1.4. Weather effects

When discussing climate change, it is important to differentiate between the notions of "climate" and "weather". While both could consist of similar or even same parameters, weather refers to conditions (temperature, precipitation, humidity, etc.) during a short period of time, while climate refers to those conditions during a longer time interval. We can, however, observe responses to weather effects in order to determine possible responses to climate change, as they are likely to reflect one another. Considering that this type of research on saproxylic insects is scarce, studies conducted on other insect species can be taken into consideration and used to provide some guidelines.

Studies on butterflies show a positive relationship between abundance and higher summer temperatures, especially when combined with lower amounts of precipitation (Pollard, 1988;

Roy et al, 2001). The predictions of increased abundance connected to increased temperature are not only existent for common species, but are also expected to be visible through higher numbers in indicator species (Lachat et al, 2012), those reflecting certain specific environmental conditions. Studies regarding climate change conducted on different types on insects, such as butterflies, show that an increase in temperature can also have a great positive effect on the species distribution and habitat range, allowing them to move into and utilize areas that were unsuitable for them in the past (Thomas et al, 2001). There is a possibility that an increase in temperature might also prove beneficial for some saproxylic species and as such can serve as a form of compensation for increasingly lower amounts of available dead and decaying wood (Müller at al, 2014), adding an additional component to the importance of research on saproxylic insects and how they respond to weather changes. Overall, higher temperatures are expected to have a positive effect on insect population numbers, through faster development rates and higher survival levels (Jamieson et al, 2012).

There is little research on the potential effects of precipitation, but it can to an extent be considered as a factor that can increase mortality (Bale et al, 2002), with a possible stronger negative impact on specialized species (Leckey et al, 2014). A study conducted on cereal aphids showed a higher abundance with increased temperatures, and a negative effect connected to precipitation, humidity and wind speed (Klueken et al, 2009).

While the possible effects of wind and wind speed on saproxylic insects are still not thoroughly researched, studies on the effects of windthrow suggest that this disturbance could be beneficial by providing decaying wood in the gaps it creates (Bouget, 2005; Bouget et al, 2004), and thus increasing the abundance of saproxylic species (Wermelinger et al, 2002). The impact of wind speed on abundance remains questioned and as such is difficult to predict. The range of responses can potentially vary from being detrimental, to facilitating flying.

The vulnerability of saproxylic insects, as well as their importance in the functioning of an ecosystem, highlight the need for further research, especially in the wake of climate change. How they might respond to the changes in temperature, precipitation and other factors, might be crucial to pinpoint the most vulnerable species and take the necessary measures to preserve ecosystems and their biodiversity.

1.5. Research objectives

The main objective of this thesis is to analyze potential relationships between different environmental parameters that are expected to change due to the climate changes, and different saproxylic species and their traits. Looking at how the abundance of species corresponds to changes in weather parameters, it might be possible to pinpoint certain key traits that are relevant for the saproxylic species' response, such as specialization, size, etc. The abundances of several of the most common species at the sites are analyzed in order to look for possible patterns that can be linked to traits of those species.

At the moment, studies on the effects of climate change on saproxylic insects are largely lacking, so it is difficult to draw direct comparisons, or even form firm predictions based on this particular insect group. In addition, the trait status of many species in this group is also uncertain, making it difficult to analyze the whole group in this way, or even a large group of saproxylic insects. That is why the tests in this thesis were conducted on the most abundant individual species, subsequently looking at possible patterns based on their traits.

These potential relationships can identify how certain species respond when faced with a change in an environmental parameter, and what that response would mean in the face of climate change and the future of the species. The results could potentially help to identify which species of saproxylic insects would be at a greater risk in the upcoming years and the changes that they are expected to bring, as well as identify which species could potentially benefit from those changes. This could prove beneficial to determining the climate change risk for other species who may not have been specifically studied, but share those same traits.

I expect that temperature will have a positive impact on species abundance, while wind speed and precipitation will be negative. I also expect specialist species to be more vulnerable to weather effects than the generalists, as well as endangered species showing a stronger response than the species of least concern. Widespread species should show the least response to the weather variables, while northern and southern species should respond more strongly, especially to temperature, with the northern species responding negatively and the southern positively. I also expect the species with a smaller body size to be more affected than the larger species, especially to precipitation.

The main research questions are:

1. How do wind speed, precipitation, temperature and humidity effect species' abundance in oak-associated beetles?
2. Can those effects be linked to certain traits of the species?

2. Methods

The data used in this study originally comes from the ARKO project conducted by the Norwegian Institute for Nature Research (NINA, 2015; Sverdrup-Thygeson et al, 2011). The project was designed to look at the importance of hollow oaks for beetle conservation, with the potential differences in different landscapes, and hollow oaks as hotspot habitats. The study was conducted in multiple sites across southern Norway, over several years. with varying numbers of standing hollow oak trees in each of thee sites. For an oak to be considered a hollow oak, it needs to have a diameter of 30 cm or over at breast height (DBH), a hollow that is larger than its opening, with an opening larger than 3 cm (Sverdrup-Thygeson et al, 2009). Sampling at the sites was conducted using window traps, with one trap being placed next to the hollow of the oak tree, and the other was hanged in the canopy of the tree. The traps were emptied three times each year, in the time period between May and August in the years 2005, 2007, 2008, 2009 and 2011 (Sverdrup-Thygeson et al, 2010). The original scope of the data covered 879 species, out of which 113 are redlisted (Kålås et al, 2010), over the 10 different sites. A subset of the 14 most abundant species is used for this thesis, with the details on the species and their selection explained in chapter 2.3.

2.1. Study design

For the purpose of this study and due to the nature of weather and climate trends, two sites with more long-term data were chosen, covering five separate years of collection, 2005, 2007, 2008, 2009 and 2011. These two sites were chosen based on the fact that they both provide data for the longest period of time (five years) and that the years covered are the same for both, which is not the case for all available sites in the scope of the original data. The two sites are also in relatively close proximity to each other and as such share environmental conditions so their data can be combined.

2.2. Study areas and insect sampling

The sites Budalsåsen (municipality: Larvik, county: Vestfold, UTM32 X: 558866, UTM32 Y: 6556109) and Brenndalsskarven (municipality: Siljan, county: Telemark, UTM32 X: 548999, UTM32 Y: 6567043) were chosen as the study areas for this thesis (Figure 1). The two sites contained five oaks in each site (Table 1), with one window trap hanging in front of the opening (hollow) of the oak and one trap in the canopy (Sverdrup-Thygeson et al, 2011). Window traps can yield different compositions of species depending on their placement, as they will reflect the surroundings of the trap (Sverdrup-Thygeson & Birkemoe, 2009). To address this, and to look at possible differences between the two trap placements and their surroundings (microhabitats), a "microhabitat" variable was included in the analysis.

Table 1: Locations of the hollow oaks used in this thesis, sampled for beetles by Anne Sverdrup-Thygeson (Sverdrup-Thygeson et al, 2009)

Tree ID	Name	UTM32 X	UTM32 Y	Municipality
BR1	Brenndalsskarven1	548978	6567046	Siljan
BR2	Brenndalsskarven2	548976	6567020	Siljan
BR3	Brenndalsskarven3	549006	6567020	Siljan
BR4	Brenndalsskarven4	549087	6567027	Siljan
BR5	Brenndalsskarven5	548950	6567101	Siljan
BU1	Budalsås1	558931	6556059	Larvik
BU2	Budalsås2	558951	6556047	Larvik
BU3	Budalsås3	558892	6556162	Larvik
BU4	Budalsås4	558779	6556111	Larvik
BU5	Budalsås 5	558779	6556166	Larvik

Figure 1: Locations of the study sites: Brenndalsskarven (UTM32 X: 548999, UTM32 Y: 6567043) and Budalsåsen (UTM32 X: 558866, UTM32 Y: 6556109) in southern Norway

2.3. Species selection and traits

My sample population consists of 14 saproxylic beetle species (Table 2, Figure 2) chosen based on their abundance from the larger data set. Species with more than 3 occurrences from the two sites were selected in order to avoid accidental presence. Species were then further selected based on their level of oak association and whether the species is saproxylic (oak associated and saproxylic species were selected). The 14 most numerous oak associated species were included in the sample population in order to enable the smoothest modeling of the weather effects.

Table 2: Total abundance of each species for the five years of collection (2005, 2007, 2008, 2009 and 2011): number of individuals caught in front of the hollow, the number of individuals caught in the canopy and the total number of individuals caught

Species	Hollow	Canopy	Total
Haploglossa villosula	908	95	1003
Enicmus rugosus	206	102	308
Dorcatoma chrysomelina	160	59	219
Dasytes niger	88	108	196
Euglenes oculatus	41	116	157
Xyleborinus saxesenii	78	58	136
Ptinus subpillosus	122	15	137
Dasytes plumbeus	12	111	123
Ampedus balteatus	88	30	118
Cryptophagus scanicus	55	19	74
Euplectus karstenii	73	16	89
Mycetochara maura	59	16	75
Dorcatoma flavicornis	60	10	70
Haploglossa gentilis	55	6	61
Total individuals	2005	761	2766

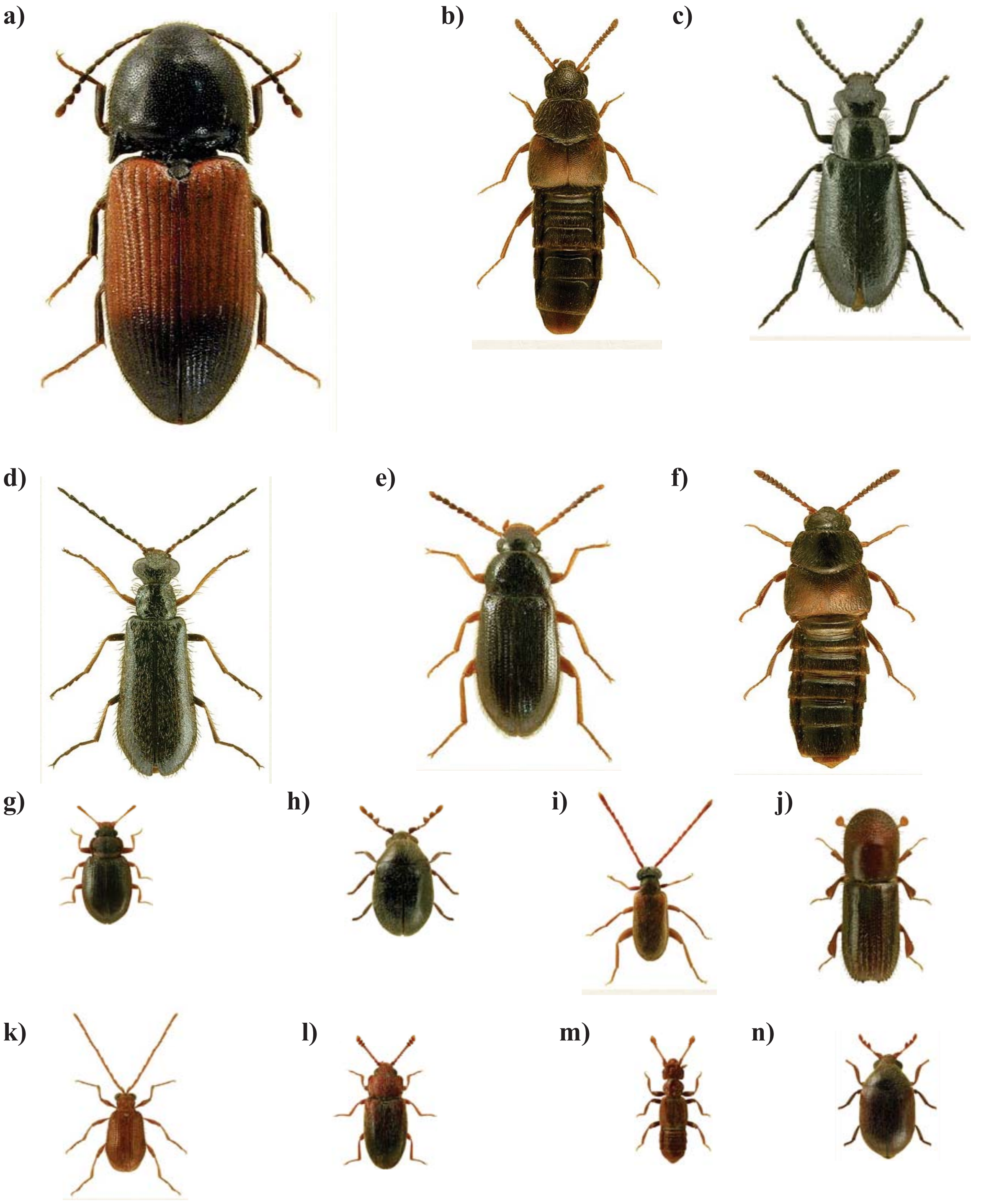


Figure 2: Images of the 14 species: a) *Ampedus balteatus*, b) *Haploglossa villosula*, c) *Dasytes niger*, d) *Dasytes plumbeus*, e) *Mycetochara maura*, f) *Haploglossa gentilis*, g) *Enicmus rugosus*, h) *Dorcatoma chrysomelina*, i) *Euglenes oculatus*, j) *Xyleborinus saxesenii*, k) *Ptinus subpillosus*, l) *Cryptophagus scanicus*, m) *Euplectus karstenii*, n) *Dorcatoma flavicornis*. (Copyright: Borowiec, 2015 (permission for use granted)**)**

Table 3: Information on the 14 species that form the sample population, including trait groups that will be examined in the discussion: size, specialization, distribution, red list status, trophic group and hollow specialization (Kålås et al, 2010; Pilskog et al, 2015; Ranius & Jansson, 2000; Saproxylic Database; Coleoptera Poloniae Database)

Species name and author	Family	Size	Specialization	Distribution	Red list status	Trophic group	Hollow specialization
Euglenes oculatus (Paykull, 1798)	Aderidae	2.3-3 mm (small)	Specialist	Northern	NT	Xylomycetophage	Hollows or nests
Cryptophagus scanicus (Linnaeus, 1758)	Cryptophagidae	1.8-2.8 mm (small)	Generalist	Northern	LC	Fungivore	Other parts of the tree
Xyleborinus saxesenii (Ratzeburg, 1837)	Curculionidae	2-2.4 mm (small)	Generalist	Widespread	LC	Xylomycetophage	Other parts of the tree
Dasytes niger (Linnaeus, 1760)	Dasytidae	3.5-4.5 mm (medium)	Generalist	Widespread	LC	Predator	Other parts of the tree
Dasytes plumbeus (Müller, 1776)		?-4.6 mm (medium)	Generalist	Southern	LC	Predator	Other parts of the tree
Ampedus balteatus (Linnaeus, 1758)	Elateridae	7.5-10 mm (large)	Generalist	Northern	LC	Xylophage	Other parts of the tree
Enicmus rugosus (Herbst, 1793)	Latridiidae	1.2-1.8 mm (small)	Generalist	Widespread	LC	Fungivore	Other parts of the tree
Dorcatoma chrysomelina (Sturm, 1837)	Ptinidae	1.7-2.5 mm (small)	Specialist	Northern	LC	Xylomycetophage	Other parts of the tree
Ptinus subpillosus (Sturm, 1837)		2-2.8 mm (small)	Specialist	Southern	LC	Detrivore	Hollow only, no nest
Dorcatoma flavicornis (Fabricius, 1792)		1.5-2.4 mm (small)	Specialist	Northern	EN	Xylomycetophage	Other parts of the tree
Haploglossa villosula (Stephens, 1832)	Staphylinidae	2.5-3.5 mm (medium)	Generalist	Widespread	LC	Predator	Hollows or nests
Euplectus karstenii (Reichenbach, 1816)		1.1-1.4 mm (small)	Generalist	Northern	LC	Predator	Hollow only, no nest
Haploglossa gentilis (Märkel, 1845)		3-4 mm (medium)	Specialist	Widespread	NT	Predator	Hollows or nests
Mycetochara maura (Fabricius, 1792)	Tenebrionidae	4-6 mm (medium)	Generalist	Southern	NT	Xylomycetophage	Other parts of the tree

The species were subsequently grouped into several trait-related groups (Table 3). The size related group was determined by the available species: one species was significantly larger than the others and was places as the "large" group. The difference between "medium" and "small" was set to 3 mm, as a general border size between the two. *Haploglossa villosula* was the only species that could be considered borderline, ranging from 2.5 to 3.5 mm, and was placed in the medium group. The distribution was separated into three groups: northern (found primarily in northern Europe, north of 50 degrees north), southern (found primarily in southern Europe, south of 47 degrees north)and widespread (widespread species, not primarily northern or southern) (Gough et al, 2015, Coleoptera Poloniae Database, 2015). The trophic groups include predator, xylophage (feeding on wood), xylomycetophage (feeding on wood and fungi), fungivore (feeding on fungi) and detrivore (feeding on detritus) (Pilskog et al, 2015). The hollow specialization was divided into three levels, species associated with "hollows or nests", species associated with "hollow only, no nest" and species associated with "other parts of the tree" (Ranius & Jansson, 2000; Saproxylic Database, 2015), in order to analyze the potential difference between cavity species and others. Other trait groups include specialization (generalist/specialist) (Pilskog et al, 2015) and red list status (divided into a "least concern" group and a vulnerable group of "near threatened and endangered") (Kålås et al, 2010).

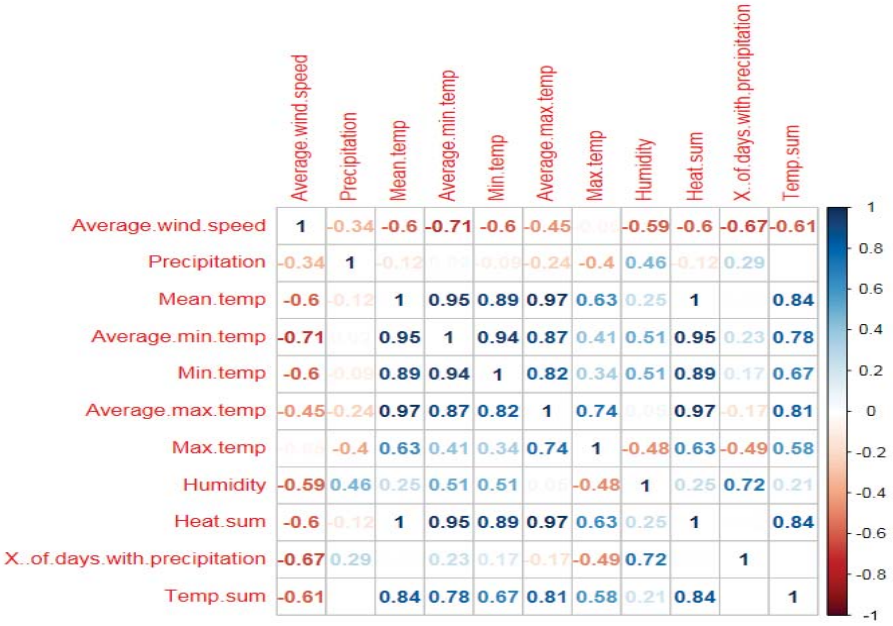
2.4. Weather data

The main environmental parameters that are examined are wind speed, temperature, precipitation, humidity and percentage of days with precipitation. The weather data was gathered from eklima (Table 4), the portal which provides information from the Norwegian Meteorological Institute (eklima, 2014). Since there is no weather data from the exact sites for the years in question, the data was gathered from local weather stations. Information from two weather stations was used, one in Hedrum and one in Skien- Geiteryggen. The two stations were selected based on their proximity to the two sites and the availability of data they provided, with the Hedrum station providing precipitation information and the Skien-Geiteryggen station providing information about temperature (eklima, 2014).

2.5. Statistical methods

All statistical analysis was conducted with the R software, version 3.1.2, using lme4 (Bates, 2010) and lmerTest (addition of p-values) (Kuznetsova et al, 2013) packages. The weather data was checked for correlations using the Pearson correlation coefficient, and the data was analyzed with a generalized linear mixed model (maximum likelihood estimation). The significance levels of the model's results are used as suggested for the model in the R software, and are as follows: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1. Significant values are also marked in bold.

All the weather variables (average wind speed, precipitation, mean temperature, average minimum temperature, minimum temperature, average maximum temperature, maximum temperature, humidity, heat sum, percentage of days with precipitation, temperature sum) were first checked for normality and possible correlation. Results showed a high level of correlation between different temperature variables (Figure 3), so only mean temperature values were used in subsequent models.



	Average.wind.speed	Precipitation	Mean.temp	Average.min.temp	Min.temp	Average.max.temp	Max.temp	Humidity	Heat.sum	X..of.days.with.precipitation	Temp.sum
Average.wind.speed	1	-0.34	-0.6	-0.71	-0.6	-0.45	-0.05	-0.59	-0.6	-0.67	-0.61
Precipitation	-0.34	1	-0.12	0.02	-0.09	-0.24	-0.4	0.46	-0.12	0.29	
Mean.temp	-0.6	-0.12	1	0.95	0.89	0.97	0.63	0.25	1		0.84
Average.min.temp	-0.71	0.02	0.95	1	0.94	0.87	0.41	0.51	0.95	0.23	0.78
Min.temp	-0.6	-0.09	0.89	0.94	1	0.82	0.34	0.51	0.89	0.17	0.67
Average.max.temp	-0.45	-0.24	0.97	0.87	0.82	1	0.74	0.05	0.97	-0.17	0.81
Max.temp	-0.05	-0.4	0.63	0.41	0.34	0.74	1	-0.48	0.63	-0.49	0.58
Humidity	-0.59	0.46	0.25	0.51	0.51	0.05	-0.48	1	0.25	0.72	0.21
Heat.sum	-0.6	-0.12	1	0.95	0.89	0.97	0.63	0.25	1		0.84
X..of.days.with.precipitation	-0.67	0.29		0.23	0.17	-0.17	-0.49	0.72		1	
Temp.sum	-0.61		0.84	0.78	0.67	0.81	0.58	0.21	0.84		1

Figure 3: The correlation matrix of the weather variables

Table 4: Weather variables used in the analysis with the corresponding unit of measure

Weather variable	Description (e-klima)	Unit of measure
Average wind speed	Average wind speed	m/s
Precipitation	Precipitation	mm
Mean temperature	Mean temperature	ºC
Humidity	Mean relative humidity	percent
Percentage of days with precipitation	Percentage of days with precipitation (calculated manually)	percent

During the writing of this thesis and the analysis of data, different statistical analysis were attempted with varying results. Due to the need for trend evaluation and the existence of several explanatory variables, multiple linear regression was the most appropriate. The data was initially used with observations with each individual trap placed at the site and analyzed with a linear model. Due to the nature of the data, containing a large number of observations with a value of 0 and at the same time including several high values, these results were deemed problematic. This was also true when a poisson distribution was included, as well as the quasipoisson distribution. The data was then pooled into two groups for each site, the group that was caught in front of the hollow and the group that was caught in the canopy of the oak. This pooling was not considered problematic since there are multiple trees used in each site, and two different sites are included in the analysis, so a difference between individual traps should not be significant. This data was then analyzed using a generalized linear mixed model with a poisson distribution. The weather variables' data was also standardized by subtracting the mean of the data points and dividing it with the standard deviation.

The final model used for this analysis and the results of which will be used and discussed in this thesis, is a generalized linear mixed model with fixed and random effects. The number of individuals was modeled with microhabitat (hollow/canopy), with average wind speed, precipitation, mean temperature, humidity and percentage of days with precipitation as weather variables, the location name (two possible sites) and the year of collection (five possible years) as the random effects, and period of collection (3 possible periods) as the covariate. Because of the potential importance of trap placement (in front of the hollow of standing oak / in the canopy), an interaction between trap placement (microhabitat) and the weather variables was also included in the model. While it is possible that this model might not be the best model to analyze the data, it is the most comprehensive one that provides the best overview over all possible responses and relationships between the variables, as well as the best method to compare responses between all the different species. The script for the model was as follows: glmer (Abundance of species x ~ Microhabitat * (Average wind speed + Precipitation + Mean temperature + Humidity + Percentage of days with precipitation)+ (1 | Year)+ (1 | LocName) + Period, data = dataset, family = poisson)

3. Results

Multiple species showed a response to microhabitat, the majority of them positive for the hollow microhabitat. The results also show that the responses to the weather variables differ greatly across species, both in terms of significance and the type of response (Table 5). All statistically significant responses to average wind speed and percentage of days with precipitation were negative, while the significant responses to mean temperature, precipitation and humidity were mixed. Out of the 14 species, six showed no statistically significant response to any of the weather variables. *Dorcatoma flavicornis* was the only species that showed no significant response to any of the possible parameters. *Dasytes niger*, *Xyleborinus saxesenii* and *Mycetochara maura* showed response to the largest number of weather variables, with all of them showing a response to four weather variables. Weather also had a diverging effect on multiple species depending on the microhabitat of collection. The microhabitat interaction responses also varied, with not many significant responses, but those that were significant were clearly positive for average wind speed and percentage of days with precipitation, and negative for humidity.

3.1. Trait groups

The trait groups show varying levels of response, with some clear patterns, both in response to the weather variables (Table 6), and the interaction between the weather variables and the microhabitat (Table 7). Medium and small sized species showed mixed significant responses, while the one species classified as large showed no significant response to the weather variables. Generalists showed a negative response to several variables, while specialists showed very few significant responses. The case was the same for species classified as "least concern" vs the threatened and endangered species, with the "least concern" group showing more significant responses. The results were mixed across the distribution groups, both in terms of type and strength of response. Responses also differed across trophic groups, with the xylomycetophagous species showing the most responses. The hollow specialized species showed very few significant responses, while the more numerous group focused on other parts of the tree showed more response.

Table 5: Results of the mixed model analysis for all 14 species and the total number of individuals, including microhabitat, weather variables and the interaction between them and the microhabitat. The significance levels are : 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Significant values are also marked in bold. (See Appendix for full model results tables for each species)

Species	Microhabitat : In front of hollow	Average wind speed	Mean temperature	Precipitation	Humidity	Percentage of days with precipitation	Period 2	Period 3	Microhabitat: Average wind speed	Microhabitat: Precipitation	Microhabitat: Mean temperature	Microhabitat: Humidity	Microhabitat: Percentage of days with precipitation
Haploglossa villosula	**2.85761*** **	-0.13552	**-1.62153** **	**-0.71243***	-0.07936	0.12048	0.81145	**-2.72753***	**0.99446***	0.17193	**2.17183*** **	**-1.18609.**	**1.49185***
Enicmus rugosus	**0.79953*** **	0.01182	0.19687	-0.02318	-0.83156	-0.18613	1.67231	2.07817	-0.16994	0.07061	-0.16202	-0.43408	0.35382
Dorcatoma chrysomelina	0.4566	1.4478	**3.6957***	0.7037	3.0566	-0.1499	-5.8259	-7.2837	0.6138	0.6980	1.2730	**-0.9532***	**1.4101.**
Dasytes niger	-0.02621	**-2.60708*** **	**-1.75761** **	**-1.23817***	1.02473	**-3.01542** **	1.99444	-0.37486	0.86251	**0.74262***	0.64400	-0.68832	1.07456
Euglenes oculatus	**-0.7748***	0.3363	1.2130	**1.9132*** **	**-2.7106.**	1.1263	3.3007	4.2499	**1.9027.**	0.3529	1.0992	**-1.3748.**	**1.9504.**
Xyleborinus saxesenii	-2.4118	**-9.3213***	-2.5885	**-4.6870*** **	**11.5161***	**-11.3472** **	-12.1094	-23.0773	**11.2448.**	0.7248	6.5586	3.5219	3.3745
Ptinus subpillosus	**3.3337*** **	-0.7522	-1.6216	-0.3374	-0.5725	0.6540	0.1828	-0.7208	0.1955	-0.3005	1.1815	0.7560	-1.0633
Dasytes plumbeus	**-2.6426*** **	-0.6089	1.0870	-0.6405	**3.4899.**	**-1.8969***	-4.0056	-7.8928	0.1191	0.6302	0.8948	-1.9201	1.6471
Ampedus balteatus	**1.10069** **	-0.18225	-0.56929	0.32171	-0.34844	0.04246	-0.11669	**-2.10630.**	-0.29278	-0.22104	0.22940	-0.32622	-0.15311
Cryptophagus scanicus	0.4648	-1.0744	**-3.5759***	**-1.0902.**	**-1.7334***	-0.2196	26.2800	30.0136	0.3066	0.0893	1.0132	0.1693	-0.2026
Euplectus karstenii	**1.98002** **	0.77289	1.75292	0.33342	-0.93027	0.19692	1.30137	1.17919	-0.26314	0.09909	-0.84045	-1.42703	1.13050
Mycetochara maura	**5.40308***	**-6.66992***	**3.57579***	**3.06391***	1.75733	**-9.05929***	**-7.45005***	-29.96999	2.93088	**-3.04103.**	-2.08348	-0.06743	6.16667
Dorcatoma flavicornis	3.471	66.447	-0.597	-5.486	-138.194	112.146	206.434	222.434	-65.481	6.570	-16.524	116.161	-99.033
Haploglossa gentilis	**1.4653***	-1.1303	-0.2467	-0.2761	2.4304	-2.4422	-1.5761	-24.9163	-1.2626	-1.1569	-1.1455	-0.9027	0.2779
Total individuals	**0.83606*** **	**-0.41598** **	0.03622	**-0.31601*** **	**0.45149.**	**-0.54339*** **	-0.10487	**-1.33313***	**0.75489*** **	0.06969	**0.60046*** **	**-1.11560*** **	**1.45964*** **

Table 6: The number of significant and not significant responses to the microhabitat and the weather variables; and significant responses in each trait group to microhabitat and different weather variables. Positive estimates are marked with a + sign and colored green, while the negative estimates and marked with a – sign and colored red. "n" shows the number of species in each trait group category (Details of the responses are shown in Table 5)

Trait/Weather Variable		**Microhabitat**	**Average wind speed**	**Mean temperature**	**Precipitation**	**Humidity**	**Percentage of days with precipitation**
Total number of effects	Significantly positive	7	0	2	2	2	0
	Significantly negative	2	3	3	4	2	4
	Not significant	5	11	9	8	10	10
Size	Large (n=1)	+					
	Medium (n=5)	- + + +	- -	- - +	- - +	+	- - -
	Small (n=8)	+ - + +	-	+ -	+ - -	- + -	-
Specialization	Generalists (n=9)	+ + - + + +	- - -	- - - +	- - - - +	+ + - -	- - - -
	Specialists (n=5)	- + +		+	+	-	
Red list status	Least concern (n=10)	+ + + - + +	- -	- + - -	- - - -	+ + -	- - -
	Near threatened / Endangered (n=5)	- +	-	+	+ +	-	-
Distribution	Northern (n=6)	- + +		+ -	+ -	- -	
	Southern (n=3)	+ - +	-	+	+	+	- -
	Widespread (n=5)	+ + +	- -	- -	- - -	+	- -
Trophic group	Predator (n=5)	+ - + +	-	- -	- -	+	- -
	Fungivore (n=2)	+		-	-	-	
	Xylophage (n=1)	+					
	Xylomycetophage (n=5)	- +	- -	+ +	+ - +	- +	- -
	Detrivore (n=1)	+					
Hollow specialization	Other parts of the tree (n=9)	+ - + +	- - -	+ - - +	- - - +	+ + -	- - - -
	Hollow / Nests (n=3)	+ - +		-	- +	-	
	Hollow without nests (n=2)	+ +					

Table 7: The number of significant and not significant responses to the interaction between the microhabitat and the weather variables; and significant responses in each trait group to the interaction between the microhabitat and different weather variables. Positive estimates are marked with a + sign and colored green, while the negative estimates and marked with a – sign and colored red. "n" shows the number of species in each trait group category (Details of the responses are shown in Table 5)

Trait/Interaction with hollow microhabitat		Average wind speed	Mean temperature	Precipitation	Humidity	Percentage of days with precipitation
Total number of effects	Significantly positive	3	1	1	0	3
	Significantly negative	0	0	1	3	0
	Not significant	11	13	12	11	11
Size	Large (n=1)					
	Medium (n=5)	+	+	+ -	-	+
	Small (n=8)	+ +			- -	+ +
Specialization	Generalists (n=9)	+ +	+	+ -	-	+
	Specialists (n=5)	+			- -	+ +
Red list status	Least concern (n=10)	+ +	+	+	- -	+ +
	Near threatened / Endangered (n=5)	+		-	-	+
Distribution	Northern (n=6)	+			-	+
	Southern (n=3)			-		
	Widespread (n=5)	+ +	+	+	-	+
Trophic group	Predator (n=5)	+	+	+	-	+
	Fungivore (n=2)					
	Xylophage (n=1)					
	Xylomycetophage (n=5)	+ +		-	- -	+ +
	Detrivore (n=1)					
Hollow specialization	Other parts of the tree (n=9)	+		+ -	-	+
	Hollow / Nests (n=3)	+ +	+		- -	+ +
	Hollow without nests (n=2)					

4. Discussion

The results indicate that average wind speed and percentage of days with precipitation are the two effects that will have the most important negative impact for these species, while other weather effects showed more mixed responses. The generalist and least concern species showed more responses than expected, together with species with a medium body size. Species with a northern distribution did not seem to be significantly effected by the weather variables, while widespread species showed a stronger response.

4.1. Microhabitat and its interactions

A large number of species has shown a clear preference for a certain type of microhabitat, either in the canopy of the hollow oak, or around the hollow of the trunk of the hollow oak. *Haploglossa villosula*, *Enicmus rugosus*, *Ptinus subpillosus*, *Ampedus balteatus*, *Euplectus karstenii*, *Mycetochara maura* and *Haploglossa gentilis*, as well as the total number of individuals of the 14 species, clearly prefered the microhabitat of the hollow of the trunk, while *Euglenes oculatus* and *Dasytes plumbeus* preferred the microhabitat in the canopy of the hollow oak. The five remaining species showed no statistically significant preference. No clear trait-related patterns could be found when it comes to microhabitat preference, as the preferences are spread across different groups (Table 6), and the two species that preferred the canopy are found in different trait groups.

In terms of traits and microhabitat interaction, three species showed a significant positive response to average wind speed and percentage of days with precipitation to the hollow microhabitat, while three species showed a significant negative response to humidity (Table 7). This suggests that the microhabitat of the hollow is positively connected with an increase in wind speed and longer periods of precipitation, and negative with an increase in humidity, in comparison to the canopy. The interaction with wind and precipitation could potentially be due to the protective environment that the hollow can provides for these species. Two out of three species that exhibited the significant negative interaction between the microhabitat of the hollow and humidity, as well as the total number of individuals, also showed a negative response to humidity alone, so it is possible that higher humidity around the hollow is the negative driver of this interaction.

4.2. Weather variables

The type of response to the weather variables and the significance of those responses differed across species, but all of them are relevant to a certain extent and need to be taken into consideration.

4.2.1. Average wind speed

Dasytes niger, *Xyleborinus saxesenii*, *Mycetochara maura* and the total number of individuals all show a significant negative relationship with average wind speed. *Xyleborinus saxesenii* and *Mycetochara maura* show an especially strong negative relationship with very high coefficient estimates, but this is potentially due to these species levels of abundance within the dataset, with very few observations and some very high values. Very few species exhibit a positive response to an increase in the average wind speed, and none of them statistically significant, suggesting that while wind may sometimes act as an aid in dispersal (Gatehouse, 1997), that is not the case with these saproxylic beetle species and its increase seems to be a hindrance. Out of the three species that had a significantly negative response to wind speed, two were medium sized and one was small. This could potentially suggest that species with a smaller body size have difficulty flying with increased wind speeds, but the number of species here is too low to claim that with certainty. All three species are also generalists and are not specialized for the hollow. The negative response to wind speed and the lack of hollow specialization could suggest that species that are hollow specialized might have a certain degree of protection from the wind in the tree cavity.

4.2.2. Mean temperature

Mean temperature has also caused mixed responses across species. *Dorcatoma chrysomelina* and *Mycetochara maura* showed a strong positive relationship with temperature, while *Haploglossa villosula*, *Dasytes niger* and *Cryptophagus scanicus* showed a negative relationship. While temperature is a variable expected to have a positive impact on insect species abundance and richness (Gossner et al, 2013, Müller et al, 2014, Rubin-Aguirre et al, 2015), it is possible that some species will not follow this pattern. All of the three species that reacted negatively are generalists classified as "least concern", and this response is split across other trait groups. It is possible that a trait that is not examined in this thesis is what is driving this response, such as a species preference for certain temperatures, or temperature thresholds. There is also the possibility of increased temperatures having an impact on the number of generations and development, by confusing the organisms that rely on environmental cues for their life-cycle regulation (Van Dyck et al, 2015).

4.2.3. Precipitation, Humidity and Percentage of days with precipitation

Precipitation seems to be an important variable for multiple species, with varying responses. *Haploglossa villosula, Dasytes niger, Xyleborinus saxesenii, Cryptophagus scanicus* and the total number of individuals all show a negative relationship with precipitation, while *Euglenes oculatus* and *Mycetochara maura* show a positive response. The responses to the humidity variable also include both positive and negative responses. *Xyleborinus saxesenii, Dasytes plumbeus* and the total number of individuals showed a positive response, while *Euglenes oculatus* and *Cryptophagus scanicus* showed a negative relationship with humidity. *Xyleborinus saxesenii's* response is particularly strong, with a very high estimate coefficient, again most likely due to the abundance levels within the dataset. Considering these responses, it seems unlikely that changes in abundance of these species following a change in precipitation or humidity will be uniform, but will probably depend on each individual species. A possible explanation for this might be the relationship between some saproxylic beetle species and the fungi in the hollow oaks (Gossner et al, 2013), with their response to precipitation and humidity being drived by the response and availability of the fungi.

The responses for these two variables are also mixed across the majority of the trait groups, with the exception of the red-list status groups response to precipitation. All of the four species that exhibited a negative response to precipitation are members of the "least concern" group, while the two species that had a positive response are in the "near threatened/endangered" group. This can be a good sign for conservation, if certain currently threatened species will react positively to the expected increase in precipitation, but it also highlights a potential vulnerability of species that are currently not considered problematic.

While the responses to the weather variable percentage of days with precipitation yielded significant negative responses, responses to both precipitation and humidity have been mixed. *Dasytes niger, Xyleborinus saxesenii, Dasytes plumbeus, Mycetochara maura* and the total number of individuals of the 14 species all showed strong negative responses to this variable, with *Xyleborinus saxesenii* and *Mycetochara maura* having high estimate coefficients. *Mycetochara maura* has also responded positively to precipitation. All of these factors combined suggest an importance of the length of the rain period, as opposed to only taking the amount of precipitation into consideration. A study on bird flocking and insect activity also found a negative effect of precipitation on insects that got stronger with the length of the precipitation period (Poulsen, 1996). This response could potentially be connected with foraging of the species, as a study on *Aphidius rosae*, a parasitoid wasp, found that the species completely stops foraging during longer periods of precipitation (Weisser et al, 1997). All of the four species that exhibited this negative response are also generalists that are not specialized for the hollow, as was the case with the responses to average wind speed, further strengthening the possibility of the tree cavity providing protection from the elements for certain species.

4.3. Traits

The only species classified as "large", did not show statistically significant responses to any variable, apart from a preference for microhabitat of the hollow. The medium and small sized species showed mixed responses, with the medium species having more response relative to their group size than smaller species. Out of five medium size species, three reacted negatively to percentage of days with precipitation and two to average wind speed, with other variables showing a mixed response. Small species' response consisted of only one to three out of eight species having a significant response, and those were mixed. It is unclear why a medium body size would be a trait that can cause stronger responses to certain weather variables, but it is possible the reason lies in the lack of special abilities that come with either a larger (more sturdy, possibly easier to withstand impact) or a smaller body size (easier to take cover).

In terms of specialization, the generalists showed more responses than the specialists, but are also the more numerous group. Out of nine generalist species, three to five species showed a response to a given weather variable, while out of five specialist species only one or none showed a significant response. The responses of generalists were predominantly negative, except for a mixed response to humidity. This suggests that abundance of generalist species could be in decline with the expected climate changes. This is a somewhat surprising result, considering that specialists of any species are usually classified as the more vulnerable. A study covering a much larger number of saproxylic beetle species (152) found that specialists were more affected by temperature (positive) and precipitation (negative), with precipitation having a much stronger effect (Gough et al, 2015). In that case the generalists did not appear vulnerable, suggesting the possibility that the generalist related vulnerability showed in this thesis might be species specific. This however does not refute the point that, while specialists are usually considered vulnerable and often the focus point of research and conservation, the generalists must not be disregarded, as they can also have species with a substantial degree of vulnerability and can be faced with population problems.

The red list status aspect of the results is also somewhat surprising. The near threatened and endangered species showed mixed responses, positive for both precipitation and mean temperature. The species classified as "least concern" however, show a much more negative response to the weather variables across the board. This can potentially add a new problem level for conservation, as the species that are at this time considered "safe" might actually be at a much greater risk of the effects of climate change than previously thought. The possible positive aspect of this would be the potential reduction in pest species abundance, as they are usually a part of this group, and as such might also be negatively affected by the expected changes.

Species with a northern distribution showed very few statistically significant responses, and those were mixed. The species with a southern distribution were a smaller group, consisting of three species, but two out of those three species showed a negative response to percentage of days with precipitation, suggesting a possible negative impact of prolonged periods with rain for these southern species. The one significant response of the southern species to temperature increase was positive, suggesting that the predictions of species moving further north under the effects of warmer weather (Williams & Liebhold, 2002) might prove to be accurate. Out of the five widespread species, three had an expected significantly negative response to precipitation, and two for wind speed, temperature and percentage of days with precipitation. The predominantly negative responses could suggest that widespread species will be the most affected by climate change. Those species should, however, be the most tolerant to temperature and precipitation changes, so it is more likely that it is some other traits of those species that are driving this response, and not purely their distribution.

Due to the individual natures of the species in the sample population, the trophic groups are numerous and some contain very few species, so it is challenging to recognize potential patterns. The xylophage and detrivore groups, each containing a single species, did not show any significant responses to the weather variables. Out of the two fungivore species, there was a single significantly negative response to precipitation, mean temperature and humidity. Since different fungal communities respond differently to precipitation (Hawkes et al, 2011), it is possible that the availability of fungi is what is driving this response. If the type of fungi required by these species is one that responds negatively to precipitation, it is expected that the fungivores would respond in the same manner, driven by the availability of the fungi. Since this group is also considered to be among the most vulnerable with weak dispersal capabilities (Ulyshen & Hanula, 2010), the connection between these species and the different types of fungi they are dependent on is of vital importance in predicting their future abundance, especially considering their mutually beneficial relationship (Stokland, et al, 2012). Out of the five xylomycetophage species, two to three showed a significant response to the weather variables. The responses were negative for wind speed and percentage of days with precipitation, positive for temperature, and mixed for precipitation and humidity. Both the fungivores and the xylomycetophagus species responded negatively to precipitation, but their response to temperature differs. This could suggest that the wood component in the species feeding habits is vital when it comes to temperature responses.

Out of five predator species, one to two showed significant responses to the weather variables. Those responses were negative, with the exception of humidity. Predator responses can be difficult to asses, due to the fact that their reaction can be a consequence of their own physiology or a response to the behavior or abundance of their prey. In this case, the predators' response seems to follow the response of the total number of individuals, with the exception of mean temperature, suggesting that it is likely that their response is driven by the abundance and availability of prey.

The responses in terms of hollow specialization, the two species associated with hollows but without nests did not show any significant response. Out of the three species associated with hollows and nests, there was one positive and one negative response to precipitation, and one negative response to temperature and humidity. The nest associated species mixed response could be due to their preference to a higher or lower level of moisture within the nest, which can vary among species (Stokland et al, 2012). Due to the lack of information and a relatively small sample size of these groups it is difficult to say with certainty, but it seems that the level of hollow specialization and nest association does not seem to be a very relevant trait in predicting the response of these species. Out of the nine species associated with other parts of the tree, three to four showed significant responses to the weather variables. The responses were negative for wind speed and percentage of days with precipitation, and mixed for the other variables.

4.4. Additional considerations

Another thing of note were two pairs of species that showed the exact same response across all weather variables. Those are *Dasytes niger* and *Xyleborinus saxesenii* (with *Euplectus karstenii* showing completely opposite responses), as well as *Haploglossa villosula* and *Ptinus subpillosus*. *Dasytes niger* and *Xyleborinus saxesenii* are both generalists, but *Euplectus karstenii* is as well. The size also differs across species, suggesting possible additional parameters driving these responses. *Euplectus karstenii* does fall under the species with a northern distribution, so it is possible that is the deciding factor of these differences. *Haploglossa villosula* and *Ptinus subpillosus* differ across their known traits, the closest of them being size, but even in that case *Haploglossa villosula* is larger on average and as such falls into the larger size group. This response could be purely coincidental, or suggest that there are other traits or parameters that can be driving certain species responses that have not been covered in this thesis.

While the primary focus of this thesis was looking into different trait groups among these beetle species and seeing how they respond to different weather variables, it is also relevant to look at the total number of individuals of all the 14 species, in order to see if there are any significant responses that can be expected in abundance in more general terms. The total number of individuals showed a significant response to the majority of the weather variables, as well as the majority of the microhabitat interactions. This suggests that the general abundance of the saproxylic beetle species could be quite sensitive to weather changes, and actually exhibit stronger responses than the species would perhaps show when examined on an individual basis. If this is indeed the case, we could be seeing great changes in abundance and consequently species composition with the upcoming expected climate changes.

5. Conclusion

This study has found that wind speed and percentage of days with precipitation are the weather effects that have a negative impact on the abundance of these saproxylic species, while temperature, precipitation and humidity have mixed effects. What we can in general expect from future climate changes for these species is that if there is a response in abundance, it will be negative with increases in wind speed and percentage of days with precipitation, while the types of responses to temperature, precipitation and humidity will be more species dependent. Different species showed different levels and strengths of response to the weather variables as expected, but in relation to different traits some patterns were more surprising. Results such as the responses of the generalists and the species found in the "least concern" group of the red list are among these. Their responses highlight the need to consider the full spectrum of species when conducting research involving climate change, as well as creating policies to combat it. While some groups can traditionally be considered as focus groups and tend to receive more attention, we must not disregard the currently common or generalized species. If they also posses a high degree of vulnerability, the number of potentially threatened species could be greater than initially thought. Additionally, changes that might occur with these more common species could have a greater impact on the communities and their ecosystems than changes in abundance of rare species could potentially have.

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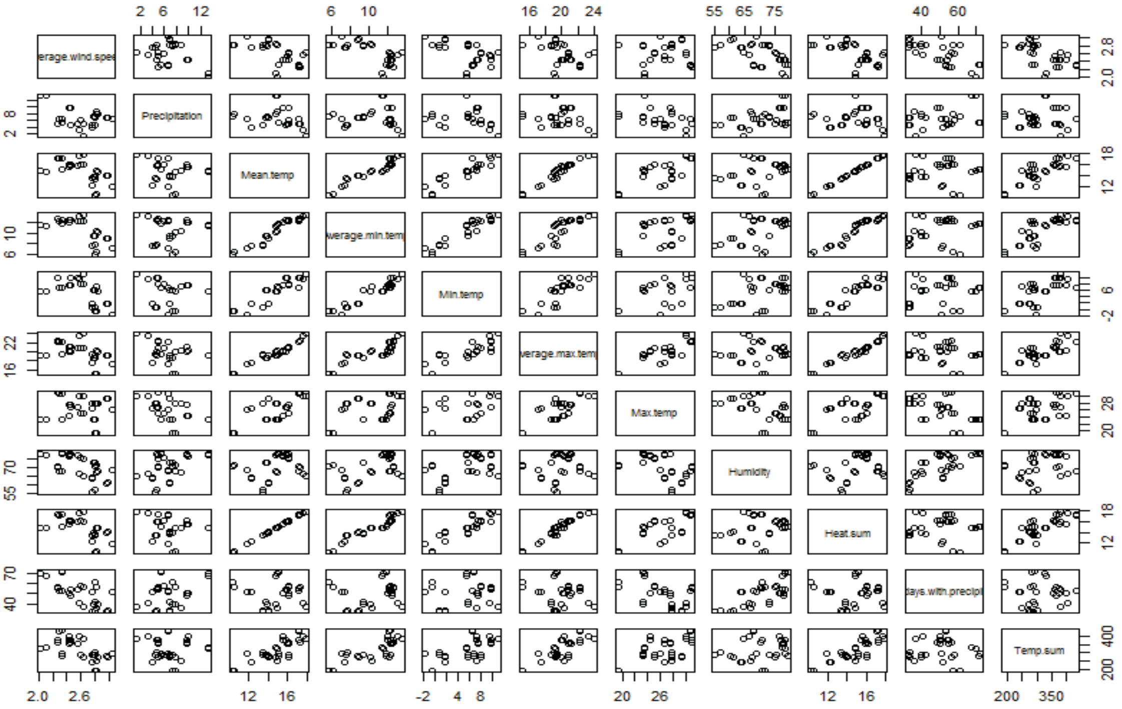
Appendix

Figure 1: Correlation matrix of weather variables



Tables with full results of the mixed model for each individual species and the total number of individuals of the 14 species

Haploglossa villosula	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.01943	0.71072	-0.027	0.97819
Microhabitat: In front of opening of hollow standing oak	**2.85761**	**0.25413**	**11.245**	**< 2e-16 *****
Average wind speed	-0.13552	0.48728	-0.278	0.78092
Precipitation	**-0.71243**	**0.33491**	**-2.127**	**0.03340 ***
Mean temperature	**-1.62153**	**0.56742**	**-2.858**	**0.00427 ****
Humidity	-0.07936	0.73652	-0.108	0.91419
Percentage of days with precipitation	0.12048	0.75817	0.159	0.87374
Period 2	0.81145	0.80022	1.014	0.31057
Period 3	**-2.72753**	**1.13316**	**-2.407**	**0.01608 ***
Microhabitat: In front of opening of hollow standing oak: Average wind speed	**0.99446**	**0.43941**	**2.263**	**0.02362 ***
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.17193	0.33757	0.509	0.61052
Microhabitat: In front of opening of hollow standing oak: Mean temperature	**2.17183**	**0.42825**	**5.071**	**3.95e-07 *****
Microhabitat: In front of opening of hollow standing oak: Humidity	**-1.18609**	**0.68699**	**-1.727**	**0.08426 .**
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	**1.49185**	**0.71350**	**2.091**	**0.03654 ***

Enicmus rugosus	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.65345	0.88868	-0.735	0.462
Microhabitat: In front of opening of hollow standing oak	**0.79953**	**0.17387**	**4.599**	**4.25e-06 *****
Average wind speed	0.01182	0.39861	0.030	0.976
Precipitation	-0.02318	0.26053	-0.089	0.929
Mean temperature	0.19687	0.47812	0.412	0.681
Humidity	-0.83156	0.68855	-1.208	0.227
Percentage of days with precipitation	-0.18613	0.46016	-0.404	0.686
Period 2	1.67231	1.02294	1.635	0.102
Period 3	2.07817	1.47577	1.408	0.159
Microhabitat: In front of opening of hollow standing oak: Average wind speed	-0.16994	0.42086	-0.404	0.686
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.07061	0.21059	0.335	0.737
Microhabitat: In front of opening of hollow standing oak: Mean temperature	-0.16202	0.35959	-0.451	0.652
Microhabitat: In front of opening of hollow standing oak: Humidity	-0.43408	0.35540	-1.221	0.222
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	0.35382	0.47069	0.752	0.452

Dorcatoma chrysomelina	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.5631	3.2835	1.085	0.2779
Microhabitat: In front of opening of hollow standing oak	0.4566	0.3690	1.237	0.2159
Average wind speed	1.4478	0.9099	1.591	0.1116
Precipitation	0.7037	0.6217	1.132	0.2577
Mean temperature	**3.6957**	**1.6532**	**2.236**	**0.0254 ***
Humidity	3.0566	2.1517	1.421	0.1554
Percentage of days with precipitation	-0.1499	1.0111	-0.148	0.8821
Period 2	-5.8259	3.8559	-1.511	0.1308
Period 3	-7.2837	5.3227	-1.368	0.1712
Microhabitat: In front of opening of hollow standing oak: Average wind speed	0.6138	0.8993	0.683	0.4949
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.6980	0.4862	1.436	0.1511
Microhabitat: In front of opening of hollow standing oak: Mean temperature	1.2730	0.9762	1.304	0.1922
Microhabitat: In front of opening of hollow standing oak: Humidity	**-0.9532**	**0.4549**	**-2.095**	**0.0362 ***
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	**1.4101**	**0.8506**	**1.658**	**0.0974 .**

Dasytes niger	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.62725	1.53383	-0.409	0.682582
Microhabitat: In front of opening of hollow standing oak	-0.02621	0.29436	-0.089	0.929040
Average wind speed	**-2.60708**	**0.68054**	**-3.831**	**0.000128 *****
Precipitation	**-1.23817**	**0.60514**	**-2.046**	**0.040748 ***
Mean temperature	**-1.75761**	**0.67247**	**-2.614**	**0.008958 ****
Humidity	1.02473	1.49306	0.686	0.492506
Percentage of days with precipitation	**-3.01542**	**1.00862**	**-2.990**	**0.002793 ****
Period 2	1.99444	1.78293	1.119	0.263299
Period 3	-0.37486	2.70950	-0.138	0.889962
Microhabitat: In front of opening of hollow standing oak: Average wind speed	0.86251	0.64148	1.345	0.178765
Microhabitat: In front of opening of hollow standing oak: Precipitation	**0.74262**	**0.32498**	**2.285**	**0.022304 ***
Microhabitat: In front of opening of hollow standing oak: Mean temperature	0.64400	0.54002	1.193	0.233051
Microhabitat: In front of opening of hollow standing oak: Humidity	-0.68832	0.64454	-1.068	0.285549
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	1.07456	0.81321	1.321	0.186377

Euglenes oculatus	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.7162	2.3011	-1.180	0.2379
Microhabitat: In front of opening of hollow standing oak	**-0.7748**	**0.3837**	**-2.019**	**0.0435 ***
Average wind speed	0.3363	0.6842	0.491	0.6231
Precipitation	**1.9132**	**0.4511**	**4.242**	**2.22e-05 *****
Mean temperature	1.2130	1.1946	1.015	0.3099
Humidity	**-2.7106**	**1.4632**	**-1.853**	**0.0640 .**
Percentage of days with precipitation	1.1263	0.7052	1.597	0.1102
Period 2	3.3007	2.6647	1.239	0.2155
Period 3	4.2499	3.7372	1.137	0.2555
Microhabitat: In front of opening of hollow standing oak: Average wind speed	**1.9027**	**1.0009**	**1.901**	**0.0573 .**
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.3529	0.3996	0.883	0.3772
Microhabitat: In front of opening of hollow standing oak: Mean temperature	1.0992	0.8788	1.251	0.2110
Microhabitat: In front of opening of hollow standing oak: Humidity	**-1.3748**	**0.7238**	**-1.899**	**0.0575 .**
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	**1.9504**	**1.0261**	**1.901**	**0.0573 .**

Xyleborinus saxesenii	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	7.4619	8.1635	0.914	0.36068
Microhabitat: In front of opening of hollow standing oak	-2.4118	2.2572	-1.068	0.28531
Average wind speed	**-9.3213**	**3.8592**	**-2.415**	**0.01572 ***
Precipitation	**-4.6870**	**1.1526**	**-4.067**	**4.77e-05 *****
Mean temperature	-2.5885	3.1186	-0.830	0.40653
Humidity	**11.5161**	**4.8118**	**2.393**	**0.01670 ***
Percentage of days with precipitation	**-11.3472**	**3.8262**	**-2.966**	**0.00302 ****
Period 2	-12.1094	12.2489	-0.989	0.32285
Period 3	-23.0773	15.4734	-1.491	0.13585
Microhabitat: In front of opening of hollow standing oak: Average wind speed	**11.2448**	**6.5238**	**1.724**	**0.08477 .**
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.7248	1.2724	0.570	0.56896
Microhabitat: In front of opening of hollow standing oak: Mean temperature	6.5586	4.8156	1.362	0.17322
Microhabitat: In front of opening of hollow standing oak: Humidity	3.5219	2.3677	1.487	0.13689
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	3.3745	3.0299	1.114	0.26539

Dasytes plumbeus	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	4.5318	2.7992	1.619	0.1055
Microhabitat: In front of opening of hollow standing oak	**-2.6426**	**0.5077**	**-5.205**	**1.94e-07 *****
Average wind speed	-0.6089	0.4729	-1.288	0.1979
Precipitation	-0.6405	0.4087	-1.567	0.1170
Mean temperature	1.0870	1.1783	0.923	0.3562
Humidity	**3.4899**	**1.9822**	**1.761**	**0.0783 .**
Percentage of days with precipitation	**-1.8969**	**0.7604**	**-2.495**	**0.0126 ***
Period 2	-4.0056	3.3784	-1.186	0.2358
Period 3	-7.8928	4.9184	-1.605	0.1086
Microhabitat: In front of opening of hollow standing oak: Average wind speed	0.1191	1.3239	0.090	0.9283
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.6302	0.5995	1.051	0.2932
Microhabitat: In front of opening of hollow standing oak: Mean temperature	0.8948	0.9892	0.905	0.3657
Microhabitat: In front of opening of hollow standing oak: Humidity	-1.9201	1.2302	-1.561	0.1186
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	1.6471	1.5306	1.076	0.2819

Ampedus balteatus	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.02288	0.69894	-0.033	0.9739
Microhabitat: In front of opening of hollow standing oak	**1.10069**	**0.36692**	**3.000**	**0.0027 ****
Average wind speed	-0.18225	0.66183	-0.275	0.7830
Precipitation	0.32171	0.39788	0.809	0.4188
Mean temperature	-0.56929	0.58252	-0.977	0.3284
Humidity	-0.34844	0.94398	-0.369	0.7120
Percentage of days with precipitation	0.04246	0.96064	0.044	0.9647
Period 2	-0.11669	0.78345	-0.149	0.8816
Period 3	**-2.10630**	**1.23897**	**-1.700**	**0.0891 .**
Microhabitat: In front of opening of hollow standing oak: Average wind speed	-0.29278	0.73738	-0.397	0.6913
Microhabitat: In front of opening of hollow standing oak: Precipitation	-0.22104	0.43923	-0.503	0.6148
Microhabitat: In front of opening of hollow standing oak: Mean temperature	0.22940	0.66301	0.346	0.7293
Microhabitat: In front of opening of hollow standing oak: Humidity	-0.32622	0.93907	-0.347	0.7283
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	-0.15311	1.04059	-0.147	0.8830

Ptinus subpillosus	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**-1.9360**	**0.8622**	**-2.245**	**0.0247 ***
Microhabitat: In front of opening of hollow standing oak	**3.3337**	**0.6617**	**5.038**	**4.7e-07 *****
Average wind speed	-0.7522	1.1690	-0.643	0.5199
Precipitation	-0.3374	0.6793	-0.497	0.6195
Mean temperature	-1.6216	0.9968	-1.627	0.1038
Humidity	-0.5725	1.3608	-0.421	0.6739
Percentage of days with precipitation	0.6540	1.5334	0.427	0.6697
Period 2	0.1828	0.8351	0.219	0.8267
Period 3	-0.7208	1.0178	-0.708	0.4788
Microhabitat: In front of opening of hollow standing oak: Average wind speed	0.1955	1.2050	0.162	0.8711
Microhabitat: In front of opening of hollow standing oak: Precipitation	-0.3005	0.6963	-0.432	0.6661
Microhabitat: In front of opening of hollow standing oak: Mean temperature	1.1815	1.0095	1.170	0.2418
Microhabitat: In front of opening of hollow standing oak: Humidity	0.7560	1.3631	0.555	0.5792
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	-1.0633	1.5634	-0.680	0.4964

Cryptophagus scanicus	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-26.5844	7150.4500	-0.004	0.9970
Microhabitat: In front of opening of hollow standing oak	0.4648	1.2203	0.381	0.7033
Average wind speed	-1.0744	0.8805	-1.220	0.2224
Precipitation	**-1.0902**	**0.5863**	**-1.860**	**0.0629 .**
Mean temperature	**-3.5759**	**1.7752**	**-2.014**	**0.0440 ***
Humidity	**-1.7334**	**0.7673**	**-2.259**	**0.0239 ***
Percentage of days with precipitation	-0.2196	0.8241	-0.266	0.7899
Period 2	26.2800	7150.4502	0.004	0.9971
Period 3	30.0136	7150.4504	0.004	0.9967
Microhabitat: In front of opening of hollow standing oak: Average wind speed	0.3066	1.0081	0.304	0.7610
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.0893	0.6720	0.133	0.8943
Microhabitat: In front of opening of hollow standing oak: Mean temperature	1.0132	1.9217	0.527	0.5980
Microhabitat: In front of opening of hollow standing oak: Humidity	0.1693	0.7828	0.216	0.8288
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	-0.2026	0.9643	-0.210	0.8336

Euplectus karstenii	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**-2.56600**	**0.92140**	**-2.785**	**0.00535 ****
Microhabitat: In front of opening of hollow standing oak	**1.98002**	**0.60232**	**3.287**	**0.00101 ****
Average wind speed	0.77289	1.14220	0.677	0.49861
Precipitation	0.33342	0.54815	0.608	0.54301
Mean temperature	1.75292	1.15073	1.523	0.12768
Humidity	-0.93027	0.81712	-1.138	0.25492
Percentage of days with precipitation	0.19692	1.05656	0.186	0.85215
Period 2	1.30137	0.91825	1.417	0.15642
Period 3	1.17919	1.10928	1.063	0.28777
Microhabitat: In front of opening of hollow standing oak: Average wind speed	-0.26314	1.24376	-0.212	0.83244
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.09909	0.58392	0.170	0.86524
Microhabitat: In front of opening of hollow standing oak: Mean temperature	-0.84045	1.15709	-0.726	0.46763
Microhabitat: In front of opening of hollow standing oak: Humidity	-1.42703	0.87333	-1.634	0.10225
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	1.13050	1.19383	0.947	0.34367

Mycetochara maura	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.80566	1.89558	-0.425	0.6708
Microhabitat: In front of opening of hollow standing oak	**5.40308**	**2.61605**	**2.065**	**0.0389 ***
Average wind speed	**-6.66992**	**3.24255**	**-2.057**	**0.0397 ***
Precipitation	**3.06391**	**1.47992**	**2.070**	**0.0384 ***
Mean temperature	**3.57579**	**1.57350**	**2.272**	**0.0231 ***
Humidity	1.75733	1.67683	1.048	0.2946
Percentage of days with precipitation	**-9.05929**	**4.38943**	**-2.064**	**0.0390 ***
Period 2	**-7.45005**	**3.07134**	**-2.426**	**0.0153 ***
Period 3	-29.96999	4898.81705	-0.006	0.9951
Microhabitat: In front of opening of hollow standing oak: Average wind speed	2.93088	2.55054	1.149	0.2505
Microhabitat: In front of opening of hollow standing oak: Precipitation	**-3.04103**	**1.68728**	**-1.802**	**0.0715 .**
Microhabitat: In front of opening of hollow standing oak: Mean temperature	-2.08348	1.28071	-1.627	0.1038
Microhabitat: In front of opening of hollow standing oak: Humidity	-0.06743	1.36156	-0.050	0.9605
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	6.16667	3.94887	1.562	0.1184

Dorcatoma flavicornis	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-208.609	17414.897	-0.012	0.990
Microhabitat: In front of opening of hollow standing oak	3.471	34.379	0.101	0.920
Average wind speed	66.447	119.030	0.558	0.577
Precipitation	-5.486	45.212	-0.121	0.903
Mean temperature	-0.597	80.208	-0.007	0.994
Humidity	-138.194	256.806	-0.538	0.590
Percentage of days with precipitation	112.146	202.534	0.554	0.580
Period 2	206.434	17415.431	0.012	0.991
Period 3	222.434	17415.785	0.013	0.990
Microhabitat: In front of opening of hollow standing oak: Average wind speed	-65.481	126.262	-0.519	0.604
Microhabitat: In front of opening of hollow standing oak: Precipitation	6.570	45.023	0.146	0.884
Microhabitat: In front of opening of hollow standing oak: Mean temperature	-16.524	89.078	-0.186	0.853
Microhabitat: In front of opening of hollow standing oak: Humidity	116.161	246.499	0.471	0.637
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	-99.033	200.525	-0.494	0.621

Haploglossa gentilis	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.9985	4.3933	-0.682	0.495
Microhabitat: In front of opening of hollow standing oak	**1.4653**	**0.5898**	**2.484**	**0.013 ***
Average wind speed	-1.1303	1.7170	-0.658	0.510
Precipitation	-0.2761	0.6461	-0.427	0.669
Mean temperature	-0.2467	1.3894	-0.178	0.859
Humidity	2.4304	2.1955	1.107	0.268
Percentage of days with precipitation	-2.4422	2.2374	-1.092	0.275
Period 2	-1.5761	1.9984	-0.789	0.430
Period 3	-24.9163	512.0002	-0.049	0.961
Microhabitat: In front of opening of hollow standing oak: Average wind speed	-1.2626	1.7763	-0.711	0.477
Microhabitat: In front of opening of hollow standing oak: Precipitation	-1.1569	0.7152	-1.617	0.106
Microhabitat: In front of opening of hollow standing oak: Mean temperature	-1.1455	1.4959	-0.766	0.444
Microhabitat: In front of opening of hollow standing oak: Humidity	-0.9027	1.9075	-0.473	0.636
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	0.2779	2.2024	0.126	0.900

Total individuals (of the 14 species)	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	**3.46608**	**0.39981**	**8.669**	**< 2e-16 *****
Microhabitat: In front of opening of hollow standing oak	**0.83606**	**0.05116**	**16.342**	**< 2e-16 *****
Average wind speed	**-0.41598**	**0.13221**	**-3.146**	**0.001654 ****
Precipitation	**-0.31601**	**0.08181**	**-3.863**	**0.000112 *****
Mean temperature	0.03622	0.18128	0.200	0.841651
Humidity	**0.45149**	**0.26674**	**1.693**	**0.090521 .**
Percentage of days with precipitation	**-0.54339**	**0.15911**	**-3.415**	**0.000638 *****
Period 2	-0.10487	0.42731	-0.245	0.806132
Period 3	**-1.33313**	**0.60739**	**-2.195**	**0.028173 ***
Microhabitat: In front of opening of hollow standing oak: Average wind speed	**0.75489**	**0.15373**	**4.910**	**9.09e-07 *****
Microhabitat: In front of opening of hollow standing oak: Precipitation	0.06969	0.07252	0.961	0.336558
Microhabitat: In front of opening of hollow standing oak: Mean temperature	**0.60046**	**0.12978**	**4.627**	**3.71e-06 *****
Microhabitat: In front of opening of hollow standing oak: Humidity	**-1.11560**	**0.14272**	**-7.817**	**5.41e-15 *****
Microhabitat: In front of opening of hollow standing oak: Percentage of days with precipitation	**1.45964**	**0.17737**	**8.229**	**< 2e-16 *****

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no