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Master Thesis

Characterisation of Habitat Requirements of European Fishing Spiders

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Abstract

Semi-aquatic fishing spiders (*Dolomedes*) are dependent on wetlands, which are among the most threatened habitats, impacted by climate change and land use. There are two species of fishing spiders, *Dolomedes plantarius* and *Dolomedes fimbriatus* in Europe. Habitat loss in central Europe causes declining populations, but new suitable habitat may become available due to climate change. In order to investigate, whether new habitat might become available, I tried to characterise the habitat requirements of *Dolomedes*. To do so, I sampled wetland sites in Norway and Sweden. I modeled timing, placement and detectability of nursery webs to specify requirements during reproduction and to identify factors impacting detectability of the species. The results suggest differences in habitat types for both species, pointing at more narrow environmental requirements of *D. plantarius*, *e.g.* concerning dependency on open water and vegetation characteristics of the terrestrial as well as of the aquatic habitat. I found placement of nursery webs determined mainly by distance to water, shade, presence of aquatic vegetation and abundance of *Phragmites*, *Carex* and *Sphagnum*; detectability was impacted by cloudiness, temperature and vegetation structure; the number of nursery webs was determined mostly by the time during the season, whereby the number decreased between July and September. Further research will be necessary to refine the conclusions and to make predictions about possible range expansion of *Dolomedes*.

Keywords: *Dolomedes plantarius*, *Dolomedes fimbriatus*, wetlands, Scandinavia, habitat suitability

Contents

1. Introduction

The near future of Biodiversity will mainly be impacted by anthropogenic land use and climate change (Sala et al., 2000). Different species' responses to climate change can be spatial or temporal and finding suitable conditions or adapting to changing conditions can prevent species and populations from extinction (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Spatial responses are possible at large scale as latitudinal and altitudinal, as well as between different micro-climates (Bellard et al., 2012). Shift in distribution range is already observed in species with high dispersal abilities (Parmesan, 2006).

Wetlands are among the most threatened, while also most important ecosystems, regarding climate change, biodiversity, hydrology and human existence (De Groot, Stuip, Finlayson, & Davidson, 2006). Conversion and loss of wetlands were reported by Davidson (2014) to have reached 87 % globally compared to the abundance in the beginning of the 18th Century. Hu, Niu, Chen, Li, & Zhang (2017) estimated 33 % wetland loss due to human activities. Wetland loss is mainly caused by agriculture and urbanization (De Groot et al., 2006). The most severe loss of wetlands globally has been described by Hu et al. (2017) and Davidson (2014) in Europe with an estimated loss of 45 % (Hu et al., 2017).

Conservation Biology is a multidisciplinary science consisting of a normative component with the goal of protecting all parts of biodiversity and a consequential descriptive component of understanding entities and antropogenic impacts on those entities (Lindenmayer & Hunter, 2010). Variable and dynamic human values are determining conservation efforts (Lindenmayer & Hunter, 2010) and have contributed to neglection of invertebrates (Clark & May, 2002) as well as freshwater species (Darwall et al., 2011) in conservation and conservation research. Although the taxonomical imbalance of research has been recognised, knowledge needed to conduct conservation is missing for wetland invertebrates, as in the case of the great raft spider, *Dolomedes plantarius* (Leroy et al., 2013). Climate change needs to be taken into account by nature conservation, as protected species may not find suitable habitat in currently protected areas in the future due to distribution shifts (Auaújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Therefore, the use of predictive models and in particular empirical niche modelling (Bellard et al., 2012) became a central tool for conservation biology to predict the future of biodiversity in changing climate conditions (Bellard et al., 2012; Kéry & Schaub, 2012).

A distribution shift from central and southern Europe towards Scandinavia is predicted for several invertebrate species at least until 2050 due to habitat alterations (Leroy et al., 2014), among them also *D. plantarius. D. plantarius* is one of the few red listed spider species in

Europe, and the only of those with a wide distribution range (Leroy et al., 2013). *Dolomedes* are semi-aquatic spiders (Stratton, Suter, & Miller, 2004) of the family Pisauridae. The European species of *Dolomedes* are closely related to the aquatic habitat, preying on land as well as on water (Gorb & Barth, 1994). In Europe, two species of the genus *Dolomedes* occur. Beside the red listed *D. plantarius*, there is the more common raft sider (*D. fimbriatus*) (Duffey, 2012). Habitats of both species are probably declining because of transformation and drying out of wetlands (Helsdingen, 1993). The literature suggests that *D. plantarius* has a narrow environmental niche compared to the more common *D. fimbriatus* (Duffey, 2012). The decline of *D. plantarius* makes it a species of conservation interest (Smith, 2000). Following the decline is difficult, as historic distribution data of *Dolomedes* are scarce (Duffey, 2012). Some authors suggest that there may be denser populations of *D. plantarius* than known (Duffey, 2012; Ivanov, Prishepchik, & Setrakova, 2017). Mis-identifications of the two European *Dolomedes* species were common especially in the first half of the 20th century (Helsdingen, 1993). Poor monitoring combined with the mis-identification history of *Dolomedes* cause an overall poor knowledge about distribution of the species.

Scandinavia is a promising future habitat for *Dolomedes*, as many riparian habitats are available and interconnected water bodies are expected to persist in the future, while the predicted suitability in terms of land use and climate is high (Leroy et al., 2013). The proportion of wetlands in northern Europe is high compared to Europe overall (Vasander et al., 2003) and shorelines are particularly protected, *e.g.* in Sweden (Lindgren, 2011). Despite the predicted climatic suitability in Scandinavia, it is unclear within this broad scale of the distribution model (Leroy et al., 2013), how well the specific habitat requirements of *Dolomedes* will be fullfilled.

1.1. Habitat Requirements

Habitat requirements and habitat differences of *D. fimbriatus* and *D. plantarius* are in general unclear (Duffey, 2012). Habitat requirements, identification, detection and coexistence with *D. fimbriatus* contain many interrelated knowledge gaps for the *Dolomedes* genus in Europe. *D. fimbriatus* and *D. plantarius* are suspected to sometimes live closely together (Duffey, 2012; Ivanov et al., 2017). It was suspected that both species do not coexist in one habitat due to slightly different habitat requirements (Helsdingen, 1993), which also has been questioned several times. For example Holec (2000) suggests coexistence can occur in habitats in transition., *i.e.* a habitat can change from a suitable *D. plantarius* habitat into a suitable *D. fimbriatus* habitat with the possibility of a temporal overlap of both species during the

transition.

The presence of *Dolomedes* has been hypothesised to be associated with certain habitat characteristics in the literature based on observational data (Duffey, 1995, Duffey (2012); e.g. Helsdingen, 1993). I summarised information from the literature (Duffey, 1995, 2012; mostly Helsdingen, 1993) about habitat associations into broader variables reflecting surrounding landscape, characteristics of the aquatic and terrestrial habitat on the site and detectability.

1.2. Detectability and Occupancy Modelling

Despite their size and the fact that they are the only two fishing spiders occurring in Europe, the genus *Dolomedes* has a history of mis-identification and non-detection in Europe. Current status and distribution history are therefore unclear (Duffey, 2012). Mis-identification issues arise from the confusing morphology of both occurring species of the genus *Dolomedes*. While both species have a "typical" morphology (*D. fimbriatus* with white stripes, *D. plantarius* unicolour dark brown), both species can also be more similar to the typical morphology of the other species (Duffey, 2012). Safe determination is only possible by inspecting the genitals (Helsdingen, 1993).

Detection of *Dolomedes* is difficult due to the semi-aquatic lifestyle, which includes fleeing behaviour on the water and under the water surface when the spider is disturbed (Gorb & Barth, 1994), the general inaccessibility of wetlands and general detection issues concerning invertebrates (*e.g.* Noreika et al., 2015). In Belarus, *D. plantarius* was found in several previously unknown sites when searching for the species (Ivanov et al., 2017). The authors claim that the perceived rarity of *D. plantarius* may be explained partly by the lack of interest as well as the lack of specialists (Ivanov et al., 2017).

Observed non-detection can be caused by either detection failure within an occupied site or by the species really being absent (Royle & Nichols, 2003). A review by Kellner & Swihart (2014) showed that only few studies account for imperfect detection. Detection issues were addressed even less in studies on invertebrates than on other taxa (Kellner & Swihart, 2014). Occupancy modelling offers the possibility to separate the ecological from the observational component of the detection process (Kéry & Schaub, 2012). Thereby, it is possible to obtain the probability of presence of a species in a site, even if the animal was not detected or is currently not present (Kéry & Schaub, 2012). If species are difficult to detect one solution is to search for signs of the species rather than for the animal itself (*e.g.* Charbonnel et al., 2014). While Pisauridae do not build webs for catching prey, they build webs as part of

maternal behaviour (Foelix, 2010). It is possible to use nursery webs as units of detection during the breeding season of *Dolomedes.*

Even though direct dependence of spiders on specific host plants is not known (Jiménez-Valverde & Lobo, 2007), relationships between spiders and vegetation structure have been found (Foelix, 2010; Jiménez-Valverde & Lobo, 2007). *Dolomedes* species have been associated with certain wetland types, plant taxa and vegetation structures (summarised in Table 1 in accordance to Duffey, 1995, 2012; Helsdingen, 1993). The nursery web of *Dolomedes*, on which the survival of the offspring depends, causes a potentially close relationship between *Dolomedes* and the vegetation of their habitat.

1.3. Nursery Webs: Placement and Timing

Maternal behaviour is common in spiders. Nursery web spiders (Pisauridae) show maternal care for their offspring in pre- and post- emergence stages. In the pre-emergence stage, they carry the egg sac in their chelicerae for two to three weeks. In the case of Pisauridae, a cocoon for the eggs is built and carried in the chelicerae. Before the spiderlings leave the cocoon, the mother builds a nursery web in the vegetation, in which she places the cocoon and guards the spiderlings thereafter (Foelix, 2010).

Dolomedes build their nursery webs close to the water in the marginal vegetation. If suitable vegetation is available, they even build their webs above the water surface, maybe to reduce predation risks (Duffey, 2012). Vegetation characteristics such as tussocks and flexible and crossing vegetation structures are assumed to be important for nursery web building (Duffey, 2012). Certain plant groups, such as *Carex*, *Juncus* and *Stratiotes alloides* are known as host plants for nursery building of *Dolomedes* (Duffey, 2012). Reproduction of *Dolomedes* usually takes place in the early summer, with decreasing reproduction events later in the summer (Pearson, 2008). Thereby, detectability of nursery webs (which is probably higher compared to detectability of spiders) is bound to time of reproduction and is thereby related to time of the year and probably other factors such as elevation, latitude and climatic factors. The age of dispersal of *Dolomedes* has been reported with variation between three days and one month (Duffey, 2012). There is no evidence for air dispersal in *D. plantarius*, while *D. fimbriatus* may disperse in the air, as juveniles were often found far from open water (Duffey, 2012). *D. plantarius* may disperse by water as hypothesised for *Dolomedes* species in America by Carico (Carico, 1973; Duffey, 2012).

1.4. Study Questions and Approaches

1. Which habitat characteristics are associated with the presence of *D. fimbriatus*, *D. plantarius*, or with the presence of both species?

2. How probable is it to detect *Dolomedes* in a site, using nursery webs as detection units and which factors impact detectability?

3. How does the number of detected nursery webs relate to the time in the year (summer)?

4. Where do *Dolomedes* place their nursery webs?

On site scale (1), I looked at habitat characteristics for both species, investigating potential causes of niche partitioning and coexistence of *D. fimbriatus* and *D. plantarius*. (2) Because of the often mentioned difficult detection of *Dolomedes*, I tried to estimate the detection probability of nursery webs to assess the probability of presence of the species in a site, when I did not detect any individual. (3) Because timing during the breeding season is a determining factor of finding nursery webs, I investigated the number of nursery webs in relation to time during our fieldwork, elevation and latitude. (4) On the finer scale, I investigated habitat requirements for nursery web placement within occupied habitats to define habitat requirements for reproduction of *Dolomedes*.

Table 1: Habitat association of Dolomedes plantarius and Dolomedes fimbriatus, summarised from Duffey 1995 (D1), Duffey 2012 (D2) and Helsdingen 1993 (H) with consequential variables collected. Plant groups, marked in this table with 'sp' and 'spp' are in the following text named without those to facilitate readability.

	D. plantarius	D. fimbriatus	Variables collected
Habitat type	Fenlands, tree-less, open habitats, large rivers, ditches with extensive cattle breeding (H),	Marshes, bogs, meadows, sparsely forested areas, swampy forest, wet heathland (H), oligotrophic wetlands (D1)	Vegetation type, type of surrounding, cattle grazing
Water dependency	Living on the water surface, preying, building nursery webs in vegetation above water surface (H), clear and clean, standing or slow flowing water (D2)	Needs water surface only during mating period, otherwise wet soil is sufficient (H), ground waterlogged (D1)	water type, water speed, water clearness
Aquatic vegetation	Stratiotes aloides (nursery building), Hydrocharis morsus-ranae (indicators for mesotrophic waters) (H), vegetation at the water edge (D2)		aquatic vegetation, type of aquatic vegetation, Abundance of Stratiotes, Nuphar and Hydrocharis
Terrestrial vegetation	Cladium mariscus, Carex spp., Calamagrostis canescens, Juncus spp., Phragmites australis, Schoenus nigricans, Typha spp, Rumex sp. Marginal vegetation (D1, D2)	Sphagnum spp., Erica tetralix, Calluna, sedges, Juncus, Carex, Cladium mariscus, Phragmites australis (D1)	Abundance of Carex spp., Juncus spp., Sphagnum spp., Typha spp., deciduous plants
Vegetation structure	Aquatic macrophytes with floating leaves on the water, tussocs (D2)	Tall herbs for nursery building (H)	horizontal cover (10, 30, 50 cm height), average height, maximum height, abundance of crossing structures
Detectability	dives when disturbed, cryptic (H)		Sampling type (dependent on water body present), temperature, cloudyness, rain
Threats	drying out of wetlands, changes in land use, decrease in range and quality of wetland areas (H)	agricultural drainage (H)	
Microclimate	no shading bushes (D1), shading reed may have stronger negative effects in colder climates (D2)	humid vegetation (D2)	shade, humidity at ground level and at 20 cm
Nursery web building	above water surface (H)	high in tall herbs (H)	nursery height, nursery host plant
Elevation, Latitude, Longitude	lowland species (D1)	up tp 1200 m (D1)	elevation, lat/ long

chemical environment	avoids waters with low ph, mesotrophic wetlands (D1)	oligotrophic wetlands, more flexible (D1)
flexibility	less flexible (D1)	wide range of environmental situations, elevation, latitudinal distribution, type of wetlands, shading (D1)

2. Methods

2.1. Study Area

The study sites were located in Sweden and Norway and are displayed in Figure 1 (background map obtained from OpenStreetMap contributors, 2017). A list of study sites with GPS positions is available in Appendix A.
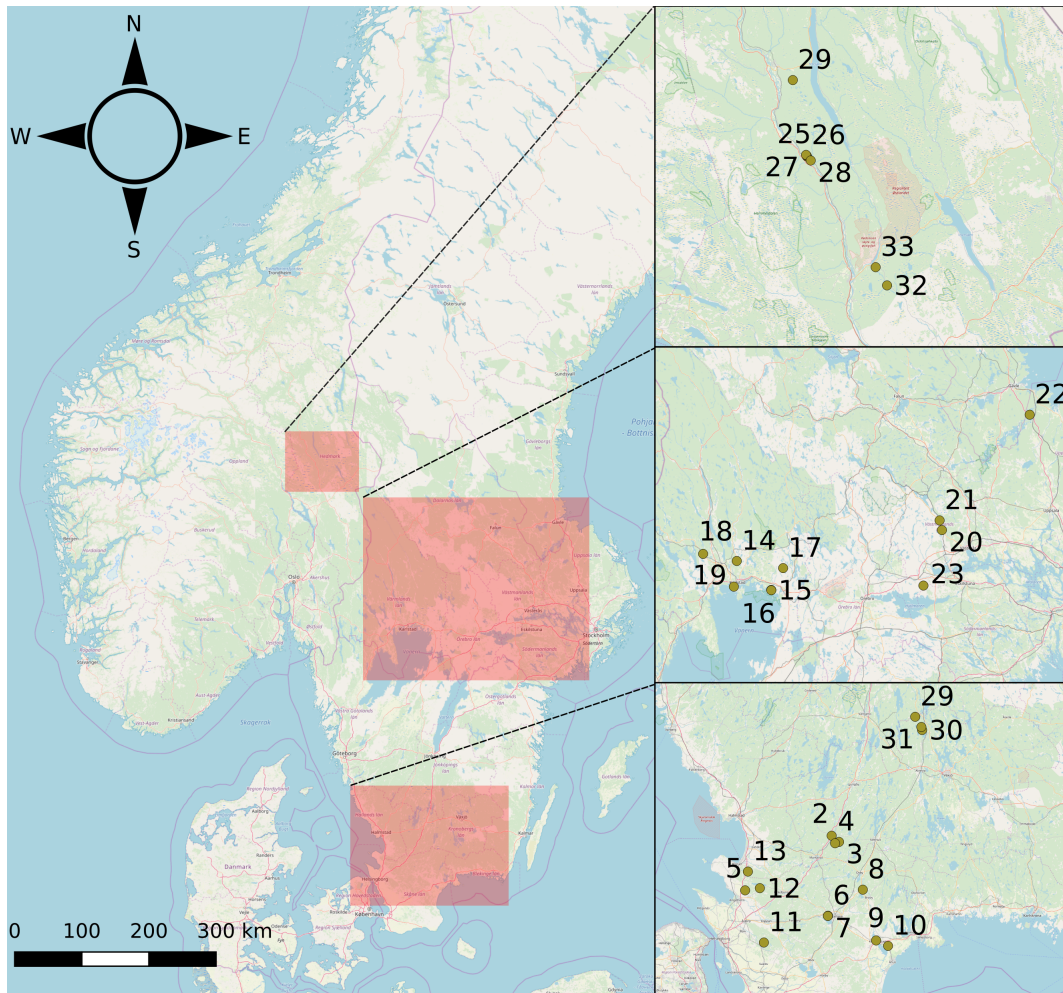

Figure 1: Overview map of the study area in Sweden and Norway (left) with detail maps of the three study areas (right). The background map is obtained from OpenStreetMap.

2.2. Data Collection

2.2.1. Choice of Study Sites

I chose study sites based on prior observations extracted from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/, full list of citations available in Appendix A) using the R package rgbif (Chamberlain, Barve, Mcglinn, & Oldini, 2019). Additionally, I visited highly suitable habitats according to the suitability map (for *D. plantarius*) by Leroy et al. (2013). The resolution of the suitability as well as the accuracy of the GBIF positions was low. Therefore, I did a selection of samling area within the highly suitable habitat and close to the GBIF positions based on information from the literature (see Table 1).

I chose water bodies with riparian vegetation and other types of wetlands (bogs, fens, meadows) for data collection. Because the model by Leroy (Leroy et al., 2013) is only valid for *D. plantarius*, I decided (outside of high suitability for *D. plantarius*) the potential suitability for occurrence of *D. fimbriatus* (implying potential data collection) according to the visual impression of the wetlands. I considered a wetland as potentially suitable, if it provided water and riparian vegetation or plant species which are indicating wetness (*e.g. Juncus, Carex, Sphagnum*), as *D. fimbriatus* is also known to occur in habitats without open water (see Table 1). A study site was defined by natural borders or ended after 5 transects (*i.e.* 40 m along the water body, see transect description below).

2.2.2. Spider Detection and Handling

I searched for spiders visually and with a sweep net in the whole study site. In case of wind, cloudiness or rain, spiders tend to hide under leaves. Because the detectability of free-ranging spiders varies with weather conditions (*e.g.* Noreika et al., 2015), I conducted the field work during the breeding season, when nursery webs are potentially present. Females can often be found close to nursery webs, which is useful for identification, as only adults can be identified with certainty. In case of wind or rain (Beaufort scale > 3, equivalent to 12-19 km/h wind speed), I did not do spider detection attempts to keep detection conditions equal. Additionally, I recorded cloudiness, rain and wind as variables at the beginning of each data collection. We searched for nursery webs and spiders between 10 min (2 people) and 20 minutes (1 person) on each site. If possible, I walked in the water and searched the edge of the vegetation both visually and with an insect net, while wading through the water. If accessing the water was not possible (*e.g.* due to quality of the substrate, strength of stream or water depth), I moved carefully across the riparian vegetation to the contact zone

of marginal vegetation and water and applied the same search strategy. I found most adult females in nursery webs or in the nearby vegetation, or on the water. I captured the spiders in a glass container. If the spider dived, I tried to catch it with a fishing net from the water and transferred it into a glass container. Once inside the container, it was pressed gently with a soft sponge against the glass, to inspect epigyne or pedipalpen with a magnifying glass to record the species, i.e., *D. fimbriatus* or *D. plantarius* (A picture of the identification process is available in Appendix A). I released all spiders after the identification. I georeferenced all detected nursery webs and successfully captured spiders.

2.2.3. Collection of Habitat Data

I collected all data using the data collection software KoBoToolbox (2002). I used an anemometer (*Multi-Purpose Anemometer*, n.d.) to measure temperature, humidity and wind. I collected habitat data at two resolutions. I collected variables regarding vegetation type, land use and surroundings at site level, thereby for the whole study site (see Table 2). As *Dolomedes* are considered to be semi-aquatic, measurements on plot level are most concentrated around the water body or in the wet center of study sites without open water. The focus on the shore-area (or wettest area in the site) is reflected by the higher density of plots (see Table 2). Because of the low abundance of nursery webs, I additionally collected the same measurements around nursery webs, which I found in the whole site. I georeferenced all data points (*i.e.* longitude, latitude and precision of the position for sites and plots; using Blackview, 2013), assigned an individual ID to them (*i.e.* site ID, plot ID) and recorded starting time and date of the data collection. I extracted elevation for all habitat data from the digital elevation model (DEM).

Data Collection on Site Level

I collected variables on site level concerning the vegetation of the site, water characteristics, information about the surrounding and variables which might influence the detectability of invertebrates. Measured variables are displayed in Table 2.

Table 2: Variables collected on site level. Variable name and explanation or levels in case of categorical variables.

Variable	Description
reason visit	suitable habitat / GBIF / other
Dolomedes fimbriatus	present / absent
Dolomedes plantarius	present / absent
site name	unique name
time stamp	date and time (start of data collection)
temperature	measured with aerometer
wind	measured with aerometer on Beaufort scale
cloudiness	yes / no / partly
cattle grazing	yes / no
water clearness	clear / brown / murky / no water
water speed	fast / slowly / standing / no water
water type	bog / creek / drainage channel / lake / pond / river / other
aquatic vegetation	yes / no
type aquatic vegetation	Hydrocharis / Nuphar / other rooted / other unrooted / no
surrounding	buildings (non-industrial / industrial) / fields / forest / infrastructure / other
surrounding forest	if surrounding is forest, which type
vegetation type	coniferous forest, deciduous forest, open wet, open dry, dry with wet indicators
dominant plant group	Calluna / Cyperaceae / Equisetum / Juncaceae / Menyanthes / Myrtillus / Phragmites / Poacea / Quercus / Sphagnum
dominant tree at site	Betula / Pinus / Quercus / Salix / Ulmus / other

Data Collection on Smaller Spatial Scale

Within each site, I placed transects to arrange sampling plots systematically along them (see Figure 2). If open water was present, I placed transects perpendicular from the water body with a distance of 10 m to each other. If no open water was present, I placed transects in a gradient from wet to dry. If no gradient was detectable, the transects started (at random) from a habitat edge, *e.g.* a forest edge, with the goal to represent the area of interest. I recorded the applied sampling type for each site.

I placed the transects perpendicular to the water body (if present). I measured one to three terrestrial plots and one aquatic plot (if open water present) per transect. I measured aquatic vegetation and habitat characteristics (see Table 3) in one half circle (aquatic plot, r = 1.5 m), centered where the transect met the water body.

Terrestrial plots (1.5 m radius) were located at two, seven and twelve meters from the water edge. In some cases the riparian vegetation was limited to the first few centimeters after the water edge, in which cases I inserted a fourth terrestrial plot in the shape of a half circle (r = 0.5 m) with its center at the water edge (see *tw* plot on Figure 2). The shape of the additional plot differed from the others to avoid overlapping. Additionally, I collected the same variables around all detected nursery webs (r = 1 m).

To collect abundance data of vegetation on an ordinal scale reduces precision and effort (Podani, 2005). I used the extended Braun-Blanquet scale (see Table 4; Reichelt & Wilmanns, 1973) for quantification of vegetation variables, which is an ordinal scale traditionally used for compositional vegetation data (*e.g.* Damgaard, 2014). I modified it slightly to quantify targeted groups of plant species as well as structural vegetation characteristics (see variables in table 2 and 3).
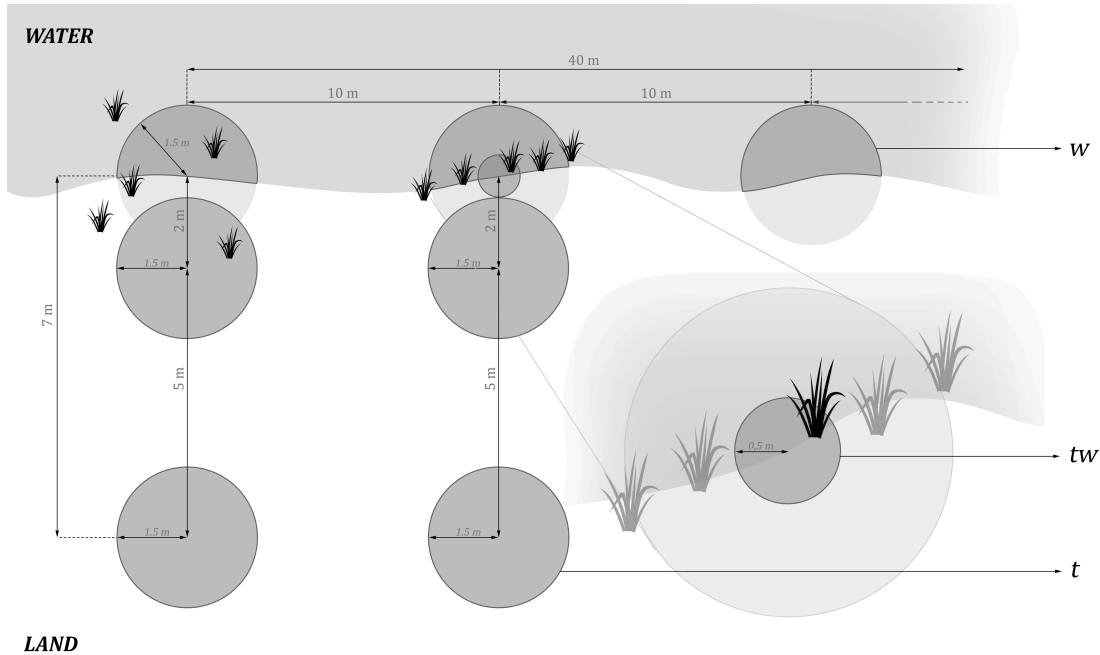
Figure 2: Displayed are the different plot types, the aquatic plot (w), the terrestrial plot (t) and the additional plot at the water edge (tw). Example of transects without (left) and with (right) inserted plot (r = 0.5) to represent marginal riparian vegetation.

Table 3: Variables collected on plot level on aquatic and terrestrial plots.

Variable	Description
aquatic plot variables	
Dolomedes detection	spider / nursery web / no
aquatic vegetation	Braun-Blanquet scale
Hydrocharis /Nuphar	Braun-Blanquet scale
Stratiotes sp.	Braun-Blanquet scale
vegetation touching water	Braun-Blanquet scale
vegetation covering water	Braun-Blanquet scale
substrate	mud / sand / stones / other
covered by tree	yes /no
terrestrial plot variables	
Dolomedes detection	spider / nursery web / no
plot type	nursery web search / transect plot
distance to water	no water / 0 m / 0.7 m / 2 m / 7m
humidity	measured at ground level and at 20 cm height
dominant plant group	dominant group of plants in plot
horizontal cover	measured at 10, 30, 50 cm
maximum height	maximum height of vegetation, measured with accuracy of 10 cm
average height	Mesured 5 times randomly with accuracy of 10 cm

tussocks	tuft of grasses or sedges, measured with Braun-Blanquet scale
large leaves	yes /no
litter	yes /no
shade	yes /no / partly
crossing structures	amount of crossing vegetation structures, measured with Braun-Blanquet scale
Carex spp.	Braun-Blanquet scale
Juncus spp.	Braun-Blanquet scale
Typha spp.	Braun-Blanquet scale
Phragmites spp.	Braun-Blanquet scale
Sphagnum spp.	Braun-Blanquet scale
deciduous plants	Braun-Blanquet scale
aquatic vegetation	yes /no
nursery web detection	yes /no
nursery height	height of nursery web above the ground or water
nursery plant	host plant of nursery web
number nursery in plot	number of nursery webs in one nursery plot (r = 1m)

2.3. Data Preparation and Exploration

I prepared and analysed all data in R (R Core Team, 2018), using the interface R Studio (RStudio Team, 2012). I prepared the data using the package dplyr (Wickham, Francois, & Henry, 2018). I explored the data using the packages ggmosaic (Jeppson, Hofmann, & Cook, 2018) and psych (Revelle, 2018) for categorical and ordinal data and ggplot2 (Wickham, 2016) for numerical data, following the protocol for data exploration by Zuur, Ieno, & Elphick (2010).

I discarded site 29 (Koppang), because I found a nursery web, but no spider. It was not possible to assign the nursery without doubt to a *Dolomedes* species, as it potentially could have been a web of another Pisauridae species. I discarded site 34 from the analysis, because I found *Dolomedes*, but could not identify the species, because I could not capture any individual. In three sites (site 3, 4 and 22), I could not conduct systematic transect sampling (due to high water or inaccessibility), therefore I collected only site specific data. Those sites are included in analysis on site level, but excluded from the occupancy modeling and nursery web analysis, which require the spatial sub-units (*i.e.* plots).

I collected variables on ordinal scale (Braun-Blanquet scale) to reduce measurement time and observer error. I reduced the levels of the variables collected on the extended Braun-Blanquet scale (Reichelt & Wilmanns, 1973) to 5 levels to facilitate model convergence and interpretability. Reduction of the levels was necessary due to small sample size. Each level of

Table 4: Extended Braun - Blanquet scale and simplification.

%	Number of individuals	Original scale	Simplified scale
0	0	no	0
< 1	1	r	0
< 1	2 - 5	+	0
< 5	6 - 50	1	1
< 5	> 50	2m	1
5 - 15		2a	1
16 - 25		2b	1
26 - 50		3	2
51 - 75		4	3
76 - 100		5	4

a variable is treated in models as one variable and leads to the estimation of one parameter, which makes it too costly to use the initial scale with the size of my data set. Additionally, convergence problems can emerge from unobserved levels or unobserved combinations of variable levels. The initial levels of the scale and the reduced levels are shown in Table 5.

I used the package psych (Revelle, 2018) to calculate the so-called polychoric correlation coefficient (Ekström, 2011) to assess associations between ordinal variables and to adjust model building in case of correlations. I used the suggested correlation threshold of 0.7 to exclude correlated variables from the same model (Dorman et al., 2012).

2.4. Data Analysis

My analysis consist of data description (site level), occupancy modelling (site and plot level), nursery web timing (site level) and nursery web placement (plot level). In the broad sense, they all serve the description of habitat requirements of *Dolomedes*. How all analysis types of this study relate to each other is displayed in Figure 3.
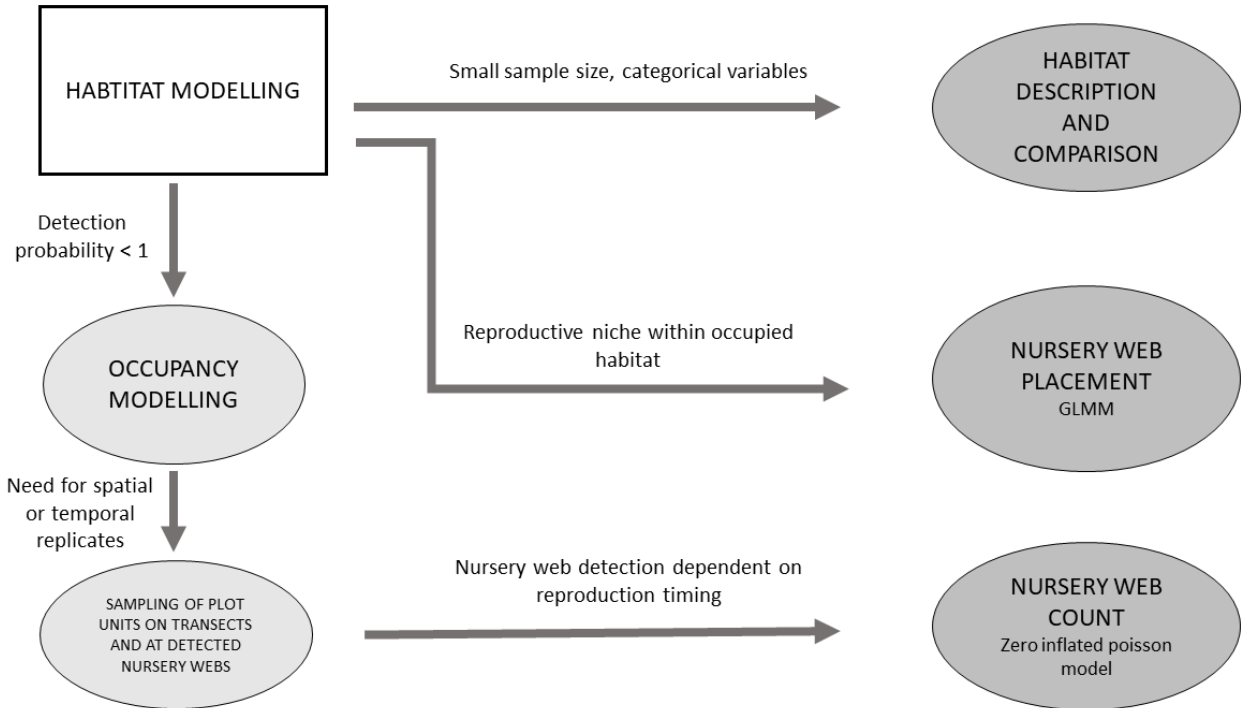

Figure 3: Overview of different analysis types and their relationship among each other.

2.4.1. Habitat Description

I compared sites in which *D. fimbriatus*, *D. plantarius*, both species and none of both species were detected. I visualised the comparison using the packages ggmosaic (Jeppson et al., 2018) and ggplot2 (Wickham, 2016). The small sample size and many categorical variables prevented me from fitting complex models (*i.e.* would have lead to overfitting), which is why I present descriptive results regarding habitat characteristics.

I did not include the variables on finer spatial scale in this analysis, because the sample sites represent a subjective, standardized measure, while the 'real' habitat only occurs in small proportions of the sample site. Therefore, the effect of the fine-scale variables are likely

diluted, when bringing them into site-specific analysis. Instead, the fine scale variables are related to the detection/ non-detection of nursery webs, which were measured on the same spatial scale.

2.4.2. Occupancy Modeling

Nursery webs are a convenient sign of *Dolomedes*, facilitating their detection. Furthermore, placement of nursery webs functions as one important indicator for *Dolomedes* habitat because it is determining reproductive success and survival. The nursery web reflects one part of the annual life cycle and thereby certain habitat requirements.

To model detection of *Dolomedes* I used a hierarchical state-space model. The hierarchical process allows to separate the ecological component from the observational component of the detection process (Kéry & Schaub, 2012). I used the single season occupancy model by (MacKenzie et al., 2002) within the unmarked framework (Fiske & Chandler, 2011). The single season occupancy model (MacKenzie et al., 2002) models detection and occupancy in a hierarchical binomial process, using zero-inflated binomial models. As unit of detection I chose the nursery web of *Dolomedes*, because detection of nursery webs is less vulnerable to weather conditions and disturbance, compared to detection of spiders. I measured nurserys webs which were close together within one nursery web plot, which was my unit of detection.

I pooled both species of *Dolomedes* for this analysis type for the following reasons:

1. I assume, that the detectability of nursery webs is similar or equal for both species, which may not be the case for (moving, individual) spiders.

2. The data are too sparse for separated models for both *Dolomedes* species.

3. If not encountering an adult spider in or in close proximity to a web, it is not possible, to distinguish nursery webs of *D. fimbriatus* and *D. plantarius*. Therefore assigning of nursery webs to one species relies on the assumption, that only the detected species of *Dolomedes* occurs. Where both species occur, it is not possible to distinguish based on this assumption either.

4. The model assumes the absence of wrong identifications.

State-space-models need repeated observations to model detectability, using usually temporal replicates. As temporal replicates were not feasible in this study design, I used spatial

replicates instead, as discussed in Charbonnel et al. (2014). As spatial replicates I used the plots measured in each site.

To model occupancy, I considered the variables **type of water, speed of water, surrounding** and **type of surrounding forest** as covariates. To model the observation process, I considered variables related to climatic and micro-climatic conditions (**temperature, cloudiness, rain, shade**), vegetation structure (**crossing structures, maximum height, horizontal coverage**) and sampling related variables (**sampling type, water type**).

I built intercept-only, univariate, and additive models for both model formulas (process of occupancy state and process of observation) and formed meaningful combinations of both formulas. In total, I built 37 models. I conducted model comparison using the Akaike Information Criterion (AIC, Burnham & Anderson, 2002). After finding the best model according to AIC, I used parametric bootstrapping provided by the unmarked package, to asses model fit (Fiske & Chandler, 2011). I visualised the estimates using the package forestplot (Gordon & Lumley, 2017) and created tables of model selection and model building using the packages knitr (Xie, 2018) and kableExtra (Zhu, 2019).

2.4.3. Nursery Web Count

I fitted a zero-inflated Poisson regressions to model the count of nursery webs per site. I considered **elevation, latitude, longitude** and time of the fieldwork (**week number**) as predictors.

Previous to model building, I standardised continuous predictors and checked for correlations. Because the correlation between elevation and latitude exceeded 0.7 (-0.71 Pearson correlation), I decided to include elevation only (Dorman et al., 2012). Elevation is inseparable of longitude in this case, as an increase in elevation corresponds to a simultaneous increase in latitude. As a measurement of time, I introduced a variable for the number of week during the field season.

When counting nursery webs, there are different sources of zeros possible:

1. The species may be absent in the site.

2. Within occupied habitats, nursery webs are a temporally rare event and can be absent in the moment of the observation.

3. If they are present, they may not be detected. A combination of true and false zeros (Welsh, Cunningham, Donnelly, & Lindenmayer, 1996) indicates the use of zero inflated mixture models (Martin et al., 2005). Due to the low number of observations, I could only fit relatively simple models.

I built intercept-only, univariate, additive and interaction models using the package pscl (Zeileis, Kleiber, & Jackman, 2008). I compared the models with the Akaike information criterion with correction term for small sample size (AICc, Burnham & Anderson, 2002), using the package MuMin (Bartoń, 2018). Overall, I built 11 models.

2.4.4. Nursery Web Placement

Lasso Regression to Identify Relevant Variables

The data set was too small to fit complex models including all variables. Therefore, I used regularisation to reduce the number of variables to consider. To identify the most important variables to explain nursery placement, I used the Least Absolute Selection and Shrinkage Operator (lasso; Tibshirani, 1996), fitted with the package oem (Huling & Chien, 2018). The lasso regularises parameters to zero, *i.e.* drops them and is thereby useful for variable selection. As each level of a ordinal variable acts as one variable, I used group lasso penalty, to force all levels of a given categorical variable to enter the model at the same moment. Maximum likelihood estimation was used for fitting lasso regressions. I standardised all continuous variables previous to model fitting.

For better readability of the plots, I split the variables into groups (1. grass-like plant groups, 2. other plant groups, 3. structure, 4. humidity, litter, distance to water) and fitted group lasso regressions for each variable group separately. Previous to fitting the model, I reduced the observations of each group to complete cases. Therefore, each of the lasso regressions is fitted to a slightly different data set, to base the variable selection per group to the largest number of observations possible. The response of each lasso regression was **nursery web presence/ absence** (within occupied sites), following a binomial distribution.

I identified the most influential variables from each group lasso regression by inspecting the visual output of each lasso regression and the cross validation plot (an example is displayed in Appendix E. I combined the selected variables of each group in one additional lasso regression.

Modeling of Nursery Web Placement

I used logistic regressions, to assess the probability of the presence of nursery webs given habitat characteristics in occupied sites. I used for this models the systematic transect plots as well as the additional plots, which I measured around detected nursery webs in the whole site, *i.e.* independent of the transects (n = 234 in 20 occupied sites). I used **nursery web presence/ absence** as response or, more accurately 'detection-non-detection' (Kéry & Schaub, 2012).

I used the predictor variables in the logistic regressions, which I identified with regularisation in the previous step. Because of the nested structure of the study design (plots within sites), I used a random intercept for **site ID** to avoid pseudo-replication (Harrison et al., 2018). I built overall 45 generalised linear mixed models with single predictors, additive models and interaction models.

I fitted all models in STAN (Carpenter et al., 2017) via the R package rstanarm (Goodrich, Gabry, Ali, & Brilleman, 2018), using the default weakly informative priors of the package. While the default prior does not strongly influence the posterior distribution, it reduces the posterior uncertainty and helps to stabilize computation compared to an uninformative prior (Muth, Oravecz, & Gabry, 2018). I fitted all models with 4000 iterations and controlled for effective sample size above 2000 and a Rhat (MCMC convergence statistic) under 1.1 (Muth et al., 2018). I compared the models using the leave one out cross validation using the package loo (Vehtari, Gabry, Yao, & Gelman, 2018). For the final model, I checked convergence of the Markov chains (Muth et al., 2018), using the package shinystan (Gabry, 2018). To assess model fit, I used posterior predictive checking. I compared visually the prior and posterior distribution of the parameter estimates (Goodrich et al., 2018). I visualized the estimates of the Bayesian models using bayesplot (Gabry & Mahr, 2018).

I decided for Bayesian modeling in order to obtain the full posterior distribution of the parameter estimates. Due to my small data set, I expected large uncertainty of my estimates. Credible intervals offer better possibilities for interpreting this uncertainty by displaying its assymetry and by simplifying the interpretation of uncertain parameter estimates (Gelman et al., 2013).

3. Results

3.1. Habitat Description

I detected *D. fimbriatus* in 12 sites, *D. plantarius* in 6 sites, both species in 4 sites and no *Dolomedes* species in 9 sites (n = 31). I related habitat characteristics descriptively with the detected species of *Dolomedes*. The positioning of the sites in longitude and latitude and the detected species is displayed in Figure 4.
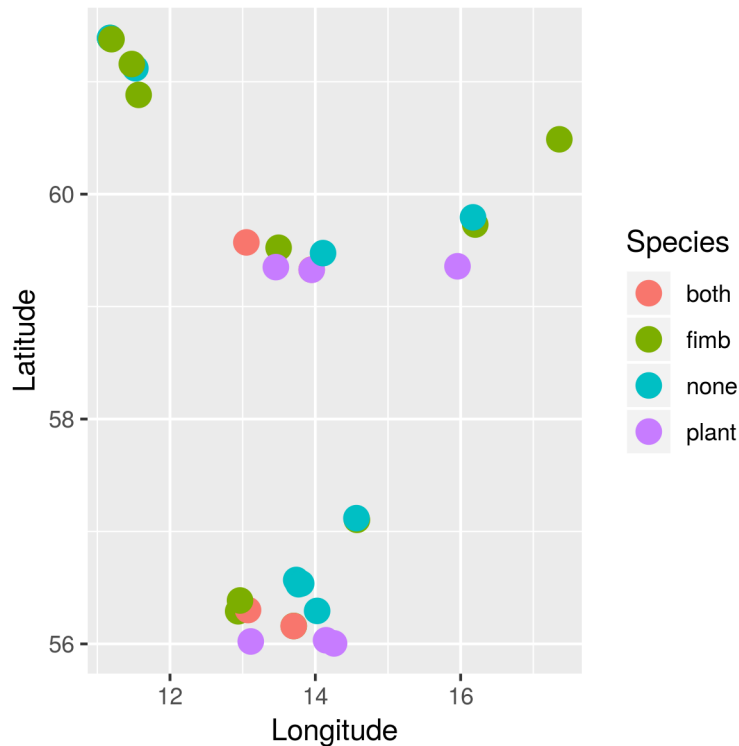
Figure 4: Species of *Dolomedes* (colour) in relation to longitude and latitude.

3.1.1. Description of Terrestrial Vegetation on Site

In most visited sites the vegetation was open and wet. Otherwise, *D. plantarius*, alone or together with *D. fimbriatus*, occurred in deciduous forest, while *D. fimbriatus* occurred in dry open areas and coniferous forest. *D. plantarius*, alone or together with *D. fimbriatus* occurred in sites in which the dominant plant groups were exclusively *Carex*, *Phragmites* and *Juncus*. The dominant plant group in absence (non-detection) sites and sites occupied by *D. fimbriatus* was more variable. In contrast to sites occupied by *D. plantarius* and both species,

Sphagnum or *Equisetum* are the dominant plant group in a proportion of sites occupied by *D. fimbriatus. Phragmites* did not occur as dominant plant group in any of the sites occupied only by *D. fimbriatus.* The dominant tree species was in all sites with both species *Betula*, in *D. fimbriatus* sites mixed with the largest proportion of *Pinus* (but also *Betula* and *Salix* occurring). In *D. plantarius* sites only deciduous trees were dominant (most often *Salix* and *Ulmus*). A higher proportion of the sites which are occupied by *D. plantarius* or by both species were grazed by cattle than of the sites occupied by *D. fimbratus* or none of the species.

3.1.2. Surrounding Landscape Type

Most sites occupied by *D. fimbriatus* were surrounded by forest. The sites occupied by *D. plantarius* were mixed regarding the landscape level, with also infrastructure and fields surrounding them. The sites with both species of *Dolomedes* were a mixture of the sites occupied by only *D. fimbriatus* and *D. plantarius* with mostly forest, but also fields and non-industrial buildings in a small proportion. The proportion of deciduous forest surrounding occupied sites was higher for *D. plantarius* and sites with both species than for *D. fimbriatus* and absence sites. A proportion of sites occupied by *D. fimbriatus* were also surrounded by pine forest and mixed forests consisting of pine and deciduous forest. Sites in which both species occurred were surrounded to a high proportion by deciduous forest and the remaining sites by mixed pine-deciduous forest.

3.1.3. Description of the Aquatic Habitat

All visited sites which were not occupied or occupied by *D. plantarius*, had either slow flowing or standing open water. One site with both *Dolomedes* species had no permanent water body. *D. fimbriatus* occurred mostly in sites with standing water, but also with slow and fast flowing water and in sites without open water. I found *D. plantarius* most often in river sites (beside a small proportion of ponds, lakes and others). I found *D. fimbriatus* most often in bogs, followed by lakes, ponds and creeks. I found both species in river sites, lake sites and a drainage channel. Sites in which I found *D. plantarius* or both species always contained aquatic vegetation, while absence sites and *D. fimbriatus* sites also occurred in sites without aquatic vegetation. The categories of water clearness (clear, murky, muddy, brown) did not show any association with the occurrence of *Dolomedes*. The proportion of vegetation touching the water surface was highest for sites with *D. plantarius* or both species occurring compared to sites in which only *D. fimbriatus* plots. In *D. plantarius* sites, the water plots were almost always covered by overhanging marginal vegetation, whereby

this was often not the case in *D. fimbriatus* sites. Sites in which both species occurred were in-between with a lower proportion of plots without covering vegetation. Rooted aquatic vegetation (*Hydrocharis*, *Nuphar* and other species) were present in high abundances in *D. plantarius* sites and sites with both species. *Stratiotes* were rare overall, and only occurred in *D. plantarius* sites.

3.1.4. Detectability related Variables

The reason for choosing sites for data collection was for sites in which I detected *Dolomedes plantarius* always known occurrence (GBIF.org, 2001). I found *D. fimbriatus* mostly in sites which I selected within the potentially highly suitable habitat (Leroy et al., 2013). I chose sites with both *Dolomedes* because of known occurrence of one of the *Dolomedes* species (GBIF.org, 2001) and once without previous knowledge of occurrence. The median of the temperature (collected at the start of data collection in each site) was lower for absence sites compared to the sites in which *Dolomedes* were detected, which is probably partly caused by the (on average) higher latitude of absence sites. The temperature was high at all data collection events in a range between 24 and 34 degrees.

Overall, I sampled more sites systematically from the water edge (systematic water sampling type) than from a 'wet centre' of the site (systematic wet sampling type). The sampling type is related to the presence of open water and thereby to the habitat type. *D. fimbriatus* occurred more often in the systematic wet sites compared to *D. plantarius*, while sites with both species were mixed in sampling type.

Additional figures of the described observations are displayed in Appendix B.

3.1.5. Elevation, Longitude and Latitude

In my sample, *D. plantarius* sites have a small range of elevations at low elevation, while I found *D. fimbriatus* at a wider range. Sites in which I detected *D. plantarius*, whether alone or together with *D. fimbriatus*, were at a lower elevation than absence sites or sites with *D. fimbriatus* alone. Sites with both species are on average higher than *D. plantarius* sites but lower than *D. fimbriatus* sites (see Figure 5). Latitude and elevation are correlated, so that latitude shows a similar pattern as elevation.
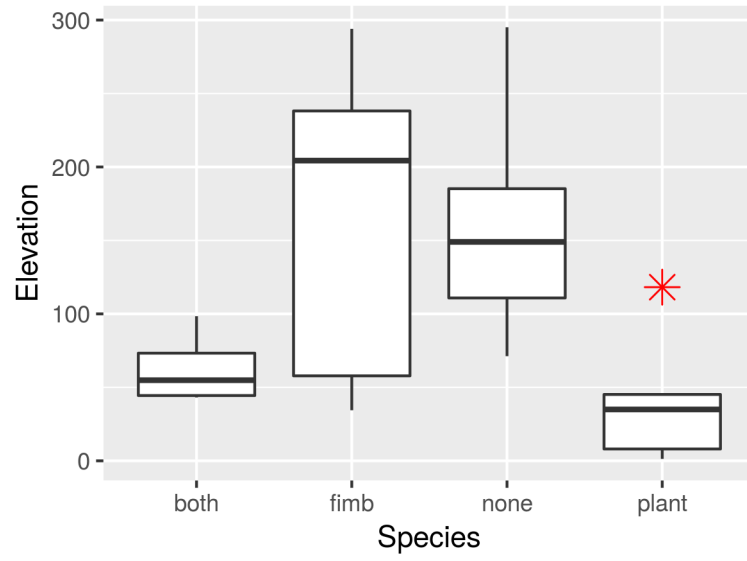
Figure 5: Boxplot showing the elevation range of sampled sites with presence and absence of *Dolomedes* species.

3.2. Occupancy Modeling

I modeled occupancy and detection, using nursery webs of *Dolomedes* as detection units. The overall sample size of sites was n = 28, the number of spatial replicates within sites was n = 329. I used 1 nursery sampling (with 2 nursery webs in one plot) collected on the systematic transect and 35 nursery sampling (43 nursery webs) in additional plots (measured because of nursery web detection on a site).

3.2.1. Model Selection

I conducted model selection with AIC. The results of the model selection are displayed in Table 5. The full AIC table is displayed in Appendix C. Model formulas of the 6 best models are displayed in Table 6.

Table 5: Results of the model selection of the 6 best models. Models were fitted in unmarked, using a one-season occupancy model. The table displays the negative log-Likelihood (negLog-Like), delta AIC (delta), Akaike Information Criterion (AIC) and the model weight (AICwt). A full table of the model selection is available in Appendix C.

model	negLogLike	delta	AIC	AICwt
ms5	89.36	0.00	202.71	0.45
m24	90.95	1.18	203.90	0.25
m11	92.86	3.00	205.71	0.10
ms2	89.36	4.00	206.71	0.06
ms4	92.57	4.43	207.14	0.05
ms8	92.86	5.00	207.71	0.04

Table 6: Model formulas for detection and occupancy part of the best models according to AIC.

Model Name	Detection	Occupancy
ms5	crossing str + temp + clouds + sampling type	aquatic vegetation + sampling type
m24	crossing str + temp + clouds	aquatic vegetation + cattle grazing
m11	crossing str + temp + clouds + sampling type	intercept only
ms2	crossing str + temp + clouds + sampling type	aquatic vegetation + water speed
ms4	crossing str + temp + clouds + sampling type	elevation
ms8	crossing str + temp + clouds + sampling type	latitude

3.2.2. Presentation of the Final Model

The final model contained the predictors **crossing vegetation structures, temperature, cloudyness and sampling type** for the modeling detection. Covariates for the occupancy in the final model were **aquatic vegetation** and **sampling type**. The parameter estimates are displayed in Figure 6 (occupancy) and Figure 7 (detection).
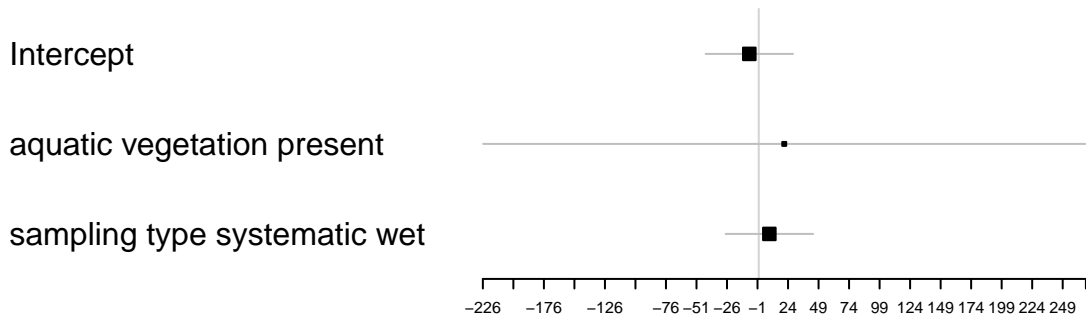

Figure 6: Estimates for Occupancy of the final model with the predictors aquatic vegetation (presence / absence) and sampling type. The intercept is a combination of aquatic vegetation absent and sampling type from the water edge (wet if there was no open water, water, if there was open water). Estimates are displayed on logit scale.
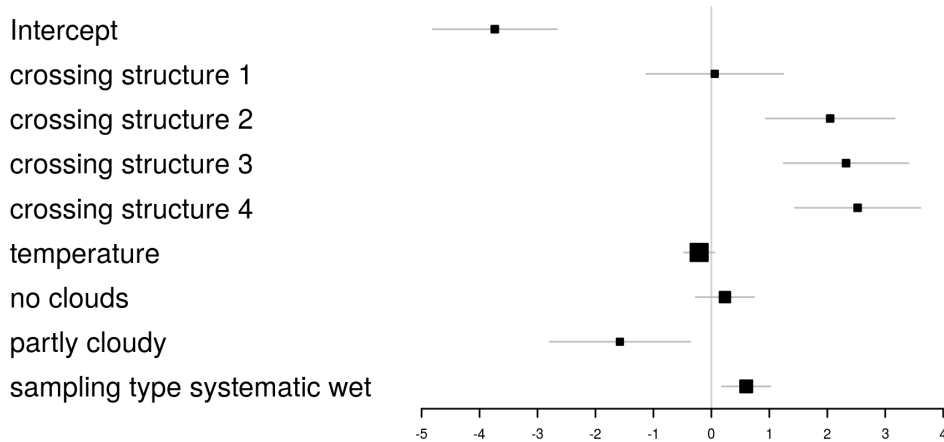
Figure 7: Estimates of the detection process of the final model. The variable crossing structure indicates the abundance of crossing vegetation structure, 1- 25 %, 2 = 26 -50 %, 3 = 51 -75 %, 4 = > 75 %. I measured temperature and cloudiness at the beginning of the data collection in each site. Wet sampling type indicates systematic sampling in sites without open water. The intercept is a combination of no crossing structures, mean temperature, cloudy and sampling type in sites with open water. Estimates are displayed on logit scale.

3.3. Count of Nursery Webs

I found 43 nursery webs in 31 sites during 8 weeks of data collection (n = 31). Nursery webs are as part of the brood development bound to the reproductive time. I used nursery webs as detection unit in the occupancy modeling, for which better understanding of the timing of nursery webs would be beneficial. To explore the dependency on time, I fitted a zero-inflated Poisson model. I visualised the nursery web count data for both species in Figure 8 and in relation to elevation and time during the data collection (*i.e.* week number) in Figure 9.
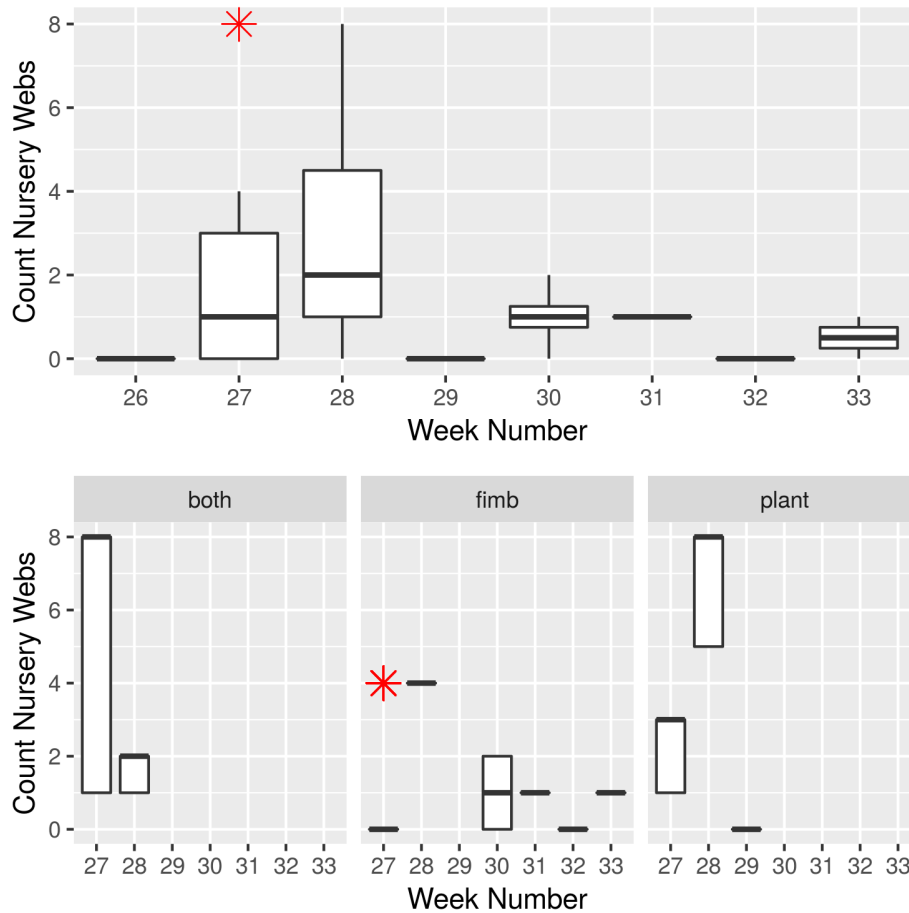

Figure 8: Boxplots displaying the relationship between week number during the data collection and the number of counted nursery webs per site for all sites pooled (upper figure) and separated by *Dolomedes* species (lower figure). Outliers displayed with a red star, black lines represent median.
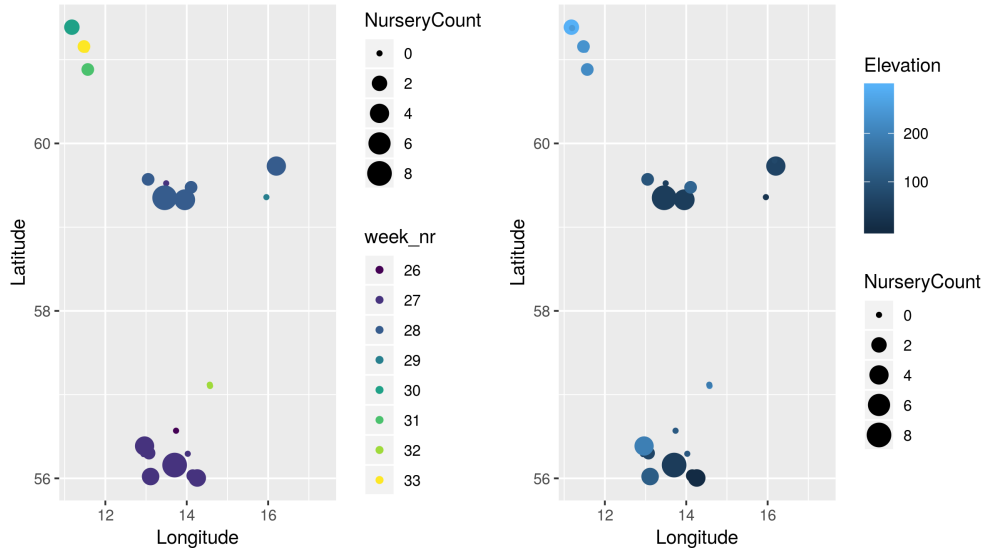
Figure 9: On the left: Plot displaying the relationship between week number (colour), number of counted nursery webs (dot size) and longitude and latitude. On the right: displaying the relationship between elevation (colour), number of nursery webs per site (dot size) and latitude and longitude.

3.3.1. Model Selection

I modeled the number of nursery webs found per site using time of the year (week number), longitude, elevation (correlated with latitude) and species as predictors and compared them with AICc (Burnham & Anderson, 2002). The results of the model selection are displayed in Table 7. There is uncertainty in the model selection, as shown by the distribution of the model weights. The full table of the model selection is displayed in Appendix D.

Table 7: Model selection of Nursery Count model with AICc. Displayed are the degrees of freedom (df), the log-Likelihood (logLik), the Akaike Information criterion with correction term for small sample size (AICc), the delta AICc (delta) and the model weight (weight).

	df	logLik	AICc	delta	weight
z1	4	-47.65	105.04	0.00	0.79
z2	4	-49.99	109.73	4.68	0.08
z4	4	-50.06	109.87	4.82	0.07
z3	6	-47.59	111.19	6.14	0.04
z0	2	-54.05	112.59	7.55	0.02
z5	8	-45.99	115.55	10.51	0.00

3.3.2. Presentation of the Final Model

The final model contained week number in both model parts (*i.e.* in the zero inflation and the Poisson part). The parameter estimate for week number and the uncertainty, quantified by the confidence interval, are displayed in Figure 10.

The model shows an uncertain (confidence interval crossing 0) and small effect of zero inflation (thereby, non-detection or other 'false zeros') and a negative effect of week number. The model describes the number of nursery webs decreasing during the time of my data collection.
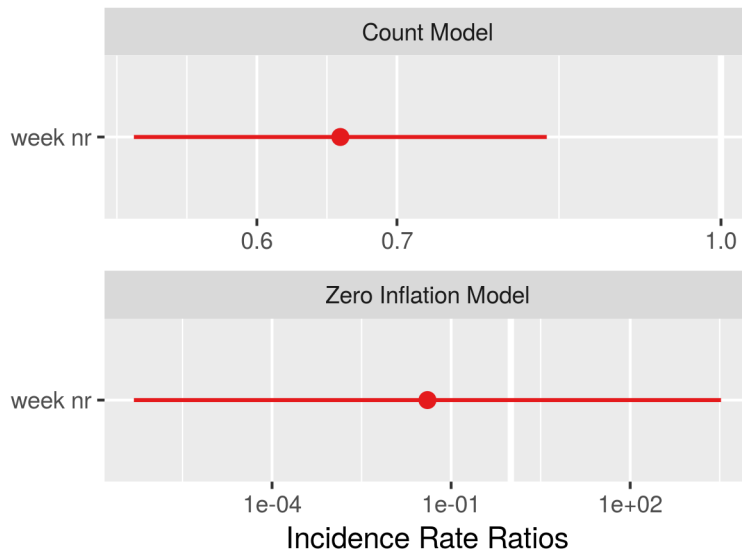
Figure 10: Final Model for the zero inflated mixture model (combination of binomial and poisson model; week nr = week number).

3.4. Nursery Web Placement

Beside the timing of reproduction, placement of nursery webs is one part of the reproductive behaviour of *Dolomedes*. It offers fine-scaled information about one part of habitat requirements and may thereby also improve detectability of nursery webs.

3.4.1. Description of the Nursery Web Micro-habitat

In sites where I detected only *D. plantarius*, I found overall 20 nursery webs. In sites in which I detected *D. fimbriatus*, I found 13 nursery webs. In sites with both species, I detected 12 nursery webs. I found nursery webs near *Typha* only on sites where *D. plantarius* was present

(alone or together with *D. fimbriatus*), but never on sites where *D. fimbriatus* was the only spider (*i.e.* identified adult) species. I found nursery webs of *D. plantarius* close to high abundances of *Carex*. In sites occupied by *D. fimbriatus*, the abundance of *Carex* was lower close to nursery webs. The abundance of *Carex* was lowest near the nursery webs in sites with both species. Only nursery webs of *D. fimbriatus* sites were associated with low to medium abundances of *Sphagnum*, while *Sphagnum* did never occur near the nursery webs of *D. plantarius* or near nursery webs in sites in which both species occur. I never found *Phragmites* close to nursery webs of *D. fimbriatus*, while I found it in low proportions close to the nursery webs of *D. plantarius*. Close to nursery webs in sites with both species, the proportion of *Phragmites* present was high, and *Phragmites* also occurred in high abundances. Nursery webs of *D. plantarius* were often associated with aquatic vegetation. A lower proportion of nursery webs in sites with both species contained aquatic vegetation. I recorded the smallest proportion of nursery webs associated with aquatic vegetation in sites occupied by *D. fimbriatus*. Near all nursery webs, I found crossing vegetation structures, but most abundant in nursery webs in sites occupied by *D. plantarius*. The horizontal vegetation cover at 10, 30 and 50 cm was on average higher near nursery webs compared to other plots, and on average slightly higher for *D. plantarius*. Average and maximum height did not show difference between species of *Dolomedes* as well as not between plots with or without a nursery web.

Nursery webs were never fully shaded and only a very small proportion of nursery web plots of *D. fimbriatus* and *D. plantarius* were in partly shaded plots. Nursery webs in sites with both species were never in the shade. The humidity at ground level and at 20 cm height above the ground was slightly higher in nursery web plots compared to plots in which no nursery occurred.

3.4.2. Plants Hosting Nursery Webs

Specification of the vegetation in the surrounding of the nursery web can point at structural and micro-climatic preferences of *Dolomedes*. One interesting aspect of the vegetation is the specific placement, *i.e.* the specific host plant, which the spider chose to place the web in. The proportions of different plant groups hosting nursery webs in my data set are displayed in Figure 11. 12 nursery webs had two or more plant species hosting them (only the main host plant is displayed in Figure 11). On average, the nursery webs of *D. fimbriatus* were located higher above the ground in the vegetation than those of *D. plantarius* (see Figure 12).
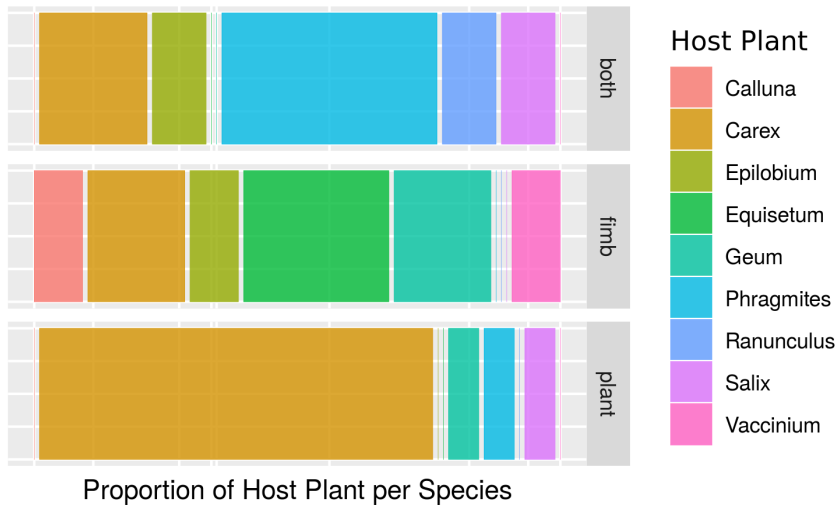
Figure 11: Mosaic plot displaying the main host plants for nursery web placement for each species. The width of the coloured area shows the proportion of each nursery web host plant.
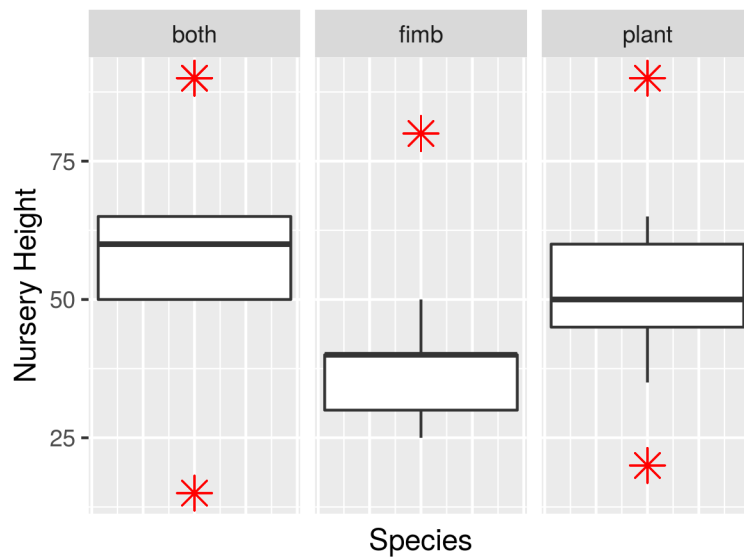
Figure 12: Figure: Boxplot showing the height of the nursery webs in the vegetation. Each vertical bar represents one category of *Dolomedes* (fimb = *D. fimbriatus*, plant = *D. plantarius*, both = both *Dolomedes* species.) Outliers are displayed as red star, median is displayed by a black line.

3.4.3. Pre-selection of Variables

After pre-selecting variables with the lasso regression, I kept the variables ***Carex, Typha, Phragmites, Spagnum*, aquatic vegetation, crossing vegetation structures, distance to water** and **shade** for further analysis. An example of the visual output of the lasso regression and the variable selection procedure are displayed and explained in Appendix E.

3.4.4. Model Selection

With the variables, which I pre-selected in the previous step, I built logistic regressions, which I compared by loo (Vehtari et al., 2018). There was uncertainty in the model selection according to the differences between the expected log predictive density of the models (see elpd_diff in Table; Vehtari, Gelman, & Gabry, 2017). I decided to interpret the first model, 'm43'.

The final model contained the predictors **aquatic vegetation, *Carex*, crossing vegetation structures, shade, distance to water, *Phragmites*, *Sphagnum*** and ***Dolomedes* species** (see Figure 12).

Table 8: Model selection with loo The full model selection table is available in Appendix E. The best model contained the predictors aquatic vegetation, Carex, crossing vegetation structures, shade, distance to water, Phragmites, Species and Sphagnum. Displayed are the expected log predictive density (elpd_kfold), the differences between the elpds of the models (diff_elpd) and the standard error of the elpd (se_elpd_kfold).

	elpd_diff	elpd_kfold	se_elpd_kfold
m43	0.00	-110.13	10.19
m28	-19.10	-129.23	11.09
m36	-20.24	-130.36	11.23
m31	-21.46	-131.59	11.22
m35	-21.72	-131.85	11.17
m32	-23.73	-133.85	11.49

3.4.5. Presentation of the Final Model

The posterior distributions of the parameter estimates (of the fixed effects) are displayed in Figure 13. The posterior predictive check as one part of the model validation is displayed in Appendix E.
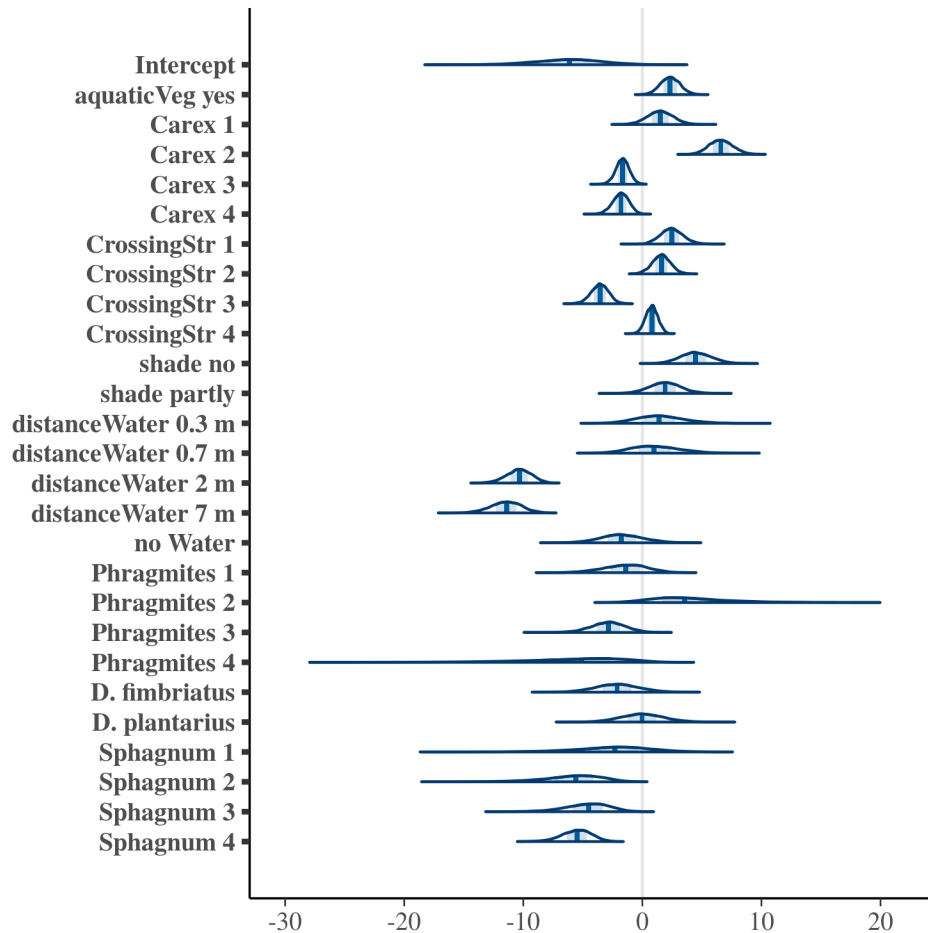
Figure 13: Posterior distributions of the estimates of the final model (m43) with the response nursery web placement (binary). The dark blue line represents the median of the probability distribution, the light blue shaded area represents 50 % of the probability distribution. Predictors of the model were aquatic vegetation, distance to water, *Carex*, crossing vegetation structures, shade, *Phragmites*, *Sphagnum* and species of *Dolomedes*. Plant abundance levels are represented by 1 = 0-25 %, 2 = 26-50 %, 3 = 51- 75 %, 4 = 76 - 100 %. I removed the random intercept (siteID) from the plot to improve readability. The intercept is a combination of abundance of *Carex, Phragmites, Sphagnum* = 0, distance to Water = 0 m, no aquatic vegetation, shaded, species = both *Dolomedes* species.

4. Discussion

In this study, I explored habitat characteristics associated with *Dolomedes fimbriatus* and *Dolomedes plantarius.* Furthermore, I tested the use of nursery webs as detection units and identified variables influencing detectability of those. To gain more knowledge about the reproductive behaviour of *Dolomedes* as well as about the nursery web as detection unit, I modeled placement and timing of nursery webs.

4.1. Habitat Description

Habitat characteristics of sites with both species and *D. plantarius* sites were in general more similar to each other than to *D. fimbriatus* sites. Still, they sometimes showed an intermediate frequency of habitat characteristics between *D. plantarius* and *D. fimbriatus* (wetland type, aquatic habitat characteristics, abundance of aquatic vegetation). This observation could be corresponding to the hypothesis of Holec (2000), that both species may occur in habitats of transition, *i.e.* in habitats, which are in the change from suitable conditions for *D. plantarius* to suitable conditions for *D. fimbriatus* or *vice versa*, can a temporal overlap of both species occur.

I found *D. plantarius* most often at slow flowing rivers, and *D. fimbriatus* most often in bogs. I observed *D. fimbriatus* in more than half of the occupied sites without permanent open water, reflecting the higher dependence of *D. plantarius* on open water. *D. plantarius*, alone or together with *D. fimbriatus*, never occurred without aquatic vegetation. In some of the sampled *D. fimbriatus* sites was no aquatic vegetation. Water speed was always slow or standing in *D. plantarius* sites, while in one of the sites with both species there was no open water.

I found *D. plantarius* alone and together with *D. fimbriatus* associated with cattle grazing. This could point at the lower tolerance of *D. plantarius* for shade, for example caused by higher vegetation. Cattle reduce the vegetation height and density by trampling and grazing, keeping thereby habitats open (Rook et al., 2004). At the same time, *D. plantarius* places nursery webs higher in the vegetation and is associated with slightly higher horizontal cover.

My study sites reflect an association of *D. fimbriatus* with forested habitats (in the surrounding and at the site), including coniferous forests. *D. plantarius* was associated with a variety of open habitats, as described in the literature, but those included also anthropogenous habitats. The association with open habitats and habitats close to human structures and

influences may be confounded, as I assume humans also rather to seek open habitats or to create them, *e.g.* in parks). Plantations of coniferous forests can acidify streams (Blacklocke, 2016). The association of *D. fimbriatus* with coniferous forest is in line with the literature, stating association with forested areas as well as higher tolerance for low pH of *D. fimbriatus*, compared to *D. plantarius* (Duffey, 1995).

Even though I sampled only a small range of elevations (between 0 m and 295 m above sea level), I found *D. fimbriatus* at a wider range of altitudes. I found *D. plantarius* only at relatively low elevations. This observation can be confounded with higher latitudes and occurrence in Norway of *D. fimbriatus*, as elevation and latitude are correlated in Scandinavia (and in particular in my data set). Interestingly, the elevation of sites with both species are on average lower than *D. fimbriatus* sites, but are relatively high compared to the *D. plantarius* sites. The differences in elevations could point at climatic conditions, restricting *D. plantarius* in its current distribution to lower latitudes and elevations compared to *D. fimbriatus*. Sites with both species present could be micro-climatically outstanding. Repeated measurements and increased monitoring over a long time frame would be needed to document, if the species persist in locations over time and if distribution shift occurs. My findings regarding habitat associations on the larger spatial scale (elevation, water type, characteristics of the aquatic habitat, cattle grazing, habitat type, surrounding forest) of *D. fimbriatus* and *D. plantarius* are in line with earlier descriptions by Helsdingen (1993), Duffey (1995) and Duffey (2012).

The need for aquatic vegetation and marginal vegetation, touching and covering the water surface for resting (by attaching the last pair of legs when staying on the water surface), was described by Duffey (1995) for *Dolomedes*. My data show especially association of aquatic vegetation with the presence of *D. plantarius*, alone as well as accompanied by *D. fimbriatus*. I also found high abundance of touching and overhanging marginal vegetation in all sites with *Dolomedes* detections, whereby the abundance is higher for *D. plantarius* compared to *D. fimbriatus*. More abundance of those structures in *D. plantarius* sites could point at less flexibility of the species, regarding the aquatic habitat. Also, because *D. fimbriatus* often occurs without permanent open water, the dependency on presence and structure of the aquatic habitat is potentially low compared to *D. plantarius* in general (Helsdingen, 1993). *Stratiotes* was associated with *D. plantarius* because of its structural qualities as well as an indicator for mesotrophic habitats (Duffey, 2012). While I found in general few *Stratiotes* in the sampled sites, it only occurred in *D. plantarius* sites. Duffey (2012) described the association of *D. plantarius* with *Stratiotes*, which he related to structural characteristics and indication of favourable pH condition, while also other abiotic factors may impact both species, *i.e. Stratiotes* and *D. plantarius* simultaneously, such as climatic conditions.

Sampling of more sites would allow to model differences between habitat requirements of *D. fimbriatus* and *D. plantarius*. Furthermore, multivariate analysis techniques as for example constrained ordination techniques could be useful to explore overlap and differences of the realised niche of both *Dolomedes* species (*e.g.* Dolédec, Chessel, & Gimaret-Carpentier, 2000).

4.2. Detectability

Detectability of Adult Spiders

I found both species of *Dolomedes* in close proximity to each other in overall four sites. All sites with only *D. plantarius* occurring were known beforehand as occupied, which was not the case for *D. fimbriatus* and sites with both species. This could be an indicator for better knowledge of *D. plantarius* sites compared to *D. fimbriatus*, for example due to more interest in a rare species. More 'unexpected' detections also point at higher abundance of *D. fimbriatus*. The fact that two of the overall four sites with both species were not recorded in the GBIF.org (2001) may indicate, that those habitats are to some extent not 'typical' *D. plantarius* sites (if the knowledge about *D. plantarius* sites is explained by interested people searching for the species) or were maybe only recently colonised by one or both of the species.

Accessibility and complexity of the study site may have affected detectability of spiders and nursery webs, and search from the water could have lead to higher detection probabilities. Especially *D. plantarius* is known to dive, when it is disturbed (Gorb & Barth, 1994) . The more vegetation movement is caused by the observer and the longer time the accessing of the water edge takes, the more probable is it to cause disturbance, lowering the probability of detection. If detection was attempted from the water or the land, could be incorporated in future protocols to model detectability.

Detectability of Nursery Webs (Occupancy Modelling)

Because detectability of invertebrates can be variable (Noreika et al., 2015) and is known to be difficult for *Dolomedes* (Duffey, 2012), I conducted occupancy modelling, using nursery webs as detection units. I assumed the detectability of nursery webs of both species to be equal, which I interpret to be supported, as the variable 'species' was not part of the final model.

Detection probability of nursery webs was higher where abundances of crossing vegetation structures was high. Increased temperatures had a potential negative effect (confidence interval overlapping 0) on the detection. Absence of clouds was beneficial for detection of

nursery webs compared to partly or full cloudy conditions. Detection probability was higher, when no open water was present (*i.e.* systematic wet sampling type).

The importance of crossing vegetation structures for detection could be caused by the importance of crossing structures for the presence of nursery webs instead (or additionally), which I could not account for due to the model structure. The impact of temperature and clouds on the detectability of nursery webs could be explained by the difference in light conditions or the humidity in the nursery webs, which could impact the visibility.

Furthermore, the age and state of the nursery web could impact detectability, as the webs degrade with time and especially after it has been abandoned. The use of nursery webs as detection units could be improved by specifying timing and duration of nursery webs by repeated visits (*e.g.* weekly) of the same sites and nursery webs. The data collection was not originally designed for occupancy modeling, causing restrictions in modeling and interpretations. Because I could only carry out a single field season, I used spatial instead of temporal replicates to model detectability as discussed in Charbonnel et al. (2014). This comes with the assumption of 'non-negligible occupancy probability', meaning it should be reasonable in each spatial replicate to find the species of interest (Charbonnel et al., 2014). This assumption may not be respected due to the narrow riparian vegetation of some sites. The sampling area exceeded in some cases the riparian vegetation. Especially for *D. plantarius*, the plots exceeding the marginal vegetation were not anymore potentially occupied (by a nursery web). To respect this assumption requires good knowledge of the habitat requirements of a species (*i.e.* in this case of the nursery placement).

Variables measured per spatial replicate were restricted by the model to the detection process. Therefore, I could not include variables collected on plot level in the occupancy part of the hierarchical model. For the presence of nursery webs, the variables on plot level (spatial replicate) were most probably of high importance for the presence of webs (as for example crossing vegetation structures, taxonomical plant groups, see section 4.4., nursery web placement).

The use of nursery webs as detection unit is useful to reduce sampling effort, increase detectability and thereby allows overall more replicates. Nursery webs also bring the difficulty of distinct identification, as a separation between *D. fimbriatus* and *D. plantarius* is not possible. If an adult female is found and identified in or around the web and successfully captured, I assumed, that the nursery contained her spiderlings. Thereby, when applying this assumption, searching for nursery webs may still increase efficiency, when sampling species-specific. It may especially be feasible, if also temporal replicates in sampling sites are

conducted, leading to higher probabilities of encountering the female during one sampling. The use of nursery webs to encounter females is especially possible, because of the sponge-technique used for identification in this study (see Figure in Appendix A). The method enabled me to determine the spider with certainty and to release the individual after the identification. The use of this method is possible for *Dolomedes* due to their large size. If more pictures of the species were available *e.g.* on GBIF, the value of occurrence data of *Dolomedes* would be improved. Furthermore, information about the method of identification would increase usability of those data, as the determination uncertainty could be included into models. Multi-species occupancy models can be used to model presence/absence and detection probability for several species and their coexistence and interaction, including the influence of the detection of one species on the detection of the second species of interest (Richmond, Hines, & Beissinger, 2010) . This may be applicable for studying *Dolomedes* furthermore, for example by exploring, how the by the observer expected species in a site influences the detection probability of that species compared to the 'unexpected' species.

4.3. Nursery Web Count

I used nursery webs as detection unit for *Dolomedes* in the occupancy modeling. Nursery webs represent one part of the annual cycle of *Dolomedes* and are bound to the time of reproduction. According to my model, the number of nursery webs decreased over time throughout the season. The timing and abundance of nursery webs is in accordance with observations from Great Britain, regarding the highest number of broods in the beginning of the breeding season (Pearson, 2008).

It could be expectable that the pattern of less reproductive success later in the season is similar and potentially even amplified in Scandinavia compared to the southern distribution range due to on average cooler climatic conditions. However, *Dolomedes* (or Pisauridae in general) may be fairly flexible in their reproduction, as the mother carries the egg sac (Foelix, 2010). Thereby, oviposition in the first part of the egg development (pre-emergence stage) is spatially and thereby potentially micro-climatically flexible.

Sampling of sites in different altitudes and latitudes along the season, temporal replicates and repeated evaluating the state of the nursery (*e.g.* each day or week) could bring more information about when, for how long, and where nursery webs are present. To visit sites during a season repeatedly for example several times a week and observe the development of the nursery webs would add additional information to the use nursery webs as detection units for *Dolomedes*.

A linear model can not fully represent a non-linear process of abundance of reproductive events, thereby the decreasing trend can only be interpreted for the time of the data collection. A non-linear model, as for example a generalized additive model, could improve modeling of the nursery web count, if more data are available. Due to the low number of observations, interactions could not be included in the models or were penalised during model selection. An interaction effect between time during the breeding season and climate and/ or latitude and elevation is imaginable and could be investigated, if sites with more variation in those variables would be sampled.

There may also be differences in the timing and the number of nursery webs dependent on the species of *Dolomedes*. The data exploration for the species separately suggests, that there may be a difference in the reproductive timing (see Figure 8). The plot shows later and wider distributed reproductive events of *D. fimbriatus* in our data set compared to *D. plantarius*. Nursery webs of *D. plantarius* were concentrated at the beginning of the data collection. Interestingly, in sites in which both species were observed, the number of nursery webs was even more concentrated to the beginning of the data collection (see Figure 8). The effect of inter-specific competition can lead to competitive exclusion, when there is a large overlap in resource utilisation (Gause 1934 and Hardin 1960, cited in Smith & Smith, 2009). Differences in reproductive timing, habitat and nursery web host plants could allow for co-occurrence of the two species, given there is competition between the species during reproduction. Differences between the species could also result from this competition as niche partitioning (Smith & Smith, 2009). A more realistic reason for the difference in reproductive timing could be the restriction of *D. plantarius* to certain climatic conditions such as temperatures, reflected also by the latitudinal and elevational restrictions of the species (Helsdingen, 1993).

Nursery web spiders (*Pisauridae*) have been found to have lower levels of intraguild-predation compared to wolf spiders (Nicholas, Stratton, & Reed, 2011). I found more often nursery webs of *Dolomedes plantarius* in close proximity to each other (on average, 1.25 nursery webs per nursery plot, r = 1 m), while this was less the case for *D. fimbriatus* (on average, 1.1 nursery webs per nursery plot). Sites with both species present exceed the number of nursery webs per plot in the single species sites slightly, with on average 1.33 nursery webs per nursery web plot. Linking the species of *Dolomedes* to the nursery webs in the sites with both species could improve understanding of the dynamics of both species and their reproduction, when both species are present.

4.4. Nursery Web Placement

Beside the timing, also placement of nursery webs is one crucial aspect of success of the brood development in the post-emergence stage (*i.e.* after the spiderlings leave the egg sac). I identified as most influential variables for nursery web placement distance to water, shade, abundance of crossing vegetation structures, *Carex*, *Typha*, *Phragmites*, *Sphagnum* and presence/ absence of aquatic vegetation (predictors in the final model).

Nursery webs were placed where there is no or only partly shade. The literature suggests, that *D. fimbriatus* is less sensitive to shading compared to *D. plantarius* (Duffey, 1995). Descriptive exploration of differences between the species showed general high avoidance of shade for both species, but even stronger for *D. plantarius.* Spiders as ektotherm organisms adapt to temperatures by behaviour, *i.e.* by micro-habitat selection and movement (Foelix, 2010). The finding is in line with Duffey (1995), stating that large vegetation is less beneficial for *Dolomedes* in colder environments due to its shading effect. In Scandinavia, shade could be generally avoided by *Dolomedes*, when placing their nursery web, to achieve sufficient conditions for spiderling development in a relatively cold climate.

The observation, that high abundances of certain plant groups such as *Carex*, were avoided by *Dolomedes* for nursery web placement, could be caused by three different reasons. First, it may be, because there are not many observations of plots with the highest count of plants (*i.e.* 75 - 100 %). Second, there may be the need for a diverse plant community, which could be linked to the needs of the prey of *Dolomedes* as well. Third, very high abundance of vegetation (independent of the type) could cause unfavourable micro-climatic and light conditions for development of the spiderlings.

Vegetation complexity was found relevant for oviposition in invertebrates (Meiners & Obermaier, 2003) and vegetation structure is assumed to be more important for spiders than certain host plants (Foelix, 2010; Jiménez-Valverde & Lobo, 2007). I represented vegetation structure by average and maximum vegetation height and horizontal cover and the abundance of crossing vegetation structures. Abundance of crossing structures remained in the final model. Most of the probability mass of the parameter estimates for crossing structures indicates a positive effect of crossing structures on the probability of nursery placement (of level 1,2 and 4). A better understanding could be reached by applying a continuous measurements for abundances to understand the relationship among different variables better.

Among the plant groups, aquatic vegetation *Carex*, *Phragmites* and *Typha* were the most influential variables (part of the final model). *Sphagnum* was important according to the variable selection, but did not remain in the final model after model selection. *Carex* has

positive effect on the nursery placement in low abundances (up to 50 % of abundance, most of probability mass on the positive site), but in high abundances most of the probability mass is negative for nursery placement. The same can be observed for *Phragmites* and *Typha*, where low abundance levels have positive effects (most of the probability mass on the positive site), while the higher abundance levels have negative effects on nursery web placement. This may be caused by a need for diverse vegetation, which could be for example the case because of prey availability. The need for diverse vegetation also fits to the nursery webs observed, which were hosted by more than one plant species. A potential cause could be differences in rigidity and flexibility, which could be necessary for different aspects of the nursery web. Rigid structures may be necessary to support the web reliable, while bendable vegetation structures could be necessary for concealment and to create the dome-shaped structure of the nursery web.

Beside biotic factors, abiotic factors which are underlying the vegetation composition as for example light, chemical conditions and hydrology could impact presence, abundance and reproduction of *Dolomedes* (Soberón, 2007).

Potential factors, which may be correlated with the occurrence of particular plant species, but also influential for *Dolomedes*, are flooding frequency, water level and water source (Carico, 1973). *D. fimbriatus* has been assumed to tolerate more acidic environments and occur in oligotrophic wetlands, while *D. plantarius* is supposed to be more sensitive to low pH and occur in mesotrophic wetlands (Duffey, 1995). *Sphagnum* is associated with and can even enhance acidic conditions (Bragazza, 2006; Schweiger & Beierkuhnlein, 2017). The data exploration showed abundance (low to medium) of *Sphagnum* close to nursery webs of *D. fimbriatus*. *D. plantarius* nursery webs were never close to *Sphagnum* in my sample and the model may have profited from including an interaction effect between species of *Dolomedes* and *Sphagnum*. Another possibility is the association of *D. fimbriatus* with *Sphagnum* due to the general presence/ abundance of *Sphagnum* in *D. fimbriatus* sites. As it provides no structures to attach nursery webs, *Sphagnum* could also be an indicator of constant wetness and thereby favourable hydrological conditions.

The high uncertainty in the parameter estimates of *Phragmites* and *Typha* could be related to differences regarding the nursery placement between *D. fimbriatus* and *D. plantarius*. The modeling could be improved by reaching a sample size which allows for separation or including of interaction effects between several variables and the species of *Dolomedes*, which could be facilitated by collecting variables on a continuous scale.

Plant groups which I found associated with nursery web placement (*i.e. Carex, Phragmites,*

Sphagnum) indicate wet environments (Hellings & Gallagher, 1992; *e.g.* Tiner, 1993) . Determination of all plant species could enable investigating the general hydrological conditions *via* Ellenberg's indicator values (*e.g.* Diekmann, 2003).

Distances lower than 0.7 m from the open water had a positive effect (most probability mass > 0) on nursery web placement. No open water had slight negative effects on the probability of nursery presence (probability mass crossing 0, but mostly on the negative site). Distances of 2 and 7 m had negative effects. The finding could correspond to the differences between *D. plantarius* and *D. fimbriatus*. *D. plantarius* is known to place their webs very close or above the water (Duffey, 2012). Thereby, in a *D. plantarius* site with open water, the distance of 2 meters from the open water is already unlikely. In site occupied by *D. fimbriatus* there is not always open water, *i.e.* the nursery are placed independently from the water.

The data exploration showed, that the maximum distance for nursery webs detected in *D. plantarius* sites was 0.7 m. In sites with *D. fimbriatus* or both species there were also nursery webs further away from the water or in sites without any open water (descriptive result). This finding reflects the high dependency of *D. plantarius* on open water compared to *D. fimbriatus.*. The nursery web reflects only the post-emergence part of the reproductive niche of *Dolomedes.*, Still, the finding points towards relevance of open water for the reproduction and thereby also for the presence of *D. plantarius* in a site.

As *Dolomedes* are semi-aquatic, I expected humidity to be an important underlying factor for their presence and especially for the survival of the spiderlings. I assumed this, based on the dependency of *Dolomedes* on open water or wet soil for their reproduction (Duffey, 1995). I measured humidity on ground level as well as 20 cm above the ground. Both variables were not selected by the regularisation, indicating that they were not suitable to explain nursery web placement. This could be caused by the low variation of those variables in the visited sites (and especially in the occupied sites, which were used for this analysis), as they all were sampled in wetlands and where riparian vegetation occurred. The humidity I measured was only a snapshot, while the general hydrological conditions may be better represented by the plant species, which indicate hydrological conditions.

In terms of plant composition, the sites with both species rather reflect the expectations for the *D. plantarius* habitat, which supports the hypothesis of a broader environmental niche and more flexibility in terms of environmental conditions of *D. fimbriatus* (Duffey, 1995). *Typha* occurs in sites with both species as well as in *D. plantarius* sites, but not in sites in which only *D. fimbriatus* occurs, which matches the observations described by Duffey (1995). Crossing structures are relevant for both species, but the very high levels of crossing

structures occur close to nursery webs of *D. plantarius.*

Sites with both species differ from the vegetation composition near the nursery webs in sites with only one of the *Dolomedes* species occurring, regarding the *Phragmites*, *Typha* and *Carex*. *Phragmites* is more abundant in nursery plots in sites with both species compared to the sites with only *D. fimbriatus* or only *D. plantarius*. *Carex* is very abundant close to nursery webs in *D. fimbriatus* and *D. plantarius* sites, but interestingly less abundant close to nursery webs in sites with both species.

The number of nursery webs counted in sites occupied by *D. fimbriatus* was low compared to the number of webs found in *D. plantarius* sites. This may be related to differences in detectability or a lower abundance, whereby both factors are linked (Royle & Nichols, 2003). Another possibility is different timing, which maybe did not match with the timing of the fieldwork. Nursery webs of *D. plantarius* might be easier to detect, if they occur in higher densities only close to the shore line of open waters. This corresponds to the finding of the occupancy model, showing that open water (linked to the sampling type) may increases the probability of detection of nursery webs.

Nursery webs of *D. plantarius* are placed higher in the vegetation compared to nursery webs of *D. fimbriatus*. I measured even higher placement of nursery webs in sites with both species. This finding could reflect micro-climatic preferences (Duffey, 1995, 2012) or association with different vegetation types of both species. It could points at 'special' characteristics of sites with both species present.

Equisetum was one of the main nursery hosting plants for *D. fimbriatus* used for building nursery webs. Harms, Dunlop, & Schütt (2009) hypothesized plant structure to out-compete pH and plant species, while those factors are probably not only correlated, but can also be causal for each other as well as influence *Dolomedes* directly.

4.5. Coexistence of *D. fimbriatus* and *D. plantarius*

Sites with both species show many similarities to the sites only occupied by *D. plantarius*, suggesting that the habitat requirements of *D. plantarius* may be the limiting factor for the coexistence of both species. Thereby, the findings point towards a wider environmental niche which is suitable for *D. fimbriatus* than for *D. plantarius*, as mentioned by Duffey (1995). Underlying factors may cause or inhibit the potential occurrence of both *Dolomedes* species in close proximity. Further investigation could start at the characteristics of sites with both species, separating those from the single-species sites (*i.e.* low abundance of *Carex*,

high abundance of *Phragmites* as nursery host plant, cattle grazing). Exclusive habitat characteristics, separating *D. plantarius* and *D. fimbriatus* may be related to structure of the surrounding, *e.g.* the presence of coniferous forest on a larger spatial scale. On smaller spatial scale, the presence of aquatic vegetation and the presence or abundance of *Sphagnum* may exclude *D. plantarius* from the habitat. Those variables may be related to certain biochemical conditions as acidity, (see e.g. Schweiger & Beierkuhnlein, 2017) or hydrology. Chemical components of the environment, climatic and micro-climatic factors and hydrological conditions could affect *Dolomedes* and the vegetation simultaneously. One way to access more underlying factors could be a full vegetation relevé, which would allow to use Ellenberger's indicator values (*e.g.* Diekmann, 2003). Hierarchical modeling, for example structural equation model could be applied to this problem (with more data), as latent variables can be included as well as several levels of observed variables and measuring direct and indirect effects of the variables on the response (*e.g.* Malaeb, 2000). To identify which variables on which level are driving *Dolomedes* presence, could give more information about the habitat separation or co-occurrence (end on which environmental level it acts) of *D. plantarius* and *D. fimbriatus.*

The negligence of coexistence and misidentifications could interact in mutual reinforcement. Where one species is expected, the other one might be less probable to be detected, because it was not expected to occur. *D. plantarius* is a species of conservation interest, as its populations are assumed to decline (Smith, 2000 and references therein). The detectability of *D. fimbriatus* and *D. plantarius* may differ and false identification are possible in both ways (Duffey, 2012), while also insufficient monitoring is still a reason for knowledge gaps in distribution and abundance (Duffey, 2012; Ivanov et al., 2017).

In this study, I investigated habitat differences between *Dolomedes fimbriatus* and *Dolomedes plantarius* on two spatial scales. On larger spatial scale, I observed differences between the species, pointing at higher dependency of *D. plantarius* on water and open habitats compared to *D. fimbriatus.* On smaller spatial scale, I investigated detection, timing and placement of nursery webs. I found detection impacted by temperature, crossing vegetation structures, and cloudiness; I found presence of nursery webs on larger spatial scale related to presence of aquatic vegetation and sampling type (*i.e.* presence of open water). The number of nursery webs was mainly determined by the time during the field season. Placement of nursery webs was related to the abundance of *Carex*, *Phragmites* and *Sphagnum* as well as to distance to water, shade and the presence of aquatic vegetation. All model estimates and results contain large uncertainties (confidence and credible intervals crossing zero) due to the sample size and should thereby be interpreted with caution, but this study can serve as a pilot study and

provide information and starting points for future research.

4.6. Futher Research Implications

Abundance is linked to dispersal and survival of populations as well as to detection (Royle & Nichols, 2003). Relating abundance of different life stages to the number of nursery webs could bring information about survival of *Dolomedes* in the northern distribution distribution range. The relationship between abundance and aquatic vegetation could bring information, if floating structures and rooted aquatic vegetation indeed help the anti-predation behaviour of *Dolomedes* as proposed by Gorb & Barth (1994). This leads consecutively to community ecology, as variables like abundance of predators and prey of *Dolomedes* would also be relevant covariates to investigate abundance and survival. *Dolomedes* use terrestrial and aquatic habitat, causing multiple dimensions in their habitat requirements. Prey and predator species of *Dolomedes*, which can be aquatic as well as terrestrial (Gorb & Barth, 1994; Suter & Gruenwald, 2000), could for example be investigated, using molecular markers as stable isotopes and/or fatty acids (*e.g.* Neubauer & Jensen, 2015).

Some questions, emerging for me from this study are:

1. Which 'level' of habitat conditions is mostly determining suitability for *Dolomedes*? *I.e.* chemical conditions (pH), prey availability, vegetation structure, taxonomical vegetation groups (e.g. related to biochemistry) and how do those variables relate to each other?

2. How does the previous knowledge of occurrence influence the detection and correct identification of *Dolomedes* in general? How does it impact the potential detection of the expected and the not expected species of *Dolomedes* in the site?

3. Furthermore, how does the general amount of knowledge (especially habitat requirements) about a species impact detectability, and how does it impact the probability of a species to be protected (given equivalent rarity)?

4. How does the count/ presence of nursery webs relate to abundance of *Dolomedes*? Are there differences on a latitudinal gradient?

5. Conclusion and Conservation Implications

During the expected climate change, the main 'hope' for remaining suitable habitat for *Dolomedes plantarius* is Scandinavia. In Scandinavia, high abundance of wetlands, interconnectivity of open waters and wetlands and the expected climatic suitability in the future (Leroy et al., 2013). We collected our data in the current northernmost part of the the distribution range of *D. plantarius* (*D. fimbriatus* can also occur in higher latitudes, see Helsdingen, 1993). Specific habitat requirements of *Dolomedes* need further investigation, but are necessary to consider when creating protected areas or assessing potential suitability on smaller scale.

Ivanov et al. (2017) calls for better monitoring of *D. plantarius* , as it could trigger the creation of protected areas, if the species is included in the red list in Belarus in the future. This could be a valid reason for better monitoring as well in Scandinavia, given the potential distribution shift (Leroy et al., 2013).

For efficient conservation of habitat, the probability of locally specific occupancy is important. Occupancy modelling can help to decide, which areas could be necessary to protect and where to apply conservation efforts by estimating occupancy probabilities (McFarland et al., 2012). With increased knowledge about habitat requirements and dispersal abilities of *Dolomedes*, occupancy modeling can provide an useful tool for determination of particular suitable sites in Scandinavia within the broad climatic suitability predicted by Leroy et al. (2013).
The abundance of *Sphagnum* has been associated with the acidity reflected by the composition of the plant community (Schweiger & Beierkuhnlein, 2017). Plantations of coniferous forests can acidify streams (Blacklocke, 2016), which is in line with coniferous forest mainly surrounding sites by the less pH-sensitive *D. fimbriatus*. How realistic the future distribution expansion of *D. plantarius* in Scandinavia really is, should be investigated, given the high abundance of *Sphagnum* rich habitats as well as of coniferous forests in Scandinavia.

Many species will loose suitable conditions in currently protected areas in the future (Auaújo et al., 2011). *Dolomedes plantarius*, in the context of its expected distribution shift and habitat loss (Leroy et al., 2013), is one example of the need for conservation action beyond spatially restricted activity and holding on to the *status quo* by acting on larger scale, based on the knowledge we can gain, for example from empirical niche modelling (Bellard et al., 2012).

This study increased knowledge about general habitat requirements specific requirements for reproduction of *Dolomedes* and explored the use of nursery webs for detection of *Dolomedes*

in occupancy modeling. Thereby my study points at some characteristics of habitats, which could be investigated in the future regarding the potential future habitat of *Dolomedes*, as well as the co-occurrence of *D. plantarius* and *D. fimbriatus* in close proximity to each other.

Dolomedes provide a good example for the type of analysis needed which allows for imperfection, *e.g.* in detectability an prior knowledge of occurrence, demonstrating that imperfect detection is not a neglectable part of scientific monitoring of invertebrates.

Even though, *Dolomedes* are emblematic species within their taxon, there are many open questions concerning the genus. Limited knowledge can be caused by detection and identification issues (Duffey, 2012; Helsdingen, 1993; Ivanov et al., 2017) and by the bias in conservation research in disadvantage of invertebrates (Clark & May, 2002). This taxonomical bias may also be connected with the inability to integrate invertebrates in the moral community of our society (Gorke, 2010). As nature conservation is driven and motivated by the normative component, which is dependent on flexible human values (Lindenmayer & Hunter, 2010), the absence of invertebrate species from the moral community can cause direct effects on their protection.

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Appendix A: Data Collection

GBIF citations

Dolomedes plantarius

Sweden

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Norway

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Dolomedes fimbriatus

Sweden

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GPS Coordinates of Visited Sites

Table 1: Coordinates od the data collection sites (WGS 84).

siteName	siteID	today	latitude	longitude
Lagastigen	2	2018-07-01	56.56896	13.73715
Rishult	3	2018-07-01	56.53768	13.80526
Traryd	4	2018-07-01	56.53077	13.76890
Ganarp	5	2018-07-02	56.29014	12.93791
Finjasjoen1	6	2018-07-03	56.15982	13.70319
Finjasjoen2	7	2018-07-04	56.15865	13.70199
Helge	8	2018-07-04	56.29360	14.02487
Kristianstad	9	2018-07-04	56.03243	14.14738
Hammarsjon	10	2018-07-04	56.00445	14.25807
Kagerod	11	2018-07-05	56.02181	13.11127
Tassjo	12	2018-07-06	56.30147	13.07391
Ostra_Karup	13	2018-07-06	56.38631	12.96364
Forshaga	14	2018-07-08	59.52355	13.49485
Kristinehamn1	15	2018-07-10	59.32888	13.94961
Kristinehamn2	16	2018-07-10	59.32724	13.95032
Stora_Algsjon	17	2018-07-10	59.47581	14.10621
Boda	18	2018-07-11	59.57083	13.05094
Knappstaviken	19	2018-07-11	59.35121	13.45668
Magsjon	20	2018-07-13	59.72963	16.20086
Norra_Nadden	21	2018-07-13	59.79386	16.17019
Alvkarleby	22	2018-07-14	60.48788	17.35824
Hjalmare	23	2018-07-17	59.35845	15.95673
Evenstad2	26	2018-07-25	61.38844	11.17699
Evenstad3	27	2018-07-25	61.38964	11.17488
Nabbtjornet	28	2018-07-26	61.37812	11.19497
Evenstad1	25	2018-07-27	61.38632	11.17878
Elverum	24	2018-08-02	60.88289	11.56843
Aneboda	30	2018-08-09	57.10335	14.57263
Lammhult	31	2018-08-10	57.11842	14.56569
Julussa1	32	2018-08-15	61.11949	11.52348
Julussa2	33	2018-08-15	61.15736	11.47438

Identification of *Dolomedes* adults with Sponge Method

Figure 1: Identification of adult *Dolomedes* with the sponge method. The spider is pressed with the sponge gently against the glass and then identified, using a magnifying glass. Certain determination of *Dolomedes* is only possible, inspecting the genitals. After identification, I released the individuals in the same location, in which they were captured.

Appendix B: Habitat Description

Figure 2: Mosaic plots of variables for habitat characterisation. The coloured bars show the proportions of the levels of categorical variables. Each vertical bar represents one category of *Dolomedes* (fimb = *D. fimbriatus*, plant = *D. plantarius*, both = both *Dolomedes* species.)
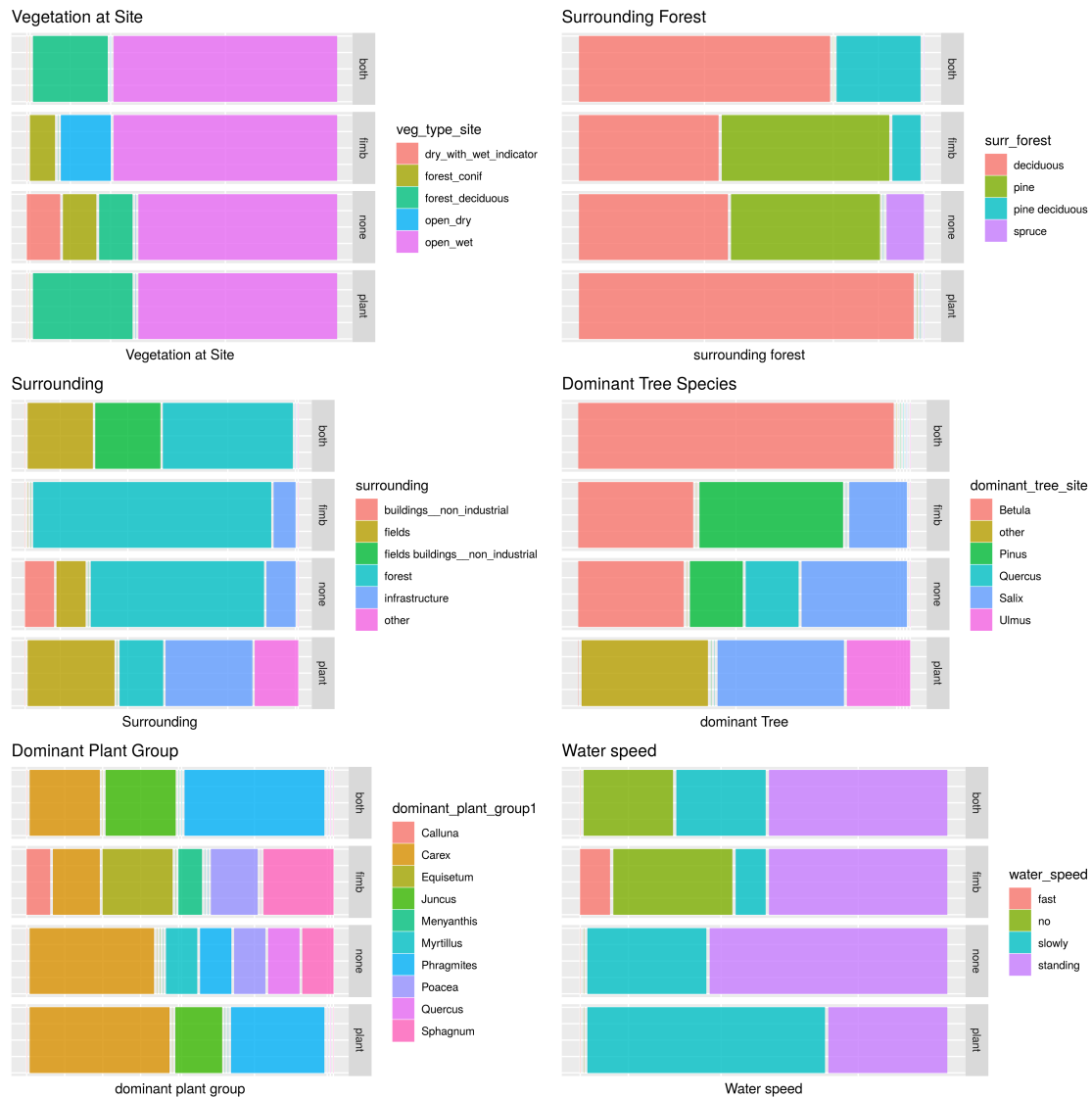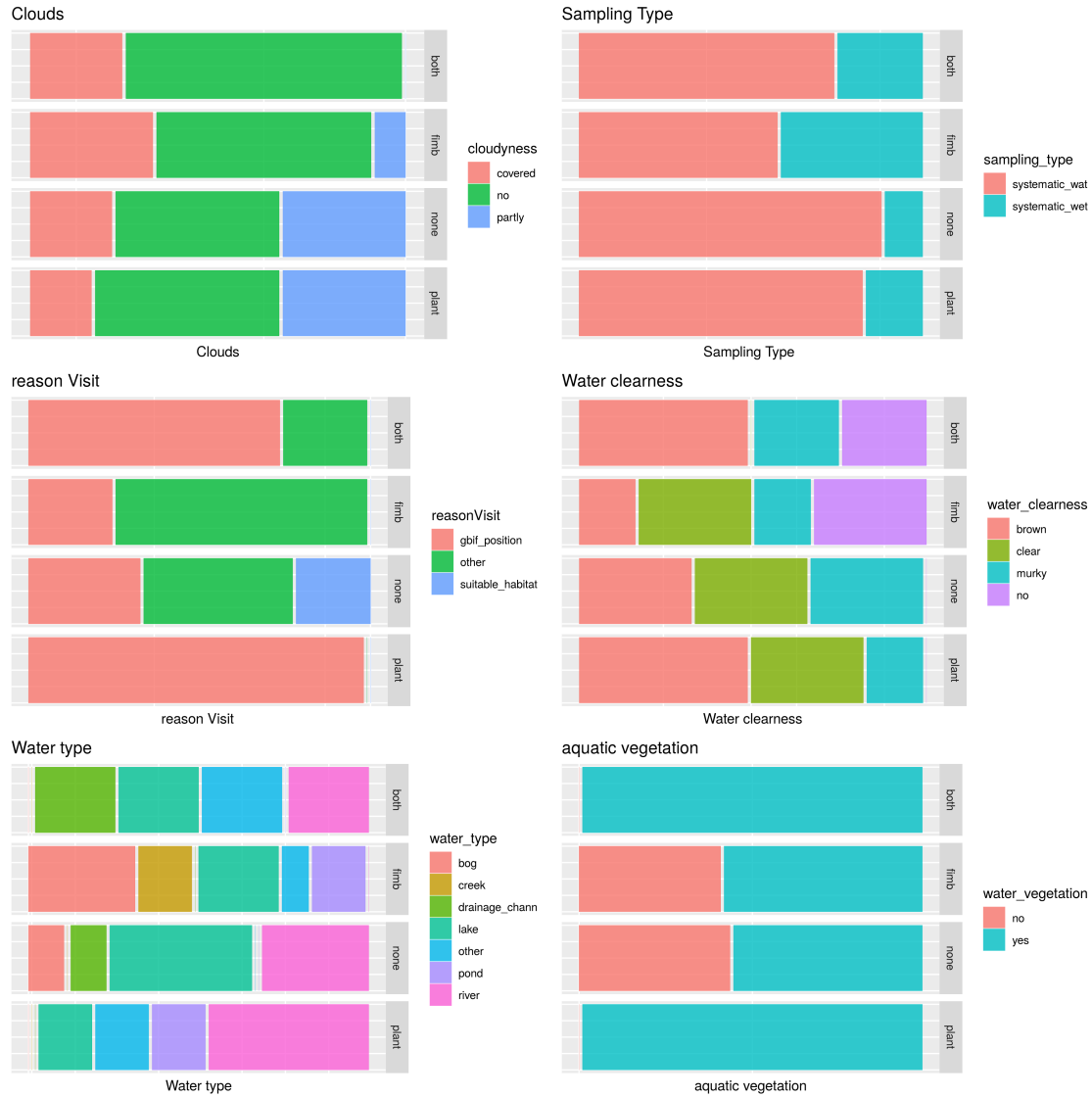
Figure 3: Mosaic plots of variables for habitat characterisation. The coloured bars show the proportions of the levels of categorical variables. Each vertical bar represents one category of *Dolomedes* (fimb = *D. fimbriatus*, plant = *D. plantarius*, both = both *Dolomedes* species.)

Appendix C: Occupancy Modeling

Model Selection

Table 2: Model selection table for occupancy modeling. The table displays the model name, the negatice Log-likelihood, the AIC value, the model weight and the cumulative model weight.

model	negLogLike	delta	AIC	AICwt	cumltvWt
ms5	89.36	0.00	202.71	0.45	0.45
m24	90.95	1.18	203.90	0.25	0.70
m11	92.86	3.00	205.71	0.10	0.80
ms2	89.36	4.00	206.71	0.06	0.86
ms4	92.57	4.43	207.14	0.05	0.91
ms8	92.86	5.00	207.71	0.04	0.94
ms7	92.33	5.94	208.66	0.02	0.97
m8	98.52	6.34	209.05	0.02	0.99
m14	96.87	7.03	209.75	0.01	1.00
ms3	91.94	15.16	217.88	0.00	1.00
m3	105.00	17.29	220.01	0.00	1.00
ms1	94.02	19.33	222.04	0.00	1.00
m2	108.26	19.80	222.52	0.00	1.00
m4	107.42	20.12	222.83	0.00	1.00
m1	107.90	21.09	223.80	0.00	1.00
m17	108.62	22.53	225.25	0.00	1.00
m23	109.02	23.32	226.04	0.00	1.00
m12	108.77	24.83	227.54	0.00	1.00
m7	105.80	24.88	227.60	0.00	1.00
m22	106.86	25.00	227.72	0.00	1.00
m19	111.03	25.34	228.06	0.00	1.00
m5	111.71	26.70	229.42	0.00	1.00
m21	110.98	27.26	229.97	0.00	1.00
m10	111.99	27.27	229.98	0.00	1.00
m0	113.02	27.34	230.05	0.00	1.00
m20	105.78	28.86	231.57	0.00	1.00
m18	111.95	29.18	231.89	0.00	1.00
m6	113.02	29.32	232.03	0.00	1.00
m15	109.26	29.80	232.51	0.00	1.00
m16	112.61	32.51	235.22	0.00	1.00
m13	110.94	35.16	237.87	0.00	1.00

Appendiy D: Nursery Web Count

Model Selection with AICc

Table 3: Model selection of nursery web count models, using AICc. The table displays the degrees of freedom (df), the log-Likelihood, the AICc, the delta AICc and the model weight.

	df	logLik	AICc	delta	weight
z1	4	-47.65	105.04	0.00	0.793287819
z2	4	-49.99	109.73	4.68	0.076356174
z4	4	-50.06	109.87	4.82	0.071181864
z3	6	-47.59	111.19	6.14	0.036794318
z0	2	-54.05	112.59	7.55	0.018239027
z5	8	-45.99	115.55	10.51	0.004140799

Appendix E: Nursery Web Placement

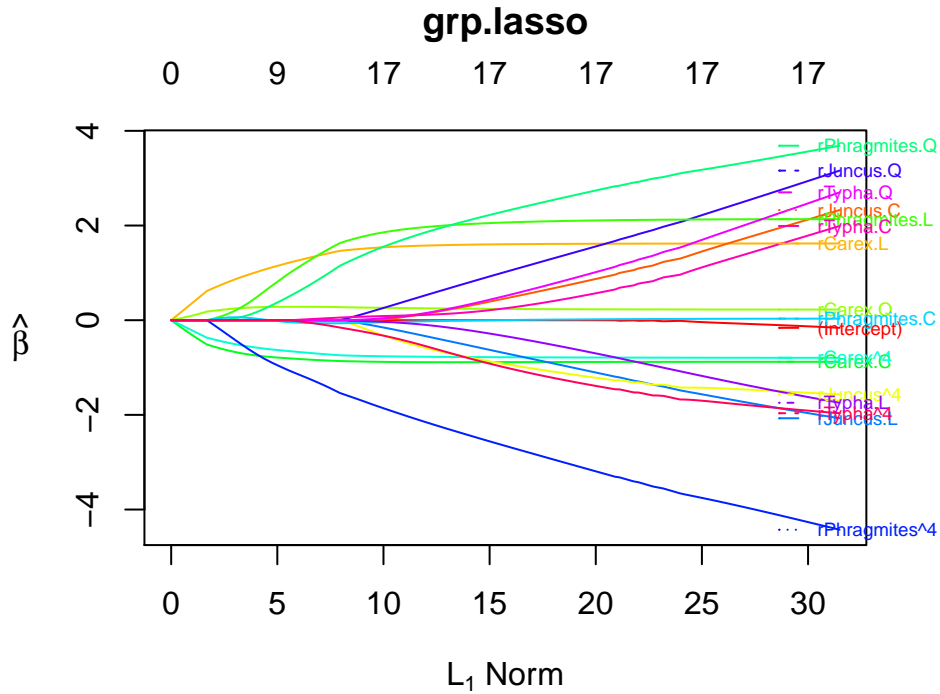**Variable Selection (Lasso Regression)**

Figure 4: Example of lasso regression (for variable group 1), fitted using maximum likelihood estimation, with the package oem. Each variable/ each level of a categorical variable is represented by one line. The earlier the variable enters the plot, the more important it is relatively to the other variables. The x axis represents the penalisation, the y axis represents the effect size of the variable.
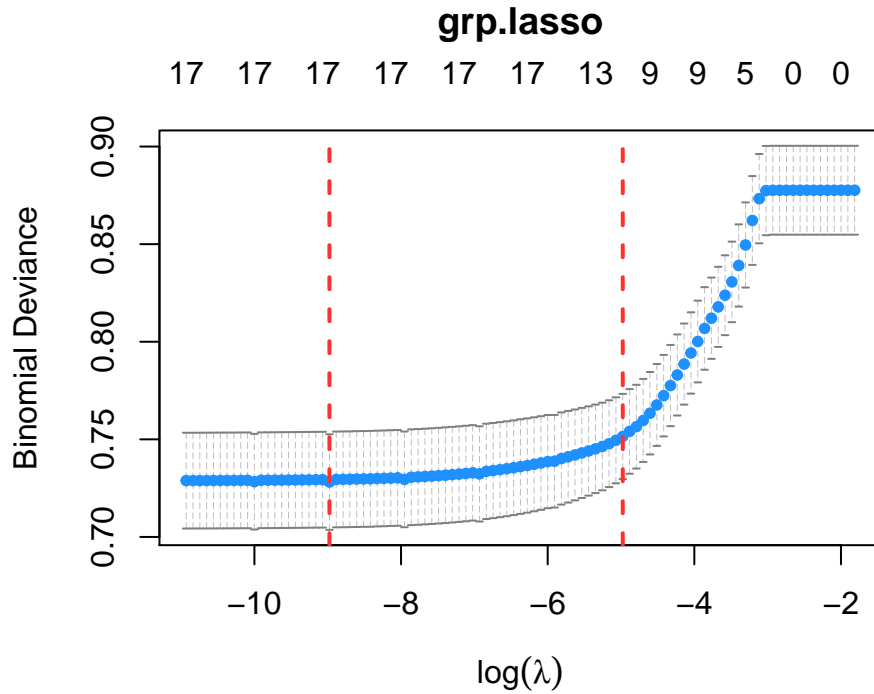
Figure 5: Example of cross validation of the lasso regression for variable group 1, fitted with the package oem. The second (right) red line in the cross validation plot indicates the number of variables, which are recommendet to keep for further use.

Table 4: Model selection with loo. The best model contained the predictors aquatic vegetation, Carex, crossing vegetation structures, shade, distance to water, Phragmites, Species and Sphagnum.

	elpd_diff	elpd_kfold	se_elpd_kfold
m43	0.00	-110.13	10.19
m28	-19.10	-129.23	11.09
m36	-20.24	-130.36	11.23
m31	-21.46	-131.59	11.22
m35	-21.72	-131.85	11.17
m32	-23.73	-133.85	11.49
m29	-25.07	-135.19	11.85
m30	-38.03	-148.15	13.11
m37	-51.45	-161.57	13.32
m1	-61.95	-172.08	13.62
m13	-67.76	-177.89	13.99
m11	-82.79	-192.92	14.69
m44	-83.85	-193.98	14.53
m12	-86.59	-196.71	15.90
m40	-88.91	-199.04	14.44

|			
m16	-96.23	-206.35	14.44
m33	-97.68	-207.80	14.46
m4	-98.20	-208.33	14.65
m18	-105.20	-215.33	14.78
m19	-153.26	-263.39	11.67
m20	-160.44	-270.56	16.79
m26	-164.34	-274.46	16.23
m22	-199.98	-310.10	13.47
m42	-220.90	-331.02	16.57
m6	-220.99	-331.12	16.96
m8	-232.74	-342.86	19.20
m38	-236.41	-346.54	20.41
m25	-242.37	-352.50	19.58
m2	-242.42	-352.54	20.21
m24	-243.50	-353.62	18.24
m21	-249.71	-359.84	18.63
m10	-266.46	-376.58	19.86
m27	-269.83	-379.96	21.29
m39	-280.05	-390.18	19.59
m3	-280.86	-390.99	19.57
m3.2	-284.15	-394.28	19.93
m9	-290.90	-401.02	20.40
m15	-296.92	-407.04	23.44
m7	-331.05	-441.18	29.55
m45	-344.58	-454.70	22.63
m23	-431.47	-541.60	22.52
m5	-590.97	-701.10	31.30
m41	-595.03	-705.16	31.70
m14	-632.32	-742.45	50.32
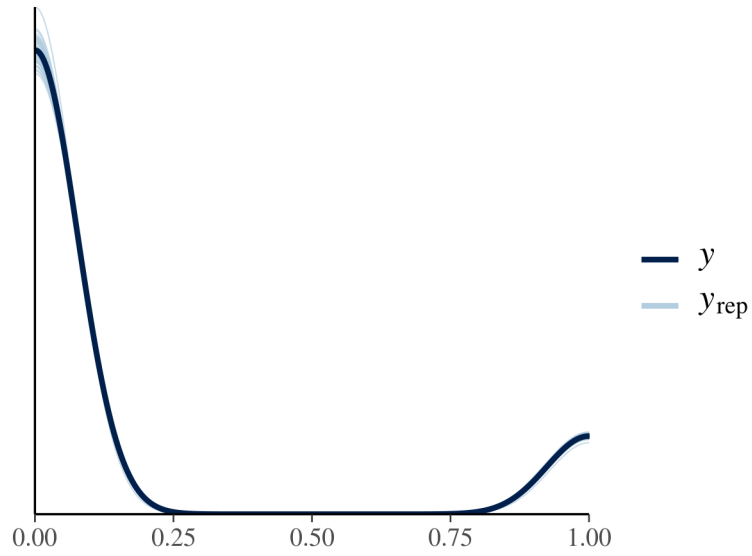
Figure 6: Posterior predictive check of the final model (m43). The dark blue line displays the data, the light blue line displays repeated predictions of the model.