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Master Thesis

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Can microclimate predict species composition of vascular plants, spiders and epiphytes?

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Abstract

Microclimate is an important determinant of species composition and distribution. However, time series of continually logged microclimate data are very complex and not directly operational in any test of the strength of relationship between microclimate and species composition.

Using Mantel tests, different indices of light, air – and surface temperature, soil moisture and humidity were correlated with dissimilarity in community composition of vascular plants, spiders and epiphytes (specifically epiphytic/epilithic mosses and lichens) to determine which indices best describe the landscape-scale distribution of one or more of the three organism groups.

At various times during the summer months of 2014-2016, microclimate and species data was collected from 130 sites covering all regions of Denmark and spanning different biotopes in relation to the degree of cultivation, succession, soil moisture and nutrient richness.

Because microclimate was not measured during the same period in all sites (soil moisture excluded), mixed effects models were used to predict new period-adjusted sets of index-values.

Based on the results from Mantel tests and how well indices could be described and predicted by mixed effects models, the 85th percentile was found to be the light index best describing species composition, while the difference between mean daytime and mean nighttime values was the best index for both surface temperature, air temperature and humidity. For soil moisture, the mean was the index best describing species composition.

Because microclimate can vary substantially within just a few centimetres or meters, I placed additional data loggers in six of the 130 sites to investigate the spatial variation of the above-mentioned light, temperature and humidity indices. Results from mixed effects models showed that with-in site variation explained 17.9 % of the total variation in light index values, 8.8 % of the total variation in surface temperature, 2.2 % of the total variation in humidity and only 0.01 % of the total variation in air temperature. How high the within-site variation was for the individual site, varied substantially though, but was high enough for all sites to potentially jump several rank positions when sites were ranked according to their index-values. To better cover the variation in light and surface temperature within sites, it would therefore be sensible to widen the spatial scale using additional loggers in all 130 sites.

1. Introduction

Understanding what drives the distribution of species is a central question in ecology.

Not only is it scientifically interesting to know by what “rules” communities assemble (Drake 1990), but this knowledge can also be applied to management and conservation issues, assessment of species invasions and prediction of the effects of climate change on species and communities. It is not an easy question to answer though, and a variety of factors and processes are involved and interplaying.

Commonly, these factors are grouped into three main determinants: dispersal constraints, environmental constraints and constraints associated with biotic interactions (Belyea & Lancaster 1999; Soberon 2007; Gotzenberger et al. 2012). Whereas dispersal constraints act at the regional level, limiting dispersal from the regional species pool into the local species pool, environmental and biotic constraints act at the local level, functioning as filters through which species present in the local species pool are sorted into the actual community (Zobel 1997; Gotzenberger et al. 2012).

In this thesis, my focus will solely be on the effect of environmental constraints, which are abiotic factors such as temperature, light intensity, soil moisture, soil pH, soil texture, nutrient richness etc. that limit the establishment, survival and reproduction of a species. In the case of plants, some species for example cannot grow in very dry or very wet conditions; others cannot exist in a shaded environment or tolerate continuous exposure to high light intensities, and others again are unable to survive at low or high temperatures (Ellenberg 1991). Every species thus has a range within the suite of abiotic factors outside which they are unable to survive – often referred to as the species’ fundamental niche (Hutchinson 1957).

Biotic constraints are interactions such as competition, facilitation, predation, parasitism, mutualism etc. between co-occurring species, which affect community composition. Traditionally, the effects of competition have been the main focus of attention, but in recent decades the importance of facilitation has been acknowledged as well (Holmgren et al. 1997; Brooker et al. 2008). Competition arises when co-occurring species are limited by the same resources, and can potentially result in the exclusion of the competitively inferior species from the community (Lhotsky et al. 2016). Conversely, facilitation has a positive effect and adds species to the

community by creating environmental conditions favourable for species that would otherwise have been excluded. Scrubs in warm and dry areas can for example facilitate the growth of species below it, by ameliorating radiation, temperature and soil moisture stress (Gomez-Aparicio et al. 2004) or nitrogen fixing legumes can provide nutrients to the soil benefitting the establishment of other species (Rodriguez-Echeverria & Perez-Fernandez 2003).

To complicate things, biotic interactions are not conserved along the environmental gradient. Several studies on plant-plant interactions has shown that generally there seems to be an increase in relative importance of facilitation when moving from a low-stress to a high-stress environment, with competition being the dominant interaction in low-stress environments and facilitation the dominant interaction in high-stress environments (Callaway et al. 2002; Sthultz et al. 2007). This is likely due to growth being limited by abiotic conditions more than resource availability in high-stress environments, while growth in low-stress environments are limited by resources.

When there are no limiting environmental or biotic constraints and a species is absent solely because it has not reached the site, the species' presence is dispersal limited. This limitation can be due to the species own dispersal abilities – e.g. how fast it can move, or be caused by external factors such as natural geographical barriers (Svenning & Skov 2004) or habitat fragmentation (Norden et al. 2014; Li & Waller 2016).

In addition to dispersal, environmental, and biotic constraints - the history and continuity of a biotope and the surrounding landscape influence both the number and identity of species present in the regional species pool. The longer a biotope has existed and the larger the area it has covered, the greater the opportunity for speciation and migration to have occurred (Zobel 1997; Gotzenberger et al. 2012). That does not mean however, that two different biotopes of historically equal temporal and spatial extent will have the same number of species. The intrinsic characteristics of the specific biotope and its community influences the number of speciation events as well, with communities having a low mean generation time showing a higher speciation rate than communities with a high mean generation time (Bruun & Ejrnaes 2006).

Furthermore, historical contingency – the effects resulting from random historical events, can also play a significant part in shaping the community. Ejrnaes et al. 2006 for example showed that the arrival order of species in a grassland microcosm greatly influenced species composition. Because

species can modify the environment to facilitate the colonization of other species or impede it through competition, it is not entirely irrelevant in which order species arrive. Depending on arrival order, two sites with identical environmental conditions and local species pools can thus end up with two different communities.

With all these factors influencing community composition and adding stochastic processes to the equation as well, it is simply impossible to accurately predict species distributions and the biodiversity at a specific site. Complex models incorporating every measurable environmental variable, biotic interactions and species niches, might result in more accurate predictions than less complex models, but they are also more difficult to understand and less general. Incorporating detailed species niches is not only time consuming and complicated, but it is not without problems either, as the realized niche of a species in one community can differ from that in another community. Niche properties derived from studies of just one or a few communities can therefore be misleading (Entling et al. 2007).

Instead of using species niches, it could be more feasible to try to derive general patterns of biodiversity by looking at environmental space. Brunbjerg et al. (*in press*) advocate for the concept of ecospace, which they define as “the multidimensional space of conditions and opportunities in which biodiversity develops” consisting of three components: position, expansion and continuity. Ecospace position is the placement of a biotope along abiotic gradients such as light intensity, temperature, moisture, pH and nutrient richness. Ecospace expansion is a measure of the build-up of organic matter that provides a home and/or resources for species – thereby expanding the number of habitats in the biotope. This could e.g. be trees providing a substrate for epiphytic mosses and lichens to grow on, flowers providing nectar for pollinators, or dead wood providing a substrate for saprophytic fungi. Lastly, continuity refers to the spatial and temporal extension of ecospace position and expansion.

Additionally, they propose an extension of ecospace into landscape metaspace to include the spatial variation in biotope ecospace – a type of measure of β -diversity.

The advantage of using the ecospace framework is the inclusion of a broad spectrum of organisms and its potential application in management and conservation. When knowing what values of

ecospace elements harbors a certain type of community, managers can strive to preserve or restore those elements in order to protect or reestablish the desired community and the species associated with it. The more parameters measured, the more precise the representation of ecospace will be, but a limited number could likely be enough for a prediction of adequate power.

1.2 Biowide – Biodiversity in Width and Depth

In line with the idea of ecospace as a measure of biodiversity, the Biowide (Biodiversity in Width and Depth) project was launched in Denmark in 2014 by Aarhus University in collaboration with The University of Copenhagen, the Natural History Museum in Aarhus and the Natural History Museum of Denmark. The main purpose of this still ongoing project is to gain a deeper understanding of the variation in the terrestrial biodiversity in Denmark. This is done by identifying every organism possible, from the smallest of insects, lichens and fungi, to vascular plants, birds and mammals in 130 sites located throughout the country and spanning the most important gradients in Danish nature. To identify any potential organisms not spotted in the field and organisms that cannot be properly identified in the lab, DNA sequencing of soils, animals and plants is also used. Furthermore, abiotic factors in the form of microclimate and soil conditions have been measured in each site along with a range of biotic expansions in the form of vegetation structure and carbon sources.

It is the microclimatic measurements from this study – more precisely measurements of air and surface temperature, light intensity, relative humidity and soil moisture, that I will use along with species data from the sites to investigate the effects of microclimate on the species distribution of selected organism groups.

1.3 Microclimate

The overall climate experienced by a larger area such as a region or a country, is referred to as *macroclimate*. Through the interaction of macroclimate with local topography, soil surfaces and vegetation cover, a considerably different climate can be formed at smaller scales – referred to as *microclimate* (Petersen and Vestergaard 2006). When looking at the effects of climate on species distributions, macroclimate is not a particularly suitable measure unless we look at distributions and patterns in biodiversity at very large-scales. At most scales, microclimate is a more appropriate measure, as it refers directly to the climatic conditions in which plants and animals live. The temperature at the soil surface of a forest is for example very different from that of a patch of grassland nearby, exposed to the same macroclimate (Suggitt et al. 2011). This difference is caused by differences in vegetation structure with the microclimate below a forest canopy generally being characterized by lower light levels, lower daytime temperature, lower wind speed and a higher air humidity than open sites with low vegetation (Aussenac 2000; Holmgren et al. 1997; Morecroft et al. 1998).

In addition to shading, soil moisture is another main factor affecting the microclimatic environment. Compared to dry soils, moist soils have a smaller surface temperature range, because of the higher thermal inertia of water in the soil, and attenuate increases in air temperature and lowering of relative humidity through evaporative cooling (Lakshmi et al. 2003). Furthermore, the slope and aspect of an area strongly influences the amount of light reaching the surface, and thereby also the associated microclimatic variables and the vegetation type (Bennie et al. 2008; Suggitt et al. 2011). Slopes facing south receive the highest amount of radiation, while north facing slopes receive the lowest. In northern temperate latitudes, north facing valleys can receive as little as 10 % of that received by south facing slopes in the winter (Austin 2005).

1.3.1 Microclimate and vascular plants

The establishment, survival and reproduction of plants rely on keeping a positive carbon balance where the rate of photosynthesis on average exceeds the rate of respiration. Microclimatic factors such as light, temperature, air humidity and soil moisture directly influences this balance and plants therefore show a range of characteristic adaptations to the microclimatic environment in

which they grow. Plants adapted to shaded environments often have larger leaves (increasing the photosynthetic surface area) and a higher production of the light-harvesting pigment chlorophyll, than plants growing in the sun (Smith and Smith 2009). This increases the rate of photosynthesis in low-light conditions. Furthermore, plants growing in the shade do not need to produce as much rubisco as species growing in the sun, because the factor limiting their photosynthetic rate is low light and not availability of rubisco. This reduces the amount of energy spent and thereby the rate of respiration (Smith and Smith 2009). Such adaptations result in shade-tolerant species having a lower light compensation point (the light intensity at which photosynthetic rate = respiration rate), a lower light saturation point (the intensity above which no further increase in photosynthetic rate occurs), and a lower maximum rate of photosynthesis (due to the lower amount of rubisco produced) than species living in high-light conditions. This allows shade-tolerant species to keep a net positive photosynthesis in low light, whereas shade-intolerant species with their higher maximum rate are competitively superior in high-light environments, but unable to survive in low-light environments.

High temperatures frequently follow high light levels, and relative humidity, which affects evapotranspiration, is directly related to air temperature (Schulze et al. 2005). Plants living in high-light environments therefore often show adaptations for coping with overheating and water stress. Common adaptations are extensive root nets to increase water uptake and smaller and more indented leaves to reduce the boundary layer and increase heat exchange through convection (Smith and Smith 2009). Some plants, like *Helichrysum arenarium* growing in dry sandy grasslands, have tiny white hairs to reflect sunlight, while other species such as the perennial *Saxifraga granulata* and the annual *Cerastium semidecandrum* survive the driest period as bulbs and seeds respectively (Petersen and Petersen 2007). If plants keep losing water, they will wilt and eventually reach the permanent wilting point from which they are unable to recover. This point differs from species to species, with species living in drier soils having a lower permanent wilting point than species living in more moist soils (Petersen and Petersen 2007).

Far from all plants living in open high-light environments are water limited though. In some habitats, both open and closed, soils can even be waterlogged for shorter or longer periods, resulting in anoxic soil conditions. To cope with this extreme, some well-adapted species are able to transport oxygen to their roots via air channels in the plant, making them able to survive and

grow in constantly waterlogged soils (Vartapetian & Jackson 1997). Other species are able to tolerate anaerobic conditions for periods ranging from just a few hours to days or weeks. Exactly how long, varies from species to species (Vartapetian & Jackson 1997).

Like high temperatures, low temperatures can also have damaging effects on plants.

When temperatures fall below freezing, there is a risk of water crystalizing in the plant cells, so to avoid this, many species are able to accumulate substances like amino acids, sugars and other compounds functioning as antifreeze (Smith and Smith 2009). Other species simply shed their leaves before the cold season or survive the winter as bulbs or seeds in the ground.

Because of the direct relation between plants and their microclimatic environment, the distribution of vascular plants is expected to be well-described by gradients of light, temperature, air humidity and soil moisture. Other environmental factors are also highly influential, with soil pH, nutrient richness and level of disturbance being examples of important factors (Petersen and Vestergaard 2006). In addition to this, is of course also the influence of historical factors, dispersal limitations and biotic constraints previously mentioned.

1.3.2 Microclimate, spiders and epiphytes

In addition to vascular plants, the distribution of other organism groups could potentially be well-described by some or all of the microclimatic variables measured in the Biowide project.

Epiphytic and epilithic mosses and lichens get all their water from rainfall, dew and air humidity. How well and for how long they are able to tolerate desiccation, how fast they can recover from desiccation and how well they function at a thallus water content above or below 100 % (fresh weigh = dry weigh) varies both between and within the two groups (Green et al. 2011).

Generally, mosses and cyanobacterial lichens do best at high water contents and store water to keep hydrated for longer periods, whereas green algae lichens do better at lower water contents, desiccate and rehydrate more rapidly and are able to hydrate solely from humid air (Green et al. 2011). The distribution of epiphytic/epilithic mosses and lichens is therefore thought to be particularly well-described by measures of air humidity.

Spiders are a diverse group of predators found in all types of terrestrial habitats. They are ectothermic animals and therefore sensitive to temperature (Wise 1993). Because many spiders roam around on or near the soil surface and have been shown to respond to small variations in temperature (Petcharad et al. 2016), surface temperature and soil moisture might be particularly good predictors of species distribution.

1.4 Aims and objectives

Vascular plants, spiders and epiphytes (specifically epiphytic/epilithic mosses and lichens), are all organism groups found in a wide range of terrestrial biotopes and distributed along abiotic gradients of light, temperature, soil moisture and air humidity. However, time series of continually logged microclimate data are very complex and not directly operational in any test of the strength of relationship between microclimate and species composition in communities of the mentioned organisms. Therefore, the aim of this work is to develop and validate the indices of microclimate that best describe the landscape-scale distribution of one or more of the three organism groups. Because we know that species within these groups are distributed along abiotic gradients (Whittaker 1967; Bultman et al. 1982; Green et al. 2011), the indices best describing the variation in species composition are also the indices best describing the microclimatic gradients when moving from open and/or south facing slopes to shaded and/or north facing slopes and from wet to dry soils.

In the Biowide project, indices of microclimate are, with the exception of soil moisture, based on measurements from a single data logger placed within each 40 x 40 m site.

The sites chosen are all fairly homogenous in relation to their vegetation type, but within sites homogenous at a 40 x 40 m scale, a certain amount of spatial variation in microclimate is still to be expected. A patch of forest might have tree-fall gaps with a very different microclimatic environment than under the closed canopy or just small openings in the canopy allowing small sun flecks to reach the forest floor in certain spots at certain times. There might be small differences in topography creating hollows of wetter and cooler soils, a small body of water or a creek running through. A grassland might have a few trees or scrubs creating shaded spots in the otherwise open

land and grazing animals might create patches of bare soil through trampling or graze selected areas more heavily than others. Within just a few centimetres or meters, the microclimatic environment can thus vary substantially.

Using the indices found to best describe the landscape-scale distribution of one or more of the aforementioned organism groups, I therefore additionally wish to investigate the spatial variation of light, air temperature, surface temperature and air humidity within sites of different vegetation structure and soil moisture content. This is achieved by placing 16 data loggers in each of six sites included in the Biowide project and will also serve as an indication of whether or not the single data logger, adequately represents the microclimate experienced in the 40 x 40 m sites.

2. Materials and Methods

The 130 sites in the Biowide project cover all regions of Denmark (Figure 1) and span different biotopes in relation to the degree of cultivation, succession, soil moisture and nutrient richness, and also include 10 sites believed to be hotspots (Appendix 1).

Each site measures 40 x 40 m and is further divided into four 20 x 20 m plots marked by coloured center – and corner poles (blue, green, red and yellow).

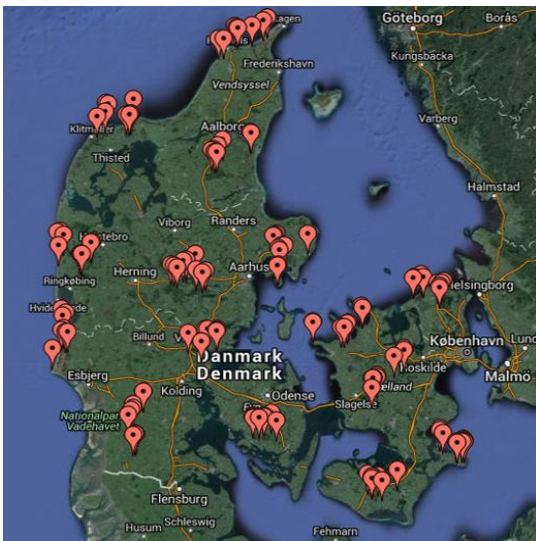


Figure 1: The location of each of the 130 study sites.

Even though the precise placement of all sites is difficult to distinguish, the map illustrates the wide coverage of regions in Denmark.

2.1 Microclimatic measurements

The microclimate was measured at 1-hour intervals during the summer months of May to August 2015, using two data loggers (type HOBO, Onset Computer Cooperation). A HOBO Pendant Temperature/Light Data Logger was placed on the soil surface and measured surface (air) temperature ($^{\circ}\text{C}$) and light intensity (lux), while a HOBO Pro v2 logger was placed under a shade-providing foil tray at a height of about 15 cm, measuring air temperature ($^{\circ}\text{C}$) and relative humidity (%). The two data loggers were placed next to each other in the red plot at all sites.

Due to the logistics of a limiting amount of people managing 130 sites across the country, the data loggers were out logging at different time spans (12 – 65 days) in different periods over the season (Appendix 2).

Soil moisture was measured in May 2016, using the Field Scout™ TDR 300 Soil Moisture Meter (Spectrum Technologies, Inc). The volumetric water content (%) was measured in 16 spots within each site, which is expected to be enough to cover the within-site variation reasonably well.

Because relative humidity (RH) expresses the proportion of water in the air compared to the air's maximum holding capacity and that maximum changes with temperature, RH is highly temperature dependant. As the temperature increases, so does the air's holding capacity, resulting in a decrease in RH.

To study the effect of air humidity on the distribution of vascular plants and epiphytic/epilithic mosses and lichens, for which we know the air's water content is particularly important, a measure such as Vapour Pressure Deficit (VPD) will be more suitable. VPD is the difference between the actual amount of moisture in the air and the amount that can be held when saturated (RH = 100 %) at a specific temperature. Consequently, VPD combines the effect of both temperature and humidity into a single value and has a more direct and linear relationship with the rate of evapotranspiration compared to RH.

VPD (kPa) was calculated from air temperature and relative humidity using the following formula from Jones (1992) and Tu (2010):

$$e_s = 0.61121 \times e^{17.502 \times T / (240.97 + T)} \text{ (kPa)}$$

$$e_a = e_s \left(\frac{RH}{100} \right) \text{ (kPa)}$$

$$VPD = e_s - e_a$$

e_s is the saturated vapour pressure, e_a the actual vapour pressure, T the air temperature in °C, and RH the relative humidity (%).

2.2 Sampling methods

2.2.1 Plants, Mosses and Lichens

In 2014, species of vascular plants were documented within a 5 m radius of the center-pole in each of the four plots. In addition to this, the sites were searched in 2015-2016 for any remaining species not documented in the 5m circles, but as this has not yet been done consistently at all sites, these observations are not taken into account in my analyses.

Species of epiphytic and epilithic mosses were documented in the 130 sites during surveys in 2014-2016, where bryologists thoroughly examined stone and wood surfaces up to 2 m for a maximum of one hour.

Species of lichens were similarly documented in 2014-2016, where lichenologists carefully examined soil, stone and wood surfaces up to 2 m in each site for a maximum of one hour.

Specimens that could not be identified in the field were sampled and later identified in the laboratory.

Most specimens were determined to species level, while only a few were determined to genus level, and some vascular plants to the sub-species level.

2.2.1 Spiders

Arthropods, including spiders, were captured using several different methods. During 2014, pitfall traps, yellow pan traps and a malaise trap were out collecting for two periods of seven days at each site. One malaise trap measuring 190 cm high at the front, 110 cm high at the back, 165 cm long and 115 cm wide, was positioned at the center of the site to collect flying and floating animals. If animals were grazing the site, an electric fence was set up around the malaise trap to avoid any destruction. Underneath the malaise trap, two yellow pan traps measuring 42.5 cm × 31 cm × 7 cm were placed to collect pollinators, flying, jumping and crawling animals along with any animals bouncing off the malaise trap. To collect animals walking and crawling on the soil surface, one yellow pit fall trap measuring 10 cm in diameter and 8 cm in depth, was placed within 5 meters from the center-pole in each of the four plots. If the area was grazed, an extra pitfall trap was placed within the electric fence at each end of the malaise trap to act as backup traps.

The 500 mL collection bottle of the malaise trap contained 95 % ethanol, while the rest of the traps contained a 5 % Rodalon solution and a drop of dishwashing soap to diminish surface tension.

Furthermore, a sweep net was used to collect any additional animals living in the vegetation, such as some web-building spiders for example.

All specimens collected were later sorted and identified in the lab. The vast majority were determined to species level with only a few specimens determined to genus level.

2.3 Data

The majority of microclimatic data was recovered, but in a few cases the data loggers went missing or the logger measuring relative humidity and air temperature had fallen onto the ground, making data unreliable.

No microclimatic data exists for VU29 Sønderbyvej and VO38 Vrøggum Kær. For NT15 Kokkærvand, EV77 Rand Skov and FM123 Ulvshale Hede, data on RH, air temperature and thereby VPD is missing, and for VO40 Lønne, VD48 Gram Slot and FL119 Musse Mose, data on surface temperature and light intensity is missing. The data for VD48 Gram Slot was recovered, but looking at light intensity, there was a “hole” in the middle where it went dark/flat for a few days before returning to light intensities similar to the ones prior to the “blackout”. Because of this anomaly, these “dark” days were removed from the dataset, leaving too few coherent days with proper data left for the site to be included in the analyses. Consequently, there is data from 125 sites for all four microclimatic variables measured using the data loggers, although it is not entirely from the same sites.

Regarding soil moisture, data exists for all 16 measurements in all 130 sites. However, there was some inconsistencies in some of the measurements. For FM125 Busemarke SØ, some values exceeded 100 %, which is likely due to its coastal location and the higher salt content in the soil water. For ES65 Tørvefladen, standing water covered the entire site and the soil would therefore be expected to be a 100 % saturated. Nevertheless, all values measured ranged between 72.5 % and 75.3 %. To account for the fact that soil that was clearly 100 % saturated could have a value as low as 72.5 %, all values from all sites were recalculated with 72.5 % as the new maximum.

When it comes to species, there is data on vascular plants and spiders from all sites. However, in the analyses, sites characterized as “field” or “ley” have been left out for vascular plants, as the species found there, are assumed to reflect agricultural use rather than a natural or semi-natural community. For mosses and lichens, some sites were not included because no mosses or lichens were found, while seven other sites have not been examined for the presence of epiphytic and epilithic mosses yet (Appendix 3). Species lists of all organism groups for all 130 sites can be found on www.biowide.dk, while the number of sites and species included in the analyses are shown in Table 1.

Table 1: Number of sites and species included in the analyses of species composition in relation to the different microclimatic variables. VPD = Vapour Pressure Deficit.

	Surface Temp. and light intensity		Air Temp. and VPD		Soil moisture	
	Number of species	Number of sites	Number of species	Number of sites	Number of species	Number of sites
Vascular plants	528	117	527	116	530	120
Epiphytes	225	103	225	102	227	106
Spiders	350	125	349	125	352	130

2.3.1 Changes in species data

A few changes have been made to the original species data (Appendix 4). Species identified to genus level have been deleted if identifications to species level existed elsewhere in the dataset. However, in cases where a significant part of observations within a genus were specified to genus level, the observations specified to species level were unified under the genus. Additionally, some sub-species have been degraded to the species level, and a few species have been upgraded to sub-species level if found at sites where it is highly unlikely to be any other sub-species.

2.3.2 Creating indices

In order to study the significance of microclimate on the distribution of species, a variety of indices for each microclimatic variable were created from the raw data.

Indices are useful when you want to investigate what aspects of microclimate are particularly important for whatever questions you wish to answer – in this case, the effects on species distribution. The distribution of some species might be limited by their ability to survive above or below certain temperatures, so for these species maxima or minima would likely be the most relevant indices. Other species might need high light intensities for a certain amount of time per day to be able to grow and compete successfully and thus the mean, median or some other percentile could possibly be an important determinant of distribution. For species that handle microclimatic variability well or only thrive in very stable conditions, an index expressing variability is likely to be a good predictor of species distribution.

If using raw data, it would contrary to indices, be difficult to extract any biological meaning behind a correlation with species composition - that is, if there even was a correlation and it had not drowned in a sea of irrelevant data or contradicting patterns.

The indices I have chosen to look at are reasonable simple and consists of mean – and standard deviation values along with a spectrum of percentile values and the relationship between them (Appendix 5). I could have chosen to make more complex indices, and it is possible that the mean difference in light intensity between 8 – and 12 o'clock times the standard deviation divided by the median² had turned out to be the light-index best describing species composition of vascular plants, but then it would have been more difficult to give a sound biological explanation of why that is. Besides, one cannot keep making indices indefinitely.

When creating indices for soil moisture, options were more limited, as only a single measurement was made at each of the 16 spots within each site. Thus, only the maximum, minimum, mean, median and standard deviation were calculated.

The indices have been calculated for both daytime, nighttime and over the course of 24 hours (all day) when relevant, because different nature types have different relationships between day – and nighttime index-values. Exposed to the same macroclimate, the temperature below the

canopy in a forest will for example be lower during the day and higher during the night compared to an open site (von Arx et al. 2013). Consequently, when looking at e.g. mean temperature over the course of 24 hours, this variation will go undetected and the two sites will have more similar mean temperatures than when looking at day and night separately.

The division between day and night was decided by looking at sunrise and sunset in Odense (located approximately in the middle of the country) at the mean day of the study-period. The first data loggers were put up the 7th May and the last ones taken down the 2nd August. The mean day of the period is therefore between the 19th and 20th of June. On both days, the sun went up at 4.36 and down at 22.04 in Odense (www.kalender-365.dk). The hours 5-21 are therefore attributed to daytime, while the hours 22-4 are attributed to nighttime.

2.4 Data analyses

To investigate the strength of the microclimatic indices as determinants of species composition the Mantel test was used (Mantel 1967). The Mantel test has been used in many similar studies (Freestone & Inouye 2006; Hore & Uniyal 2008; Potts et al. 2002) and is based on distance matrices where a Mantel statistic (r) is calculated as the (by default) Pearson correlation coefficient between two matrices.

Dissimilarity matrices representing the species composition were computed for each of the three organism groups using Bray-Curtis dissimilarity, while distance matrices for the microclimatic indices were computed using Euclidean distance. The matrices of vascular plants were based on abundance data in the sense of how many of the four 5 m circles in each site the species had been found in. For spiders and epiphytic/epilithic mosses and lichens the dissimilarity matrices were calculated on presence/absence data, which technically makes it Sørensen's similarity matrices and not Bray-Curtis dissimilarity matrices.

Next, the distance matrix of each microclimatic index was correlated with the dissimilarity matrix of each organism group in a Mantel test. Both the calculation of distance matrices and the Mantel test were performed using the package 'vegan' (Oksanen et al. 2016) in R version 3.2.3 (R Core Team 2015). The significance of the derived correlation coefficients were tested by running 9999 permutations where rows and columns of one of the matrices are randomly rearranged and the

correlation coefficient calculated after each permutation. The *P*-values are then estimated as the proportion of permutations showing a correlation equal to or stronger than the observed correlation.

2.4.1 Linear Mixed effects models

Because the data loggers were out logging at different times during May to August (Appendix 2), a substantial amount of variation in microclimate between sites can be expected to stem from random variation in weather and seasonal variation. In order to correct for this, a mixed effects model incorporating variation in weather and season was used to predict period-adjusted index values.

Linear mixed effects models are an extension of linear regression models. Whereas a linear regression model only contains fixed effects, the mixed effects model also contains a random component. This is suitable for when you have an explanatory variable with random properties that you are not specifically interested in, but still wish to account for. By including the variable as a random effect, you avoid spending an excessive amount of degrees of freedom on an effect you do not need to know the exact nature of (Zuur et al. 2009). An example of such a variable could be “sites” for which you have multiple measurements. The values measured within each site are non-independent and likely more related to each other than to those of other sites – something the random component in mixed effects models acknowledges by modelling a site-specific intercept (and slope if asked to) for each site. This is useful if you for example wish to study the effect of some treatment on species richness and want to account for the site-specific effect. However, if you wish to investigate exactly what effect each site has on richness, you will need to incorporate it as a fixed effect.

To adjust for differences between periods, the data was divided into 17 periods of 5 days, ranging from 10th May to 2nd August. The indices showing the highest correlations in the Mantel tests were then calculated for each site in each period, for which they had five full days of measurements. A number of models were created (Model 1-5) with site and seasonal variables as fixed effects and weather as a random effect. Both the season and weather variable were

specified as the mean Julian day of the period, but as a numeric and factor variable respectively. Whereas season denotes the distinctive changes happening when moving from May to August, azimuth represents an even more consistent aspect of season – namely the position of the sun. In the models, azimuth is specified as the number of days the mean day of the period deviates from summer solstice (21st June 2015), which happens to fall exactly in the middle of the full study period.

Model 1-5

- (1) `M1 <- lme(index ~ season + azimuth + site, random= ~1|weather, data = MyData, method="ML")`
- (2) `M2 <- lme(index ~ season + site, random= ~1|weather, data = MyData, method="ML")`
- (3) `M3 <- lme(index ~ azimuth + site, random= ~1|weather, data = MyData, method="ML")`
- (4) `M4 <- lme(index ~ site, random= ~1|weather, data = MyData, method="ML")`
- (5) `M5 <- gls(index ~ season + azimuth + site, data = MyData, method="ML")`

The models were run using the lme-function in the R-package 'nlme' (Pinheiro et al. 2015) and the best model for each index determined by comparing AIC scores. The linear model (gls) was included to test if the random variation in weather was in fact significant enough for it to be included and a mixed effects model needed.

Because a mixed effects model produces both a variance associated with each random factor and the residual variance, the resulting R^2 is not entirely correct, and what you would call a pseudo- R^2 . To address this problem, two types of R^2 can be calculated – the marginal R^2 , which describes the proportion of variance explained by the fixed factors alone, and the conditional R^2 , which describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2013). These were easily calculated using the `r.squaredGLMM` function in the R-package 'MuMIn' (Barton 2016).

Only a single index for each of the four microclimatic variables were chosen as “the best one”, based primarily on the correlation with species composition in the Mantel test, but also on how much of the total variation the mixed effects model was able to describe – and therefore how accurate a period-adjusted index would be. The best mixed effects model for each of the four indices was then used to predict values for the period 30/5 – 3/6, the period in which the microclimate had been measured for the most sites.

Originally, additional random variables with weather nested in cluster or region were tested as well. However, since no period exists in which microclimate in all clusters or all regions have been measured, it was not possible to predict period-adjusted indices for all sites using these models.

2.5 Variation within sites

To study how well the one data logger pair in each site represents the variation found within sites, 16 data loggers were placed (as shown in Figure 2) in each of six sites on Zealand, recording light intensity, air – and surface temperature and relative humidity every 30 min from 14th August to 2nd December 2015.

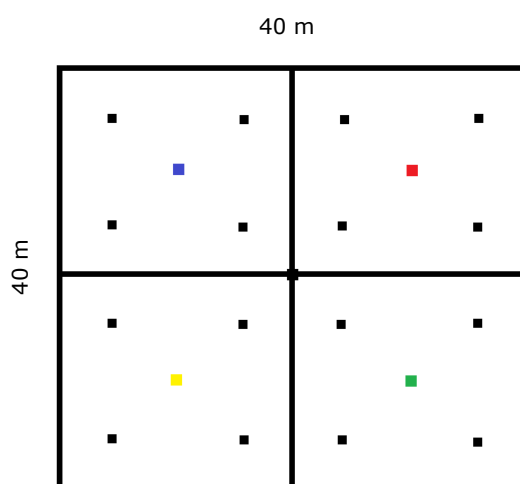


Figure 2: The placement of data loggers within each site. The coloured squares denote the center of each plot, while the black squares denote the placement of data loggers.

The six sites with additional loggers were:

SV88 Diesbjerg (early, dry, rich)

SV89 Eskebjerg Vesterlyng (early, moist, poor)

SV92 Kaldred Kær (early, wet, rich)

SV94 Røsnæs Krat (mid, dry, rich)

SM97 Suserup Skov (late, dry, rich)

SM101 Frederikskilde Skov (late, wet, rich)

These sites were selected because they cover very different nature types in relation to succession (early, mid, late), soil moisture (wet, moist, dry) and nutrient content (rich, poor). They are also located in fairly close proximity to each other, spanning two clusters in the same region (Appendix 1), and are therefore likely to experience similar weather conditions.

2.5.1 Analysis

The indices found to best describe species composition of one or more organism group, when using data collected from all 130 sites in the Biowide-project, were calculated for each of the six sites as a total and for each data logger individually. This was not done for the entire 3.5 month period, but only for the first 20 days (14/8 – 2/9), as we are interested in the variation within – and between sites in the summer period. Furthermore, including a longer period would have resulted in the removal of data from several data loggers from the dataset, as they became covered in litter or trampled down by animals as time progressed. Even within the first 20 days, two data loggers measuring light intensity and surface temperature in Suserup Skov had been covered by litter, and had to be removed from the analysis.

When calculating the indices, the division into day and night was done using the same principle as for the 130-site dataset – by looking at the time of sunrise and sunset on the mean day of the period. For the period 14/8 – 2/9, the mean day is halfway between 23/8 and 24/8. In the city of Slagelse, whose longitudinal position lies approximately in the middle of the location of the six sites, the sun rose at 6.02 and went down at 20.31 on August 23rd, while it rose at 6.04 and went down at 20.29 on the 24th (www.kalender-365.dk). The hours 6.30 – 20.00 were therefore attributed to daytime and the hours 20.30 – 6.00 to nighttime.

To investigate how much of the variation in index value could be attributed to variation between sites and within sites respectively, mixed effect models were used again. The 20-day period was divided into 4 periods of 5 days to account for periodic variation and an index-value was calculated for each logger in each 5-day period. When looking at indices of air temperature and VPD, a total of 96 data loggers were included in the model, while data from only 94 data loggers were included when looking at indices of light and surface temperature, because of the two litter-covered data-loggers in Suserup Skov.

Contrary to the mixed effects models used to predict the period-adjusted indices for the 130 sites, we are not interested in the site – or logger specific effect on the response variable, but only in partitioning the variation. It is therefore more feasible to specify site and logger as random variables. Mixed effects models were thus created with period as a fixed effect and site, and logger nested within site, as random effects (Model 6-7). Period was modelled as a factor and not a numeric variable, as there was only a weak linear tendency between time-period and the light index and possibly also with the surface temperature index, while the relationship between time-period and the air temperature and VPD indices were far from linear.

Model 6-7

```
(6) M6 <- lme(Index ~ period, random= ~1|site, data=MyData, method="REML")
```

```
(7) M7 <- lme(Index ~ period, random= ~1|site/logger, data=MyData, method="REML")
```

The marginal R^2 from the best model (lowest AIC), tells us how much of the variation in index-value can be attributed to variation between time periods, while the between-site variation is the difference between the conditional R^2 and the marginal R^2 for model M6, and the within-site variation the difference between the conditional R^2 and the marginal R^2 for model M7 minus the between-site variation:

Between-site variation = conditional R^2 (M6) – marginal R^2 (M6)

Within-site variation = (conditional R^2 (M7) – marginal R^2 (M7)) – Between-site variation

3. Results

Correlations between the raw measurements of microclimate variables are shown in Table 2. Soil moisture is not included, as it was not measured at the same time as the other variables. The correlation between surface and air temperature is the highest ($r = 0.895$, $P < 0.001$) and both temperatures have a similar high correlation with VPD ($r = 0.799$, $P < 0.001$ and $r = 0.766$, $P < 0.001$). Light intensity show the highest correlation with surface temperature ($r = 0.69$, $P < 0.001$) and the lowest with air temperature ($r = 0.419$, $P < 0.001$), while the correlation with VPD is $r = 0.512$ ($P < 0.001$).

Table 2: Correlations (Pearson's r) between four of the microclimate variables using the raw data from 122-125 sites (see Appendix 3 for which sites microclimatic data is missing). $P < 0.001$ for all correlations.

	Light Intensity (lux)	Surface Temp. (°C)	Air Temp. (°C)
Surface Temp. (°C)	0.690		
Air Temp. (°C)	0.419	0.895	
VPD (kPa)	0.512	0.799	0.766

3.1 Mantel tests

Table 3-7 show the correlations between different indices of the microclimate variables and species composition of the three organism groups. Indices with the designation "all" are calculated for the 24 hour period, while indices with the designation "day" or "night" are calculated for daytime and nighttime respectively. An overview of what exactly the different index-abbreviations mean, is found in Appendix 5.

Table 3: The correlation (Mantel r) between the Euclidean distance matrices calculated from the logarithmic values of different light intensity indices and the Bray-Curtis dissimilarity matrices calculated from species composition of vascular plants, spiders and epiphytic/epilithic mosses and lichens. P-values were obtained by running 9999 permutations.

Light intensity

Index	Vascular plants		Epiphytes		Spiders	
	Mantel r	P	Mantel r	P	Mantel r	P
MaxLight_all	0.228	<0.001	0.099	0.022	0.194	<0.001
MeanLight_all	0.346	<0.001	0.232	<0.001	0.427	<0.001
MedianLight_all	0.324	<0.001	0.245	<0.001	0.419	<0.001
sdLight_all	0.312	<0.001	0.191	<0.001	0.353	<0.001
MedianLight_day	0.336	<0.001	0.239	<0.001	0.441	<0.001
sdLight_day	0.306	<0.001	0.185	<0.001	0.340	<0.001
Light_5pct_day	0.243	<0.001	0.237	<0.001	0.400	<0.001
Light_10pct_day	0.312	<0.001	0.231	<0.001	0.402	<0.001
Light_15pct_day	0.320	<0.001	0.237	<0.001	0.406	<0.001
Light_85pct_day	0.345	<0.001	0.247	<0.001	0.455	<0.001
Light_90pct_day	0.344	<0.001	0.252	<0.001	0.441	<0.001
Light_95pct_day	0.341	<0.001	0.228	<0.001	0.402	<0.001

The distance matrices for light are calculated from logarithmic index values, as log-transformation significantly improved the correlations.

Looking at Table 3, species composition of spiders is generally showing the highest correlations with the light indices, followed by plant species composition and lastly the composition of epiphytes. The 85th and 90th percentile generally show the highest correlations with all three organism groups, with mean light intensity doing just as well for vascular plants. The highest correlation is $r = 0.455$ ($P < 0.001$) and found between spider species composition and the 85th percentile calculated for daytime. Because light intensity is zero in the far majority of nighttime measurements, this is the same correlation found when calculating the 85th percentile for the 24-hour period.

Table 4: The correlation (Mantel r) between the Euclidean distance matrices calculated from different surface temperature indices and the Bray-Curtis dissimilarity matrices calculated from species composition of vascular plants, spiders and epiphytic/epilithic mosses and lichens. P-values are obtained from running 9999 permutations.

Surface Temperature

Index	Vascular plants		Epiphytes		Spiders	
	Mantel r	P	Mantel r	P	Mantel r	P
MaxSurfaceTemp_all	0.218	<0.001	0.149	<0.001	0.271	<0.001
MinSurfaceTemp_all	0.135	<0.001	0.057	0.12	0.212	<0.001
MeanSurfaceTemp_all	0.152	<0.001	0.140	<0.001	0.178	<0.001
MedianSurfaceTemp_all	0.098	<0.001	0.084	0.009	0.109	<0.001
sdSurfaceTemp_all	0.314	<0.001	0.255	<0.001	0.393	<0.001
MinSurfaceTemp_day	0.122	<0.001	0.043	0.18	0.198	<0.001
MeanSurfaceTemp_day	0.200	<0.001	0.176	<0.001	0.248	<0.001
MedianSurfaceTemp_day	0.154	<0.001	0.158	<0.001	0.195	<0.001
sdSurfaceTemp_day	0.301	<0.001	0.245	<0.001	0.374	<0.001
MeanSurfaceTemp_night	0.067	<0.001	0.056	0.024	0.079	<0.001
MedianSurfaceTemp_night	0.059	0.002	0.063	0.009	0.078	<0.001
sdSurfaceTemp_night	0.091	<0.001	0.032	0.23	0.147	<0.001
SurfaceTemp_mean_diff	0.345	<0.001	0.286	<0.001	0.437	<0.001
SurfaceTemp_median_diff	0.330	<0.001	0.279	<0.001	0.438	<0.001
SurfaceTemp_max_diff	0.252	<0.001	0.174	<0.001	0.313	<0.001
SurfaceTemp_sd_diff	0.286	<0.001	0.248	<0.001	0.357	<0.001
SurfaceTemp_5pct_day	0.073	0.002	0.064	0.02	0.069	<0.001
SurfaceTemp_10pct_day	0.075	0.002	0.063	0.015	0.079	<0.001
SurfaceTemp_15pct_day	0.085	<0.001	0.082	0.007	0.089	<0.001
SurfaceTemp_85pct_day	0.270	<0.001	0.238	<0.001	0.336	<0.001
SurfaceTemp_90pct_day	0.278	<0.001	0.238	<0.001	0.342	<0.001
SurfaceTemp_95pct_day	0.282	<0.001	0.231	<0.001	0.345	<0.001
SurfaceTemp_5/95_day	0.313	<0.001	0.194	<0.001	0.333	<0.001
SurfaceTemp_10/90_day	0.325	<0.001	0.215	<0.001	0.370	<0.001
SurfaceTemp_15/85_day	0.314	<0.001	0.227	<0.001	0.375	<0.001
SurfaceTemp_5pct_night	0.102	<0.001	0.061	0.11	0.173	<0.001
SurfaceTemp_10pct_night	0.097	<0.001	0.061	0.087	0.145	<0.001
SurfaceTemp_15pct_night	0.089	<0.001	0.062	0.068	0.123	<0.001
SurfaceTemp_85pct_night	0.051	0.003	0.039	0.033	0.057	0.002
SurfaceTemp_90pct_night	0.054	0.002	0.038	0.045	0.054	0.004
SurfaceTemp_95pct_night	0.063	<0.001	0.032	0.095	0.028	0.063
SurfaceTemp_5/95_night	0.107	<0.001	0.047	0.18	0.216	<0.001
SurfaceTemp_10/90_night	0.136	<0.001	0.067	0.11	0.224	<0.001
SurfaceTemp_15/85_night	0.132	<0.001	0.084	0.068	0.210	<0.001

As for light, the highest correlations are generally with spider composition, followed by vascular plant composition and finally epiphyte composition (Table 4). Correlations are also of similar strength as those found for the light indices, albeit a little lower.

When looking at both plant, spider and epiphyte composition, the correlation with indices calculated for daytime is generally considerably higher than the same indices calculated for nighttime, while those calculated for all 24 hours land somewhere in between. The lower percentile indices however, deviate from this pattern; looking at vascular plants and spiders, the 5th, 10th and 15th percentile show a low correlation with species composition when calculated for daytime and a higher correlation when calculated for nighttime. Conversely, the 85th, 90th and 95th percentile have much higher correlations with species composition when calculated for daytime than for nighttime. For epiphytes, the pattern is the same, but most of the nighttime percentile-indices are non-significant. The percentile-indices calculated for all 24 hours have not been included here, but they generally have correlations somewhere in between.

The highest correlations for spiders, vascular plants and epiphytes are found with the differences between mean – and median daytime and nighttime temperatures (SurfaceTemp_mean_diff and SurfaceTemp_median_diff), but also the standard deviation for both daytime and all 24 hours (sdSurfaceTemp_day and sdSurfaceTemp_all) show some of the highest correlations for all three organism groups. For spiders and especially vascular plants, the indices depicting the relationship between the lower and higher percentile values calculated for daytime (SurfaceTemp_5/95_day, SurfaceTemp_10/90_day, SurfaceTemp_15/85_day), are generally also among the best predictors of species composition. The highest correlation found is $r = 0.438$ ($P < 0.001$) between spider composition and SurfaceTemp_median_diff, with SurfaceTemp_mean_diff being essentially just as good with a correlation of $r = 0.437$ ($P < 0.001$). Moreover, SurfaceTemp_mean_diff also shows the highest correlation with the composition of both vascular plants and epiphytic/epilithic mosses and lichens.

Table 5: The correlation (Mantel r) between the Euclidean distance matrices calculated from different air temperature indices and the Bray-Curtis dissimilarity matrices calculated from species composition of vascular plants, spiders and epiphytic/epilithic mosses and lichens.

P-values were obtained by running 9999 permutations.

Air temperature

Index	Vascular plants		Epiphytes		Spiders	
	Mantel r	P	Mantel r	P	Mantel r	P
MaxAirTemp_all	0.093	<0.001	0.057	0.1	0.108	<0.001
MinAirTemp_all	0.174	<0.001	0.068	0.07	0.215	<0.001
MeanAirTemp_all	0.080	<0.001	0.074	0.005	0.077	<0.001
MedianAirTemp_all	0.075	<0.001	0.063	0.007	0.064	0.002
sdAirTemp_all	0.181	<0.001	0.127	0.005	0.224	<0.001
MinAirTemp_day	0.148	<0.001	0.066	0.067	0.195	<0.001
MeanAirTemp_day	0.100	<0.001	0.093	0.006	0.104	<0.001
MedianAirTemp_day	0.101	<0.001	0.099	0.004	0.103	<0.001
sdAirTemp_day	0.153	<0.001	0.107	0.015	0.177	<0.001
MeanAirTemp_night	0.070	<0.001	0.070	0.008	0.065	0.002
MedianAirTemp_night	0.060	<0.001	0.070	0.006	0.063	0.002
sdAirTemp_night	0.084	<0.001	0.024	0.28	0.116	<0.001
AirTemp_mean_diff	0.255	<0.001	0.217	<0.001	0.339	<0.001
AirTemp_median_diff	0.226	<0.001	0.216	<0.001	0.313	<0.001
AirTemp_max_diff	0.183	<0.001	0.125	0.011	0.217	<0.001
AirTemp_sd_diff	0.127	<0.001	0.126	0.013	0.172	<0.001
AirTemp_5pct_day	0.080	<0.001	0.077	0.004	0.075	<0.001
AirTemp_10pct_day	0.070	<0.001	0.064	0.008	0.057	0.003
AirTemp_15pct_day	0.069	<0.001	0.063	0.007	0.063	0.002
AirTemp_85pct_day	0.108	<0.001	0.102	0.014	0.119	<0.001
AirTemp_90pct_day	0.108	<0.001	0.093	0.025	0.109	<0.001
AirTemp_95pct_day	0.111	<0.001	0.078	0.039	0.113	<0.001
AirTemp_5/95_day	0.197	<0.001	0.092	0.03	0.204	<0.001
AirTemp_10/90_day	0.226	<0.001	0.134	0.002	0.245	<0.001
AirTemp_15/85_day	0.222	<0.001	0.146	<0.001	0.269	<0.001
AirTemp_5pct_night	0.083	<0.001	0.025	0.29	0.130	<0.001
AirTemp_10pct_night	0.078	<0.001	0.052	0.13	0.089	<0.001
AirTemp_15pct_night	0.080	<0.001	0.061	0.066	0.087	<0.001
AirTemp_85pct_night	0.052	0.002	0.052	0.013	0.044	0.01
AirTemp_90pct_night	0.055	0.002	0.055	0.012	0.034	0.034
AirTemp_95pct_night	0.063	0.001	0.047	0.048	0.017	0.20
AirTemp_5/95_night	0.084	<0.001	0.014	0.38	0.173	<0.001
AirTemp_10/90_night	0.086	<0.001	0.040	0.22	0.142	<0.001
AirTemp_15/85_night	0.086	<0.001	0.044	0.19	0.125	<0.001

The correlations between air temperature indices and the three organism groups (Table 5) overall follow the same pattern as those for surface temperature, but with the highest correlations for air temperature being considerably lower than the highest correlations for surface temperature. The indices of both air – and surface temperature showing the lowest correlations with species composition are however, of similar strength. These are typically indices calculated for nighttime. As for surface temperature, the lower percentile indices have higher correlations with vascular plant – and spider composition than the upper percentile indices when calculated for nighttime, while the opposite is the case when the indices are based on daytime. Nighttime indices generally have lower correlations than the same indices calculated for daytime, but the difference is not as pronounced as for surface temperature. The difference between mean daytime – and nighttime temperature (AirTemp_mean_diff) is the air temperature index showing the highest correlation with both spiders ($r = 0.339$, $P < 0.001$), vascular plants ($r = 0.255$, $P < 0.001$) and epiphytes ($r = 0.217$, $P < 0.001$), with AirTemp_median_diff being the second best in all cases.

Table 6: The correlation (Mantel r) between the Euclidean distance matrices calculated from different vapour pressure deficit (VPD) indices and the Bray-Curtis dissimilarity matrices calculated from species composition of vascular plants, spiders and epiphytic/epilithic mosses and lichens. P-values were obtained by running 9999 permutations.

Vapour pressure deficit (VPD)

Index	Vascular plants		Epiphytes		Spiders	
	Mantel r	P	Mantel r	P	Mantel r	P
MaxVPD_all	0.119	<0.001	0.110	0.024	0.141	<0.001
MeanVPD_all	0.180	<0.001	0.202	<0.001	0.168	<0.001
MedianVPD_all	0.153	<0.001	0.190	<0.001	0.141	<0.001
sdVPD_all	0.147	<0.001	0.160	0.002	0.146	<0.001
MeanVPD_day	0.184	<0.001	0.204	<0.001	0.177	<0.001
MedianVPD_day	0.195	<0.001	0.214	<0.001	0.192	<0.001
sdVPD_day	0.139	<0.001	0.150	0.004	0.137	<0.001
MaxVPD_night	0.066	0.004	0.127	0.013	0.047	0.11
MeanVPD_night	0.087	<0.001	0.133	0.005	0.089	0.003
MedianVPD_night	0.071	<0.001	0.114	0.011	0.094	0.002
sdVPD_night	0.090	<0.001	0.123	0.007	0.068	0.02
VPD_mean_diff	0.192	<0.001	0.214	<0.001	0.201	<0.001
VPD_median_diff	0.209	<0.001	0.224	<0.001	0.221	<0.001
VPD_max_diff	0.123	<0.001	0.103	0.043	0.156	<0.001
VPD_sd_diff	0.144	<0.001	0.158	0.005	0.153	<0.001
VPD_5pct_day	0.075	0.005	0.136	0.026	0.109	0.007
VPD_10pct_day	0.107	<0.001	0.195	<0.001	0.124	<0.001
VPD_15pct_day	0.142	<0.001	0.228	<0.001	0.149	<0.001
VPD_85pct_day	0.156	<0.001	0.186	<0.001	0.151	<0.001
VPD_90pct_day	0.142	<0.001	0.167	0.003	0.126	<0.001
VPD_95pct_day	0.142	<0.001	0.160	0.002	0.122	<0.001
VPD_10pct_night	0.070	0.006	-0.051	0.22	0.117	0.002
VPD_15pct_night	0.080	<0.001	0.070	0.10	0.112	<0.001
VPD_85pct_night	0.092	<0.001	0.143	0.003	0.079	0.009
VPD_90pct_night	0.090	<0.001	0.141	0.002	0.075	0.013
VPD_95pct_night	0.087	<0.001	0.133	0.005	0.071	0.014

The correlations between species composition and VPD indices are, with the exception of a few cases, strongest for epiphytes (Table 6).

Generally however, the strength of the correlations do not differ much between vascular plants, spiders and epiphytes – at least not compared to indices of the other microclimate variables.

The highest correlation found is between VPD_15pct_day and epiphyte composition ($r = 0.228, P < 0.001$). However, VPD_median_diff ($r = 0.224, P < 0.001$), VPD_mean_diff ($r = 0.214, P < 0.001$) and Mean_VPD_day ($r = 0.214, P < 0.001$) are not far behind, and contrary to the 15th percentile, show some of the highest correlations for vascular plants and spiders as well.

Table 7: The correlation (Mantel r) between the Euclidean distance matrices calculated from different soil moisture indices and the Bray-Curtis dissimilarity matrices calculated from species composition of vascular plants, spiders and epiphytic/epilithic mosses and lichens. P-values were obtained by running 9999 permutations.

Soil moisture

Index	Vascular plants		Epiphytes		Spiders	
	Mantel r	P	Mantel r	P	Mantel r	P
MaxSoilM	0.289	<0.001	0.096	0.003	0.210	<0.001
MinSoilM	0.255	<0.001	0.044	0.1	0.162	<0.001
MeanSoilM	0.328	<0.001	0.071	0.002	0.227	<0.001
MedianSoilM	0.322	<0.001	0.063	0.002	0.223	<0.001
sdSoilM	0.014	0.27	-0.020	0.64	0.023	0.23

Soil moisture shows the highest correlations with composition of vascular plants followed by spiders and finally, epiphytes (Table 7).

Discounting the standard deviation in soil moisture (sdSoilM), which has low, non-significant correlations with all three organism groups, the remaining indices all do similarly well.

Mean and median soil moisture show the highest correlations with both vascular plant - and spider composition, with mean soil moisture being the marginally better index. The highest correlation is $r = 0.328 (P < 0.001)$ and found between mean soil moisture and vascular plant composition.

3.2 Mixed effects models and choosing the best indices

Because light intensity, surface temperature, air temperature and relative humidity have not been measured in the same time period for all sites, indices based on these microclimatic variables should be adjusted for any differences in time period that may exist.

For each microclimate variable, indices showing the highest correlations with species composition of any of the three organism groups were modelled in a linear mixed effects model as described in Materials and Methods. A single index is chosen for each variable based on how well it does in the Mantel test and how well it is modelled in the mixed effects model compared to other indices.

I have modelled most indices except the ones showing the lowest correlations. However, only the mixed effects results for indices showing Mantel statistics of similar strength for the mixed effects results to actually matter will be mentioned.

3.2.1 Light

The light index best describing the variation in species composition is Light_85pct_day ($r = 0.455$, $P < 0.001$). The next best indices are Light_90pct_day ($r = 0.441$), MedianLight_day ($r = 0.441$, $P < 0.001$) and MeanLight_all ($r = 0.427$, $P < 0.001$) (Table 3). Light_90pct_day and MedianLight_day can quickly be ruled out, as they do poorer than Light_85pct_day in the mixed effects model as well (lower conditional R^2). MeanLight_all on the contrary, can be explained to a higher degree by the mixed effects model ($R^2 = 0.937$, $P < 0.001$) than Light_85pct_day ($R^2 = 0.926$, $P < 0.001$), but given the smaller difference in conditional R^2 compared to the difference in the Mantel statistic, the 85th percentile is chosen as the best measure of the light gradient.

3.2.2 Surface Temperature

For surface temperature, the two indices best describing the variation in species composition, is SurfaceTemp_median_diff ($r = 0.438$, $P < 0.001$) and SurfaceTemp_mean_diff ($r = 0.437$, $P < 0.001$). These indices nearly have the same correlation with spider composition, while SurfaceTemp_mean_diff has a relatively higher correlation with vascular plant and epiphyte composition (Table 4). This alone would make me choose SurfaceTemp_mean_diff as the better index of the two, and the results of the mixed effects models, showing a significantly lower

conditional R^2 for SurfaceTemp_median_diff ($R^2 = 0.854, P < 0.001$) than for SurfaceTemp_mean_diff ($R^2 = 0.902, P < 0.001$) only establishes this. No other indices with correlations remotely close to that of SurfaceTemp_mean_diff in the Mantel test were better described by a mixed effects model.

3.2.3 Air Temperature

The two air temperature indices best describing species composition is AirTemp_mean_diff ($r = 0.339, P < 0.001$) and AirTemp_median_diff ($r = 0.313, P < 0.001$), with AirTemp_mean_diff also showing the highest correlations with vascular plant and epiphyte composition.

AirTemp_mean_diff is chosen as the better index, as it is also better described by the mixed effects model ($R^2 = 0.894, P < 0.001$) than AirTemp_median_diff ($R^2 = 0.861, P < 0.001$). No other indices with correlations remotely close to that of AirTemp_mean_diff in the Mantel test were better described by a mixed effects model.

3.2.4 Vapour Pressure Deficit

Several of the VPD-indices best describing variation in species composition, have correlations of similar strength (Table 6), and how well the indices are described by mixed effects models has been essential to the choice of index.

The five indices showing the strongest correlations in the Mantel test are listed in Table 8 along with the resulting marginal – and conditional R^2 from the mixed effects models. From Table 8, it can be seen that VPD_15pct_day, which does best in the Mantel test, performs very poorly in the mixed effects model compared to the other indices. VPD_median_diff, which performs second best in the Mantel test, also does substantially worse in the mixed effects model than the remaining indices. The third best indices are VPD_mean_diff and MedianVPD_day, showing the same correlation in the Mantel test. Of these two indices, MedianVPD_day is opted out even though it has a marginally higher conditional R^2 ($R^2 = 0.831, P < 0.001$) than VPD_mean_diff ($R^2 = 0.829, P < 0.001$). This is because the marginal R^2 – the R^2 , which tells us how much of the variation the fixed effects (in this case “sites”) explain – is substantially better for VPD_mean_diff ($R^2 = 0.476, P < 0.001$) than for MedianVPD_day ($R^2 = 0.414, P < 0.001$). Since we are interested in how the

site specific index values correlate with species composition, an index where “sites” is able to explain a higher proportion of the variation in index-values, is to be preferred.

MeanVPD_day, which has a slightly lower correlation ($r = 0.204$, $P < 0.001$) than VPD_mean_diff in the Mantel test, has a slightly higher conditional R^2 ($R^2 = 0.845$, $P < 0.001$) than VPD_mean_diff. Since the correlation with species composition in the Mantel test is the main criteria and the difference in conditional R^2 is relatively small, VPD_mean_diff is chosen as the best index for vapour pressure deficit.

Table 8: The VPD-indices with the five highest correlations in the Mantel test and the marginal – and conditional R^2 showing how well the variation in each index can be explained by the best mixed effects model. $P < 0.001$ for all Mantel r , marginal R^2 and conditional R^2

	Highest Mantel r	The best mixed effects model	Marginal R^2	Conditional R^2
VPD_15pct	0.228	M4	0.439	0.684
VPD_median_diff	0.224	M4	0.403	0.798
VPD_mean_diff	0.214	M4	0.476	0.829
MedianVPD_day	0.214	M4	0.414	0.831
MeanVPD_day	0.204	M4	0.462	0.845

3.2.5 Period-adjusted indices

The index for each of the four microclimate variables found to best describe variation in species composition was adjusted for differences in time-period by using the best mixed effect model for each index to predict new values for the period 30/5 – 3/6 2015.

For light, model M2 was used to predict new values for Light_85pct_day, while index-values for the remaining three microclimatic variables were predicted using model M4.

How well the adjusted indices performs in the Mantel test compared to the original indices can be seen in Table 9.

Table 9: Overview of the indices chosen for each of the four microclimatic variables and their correlation with variation in species composition of vascular plants, spiders and epiphytic/epilithic mosses and lichens, before and after being adjusted for differences in time-period. “adj” denotes the adjusted indices. P-values were obtained by running 9999 permutations.

Index	Vascular plants		Epiphytes		Spiders	
	Mantel r	P	Mantel r	P	Mantel r	P
Light_85pct_day	0.345	<0.001	0.247	<0.001	0.455	<0.001
Light_85pct_day_adj	0.340	<0.001	0.260	<0.001	0.441	<0.001
SurfaceTemp_mean_diff	0.345	<0.001	0.286	<0.001	0.437	<0.001
SurfaceTemp_mean_diff_adj	0.338	<0.001	0.294	<0.001	0.419	<0.001
AirTemp_mean_diff	0.255	<0.001	0.217	<0.001	0.339	<0.001
AirTemp_mean_diff_adj	0.249	<0.001	0.217	<0.001	0.326	<0.001
VPD_mean_diff	0.192	<0.001	0.214	<0.001	0.201	<0.001
VPD_mean_diff_adj	0.220	<0.001	0.243	<0.001	0.234	<0.001

The adjusted indices for light intensity, surface temperature and air temperature generally have somewhat lower correlations with the variation in species composition than the non-adjusted indices – except for the correlations with epiphytes, where they perform better or equally good. Conversely, the adjusted index for VPD has a higher correlation with the species composition of all organism groups, than the non-adjusted index, with the difference between the adjusted and non-adjusted index being noticeably larger than for the other microclimate indices.

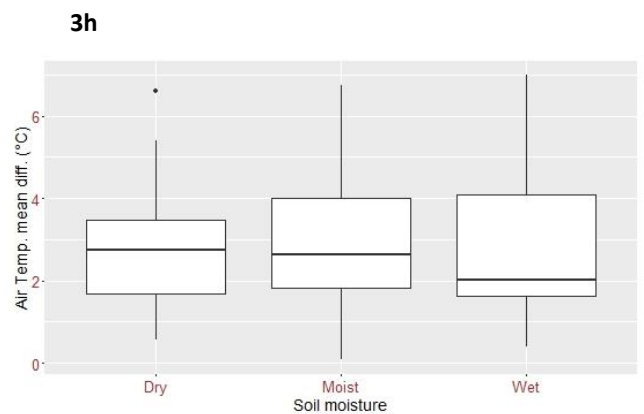
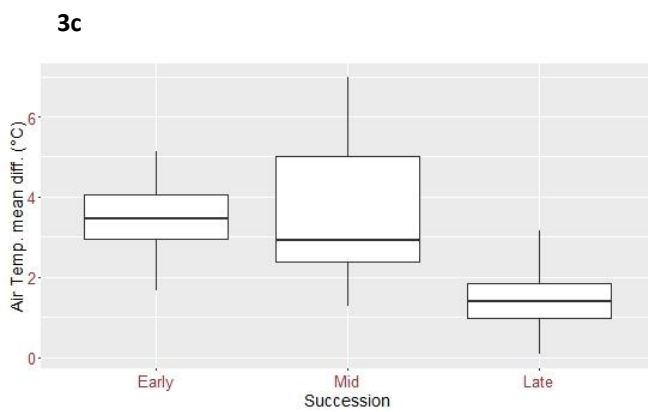
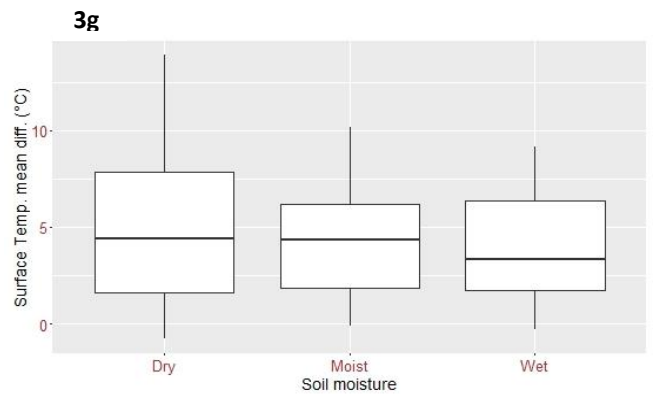
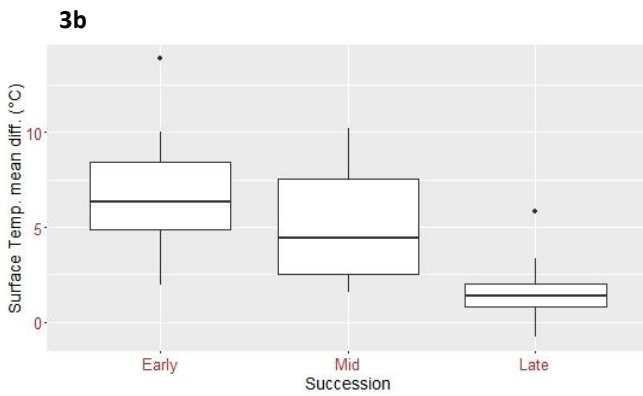
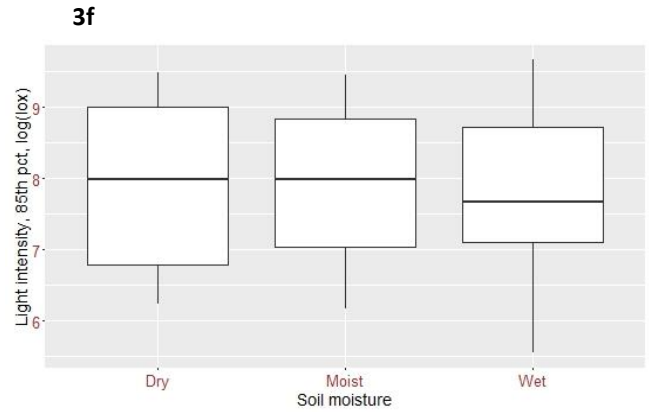
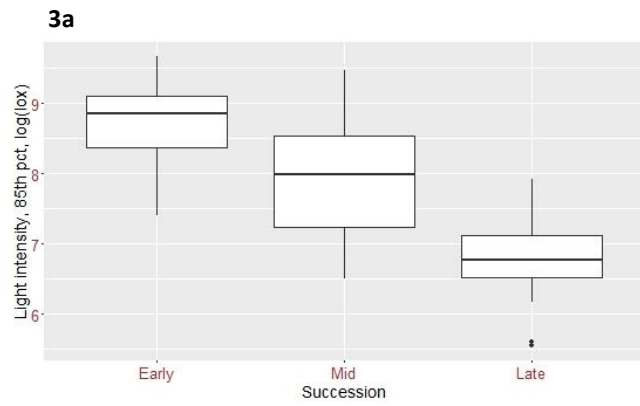
Correlations between the period-adjusted indices and the best index for soil moisture is shown in Table 10.

Table 10: Correlations (Pearson’s *r*) between the best indices of the five microclimatic variables. ** indicates $P < 0.001$, ns = non-significant. ns* = non-significant, but tendency ($P = 0.055$)

	Light_85pct_day_adj	ST_mean_diff_adj	AT_mean_diff_adj	VPD_mean_diff_adj
ST_mean_diff_adj	0.897**			
AT_mean_diff_adj	0.684**	0.820**		
VPD_mean_diff_adj	0.693**	0.832**	0.864**	
MeanSoilM	0.062 ns	-0.083 ns	-0.026 ns	-0.172 ns*

3.2.6 Microclimate, succession and soil moisture

Figure 3a-j shows how index values of the five microclimate variables are distributed among sites categorized as being in early, mid – or late succession or having dry, moist or wet soils.



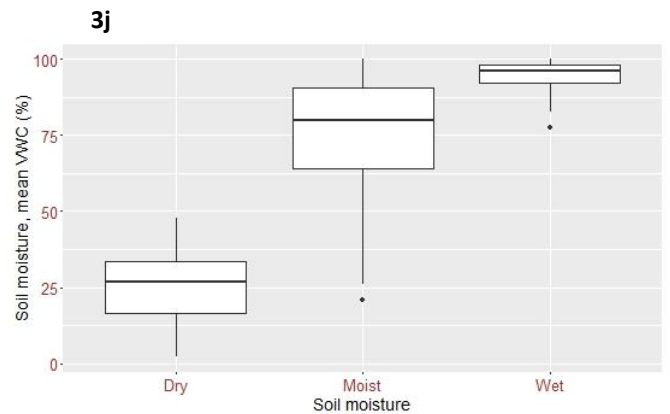
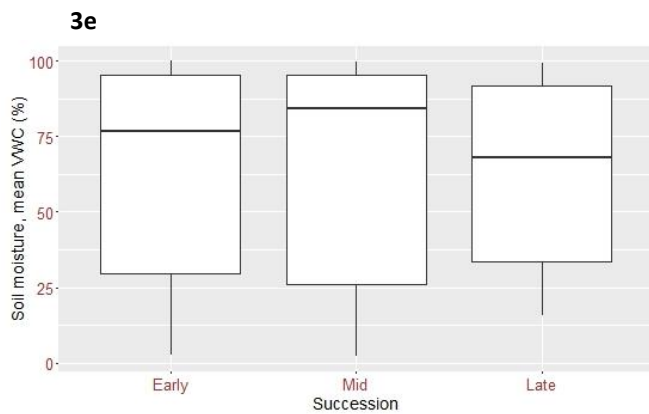
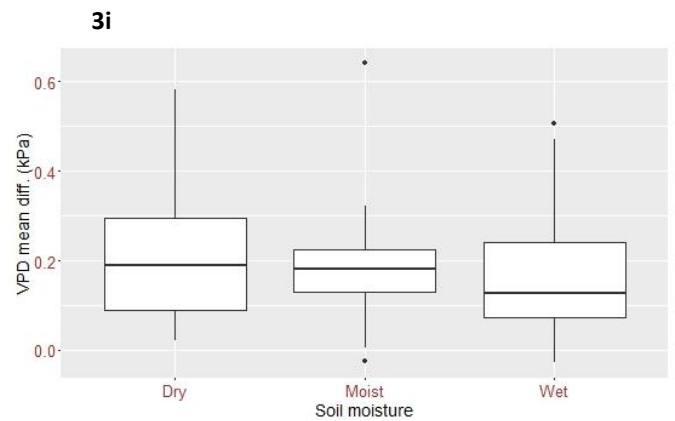
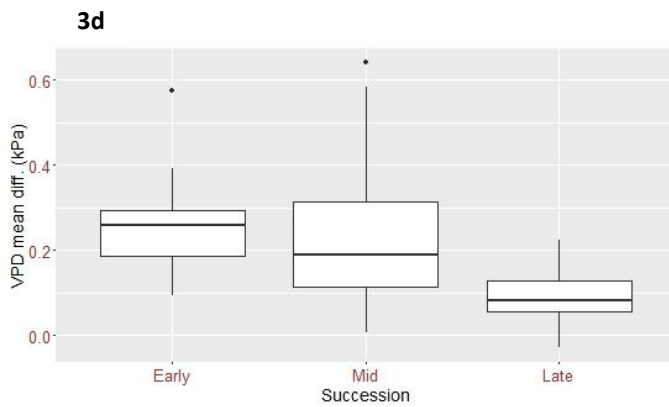


Figure 3a-j: Box plots of how the index-values for light, surface temperature, air temperature, VPD and soil moisture are distributed among sites categorized as being in early, mid – or late succession or having dry, moist or wet soils.

3.3 Within-site variation

For the six sites where 16 data-loggers had been placed to cover the within-site variation, the light, surface temperature, air temperature and VPD indices found to best describe species composition of one or more organism groups, were calculated for each data logger and each site. The indices were then modelled using mixed effects models to determine how much of the total

variation in index values can be attributed to between-period variation, between-site variation and within-site variation.

Results from the mixed effects models (Table 11) show that the majority of the total variation in indices of air temperature and VPD can be ascribed between-period variation, with 55.3 % of the total variation explained for air temperature and 59.7 % of the total variation explained for VPD. In contrast to this, only 4.8 % of the variation in light index values is attributed between-period variation, while the variation between periods explain 23.6 % of the total variation in the surface temperature index values.

Both the between-site and within-site variation is highest for the light index, with the between-site variation accounting for 74 % and the within-site variation accounting 17.9 % of the total variation. For the surface temperature index, the between-site variation explains 52.9 % and the within-site, 8.8 % of the total variation. For air temperature, the between-site variation explains 31.2 % of the total variation in index-value, while the within-site variation only explains 0.01 %. Lastly, only 21.2 % of the variation in the VPD index can be explained by between-site variation and 2.2 % by within-site variation.

Table 11: Results from the mixed effects models. The between-period and the between – and within site variation is calculated from the marginal R^2 and conditional R^2 for the two models M6 and M7 as explained in Materials and Methods.

	Light Intensity 85 th percentile	Surface Temp. Mean diff.	Air Temp. Mean Diff.	VPD Mean diff.
The best model	M7	M7	M6	M7
M6 Marginal R^2	0.048	0.236	0.553	0.597
M6 Conditional R^2	0.788	0.765	0.865	0.809
M7 Marginal R^2	0.048	0.236	0.553	0.597
M7 Conditional R^2	0.968	0.853	0.865	0.831
Between-period variation	4.8 %	23.6 %	55.3 %	59.7 %
Between-site variation	74.0 %	52.9 %	31.2 %	21.2 %
Within-site variation	17.9 %	8.8 %	0.01 %	2.2 %

In the mixed effects models, the logger-specific differences are modelled by estimating an intercept for each data-logger; box plots in Figure 4a-d show the variation in the estimated logger-intercepts for the six sites, thus visualizing the magnitude of variation present within each site. For the light and surface temperature indices, the within-site variation varies considerably between the sites (Figure 4a-b), while it is more similar for air temperature and VPD, with only SV94 Røsnæs having a substantially higher within-site variation compared to the other sites (Figure 4c-d).

In general, SV94 Røsnæs Krat has the highest or one of the highest within-site variations for all four microclimatic variables, whereas the two forests SM101 Frederikskilde Skov and SM97 Suserup Skov have low within-site variations – except for light intensity, where SM97 Suserup Skov show one of the highest within-site variations.

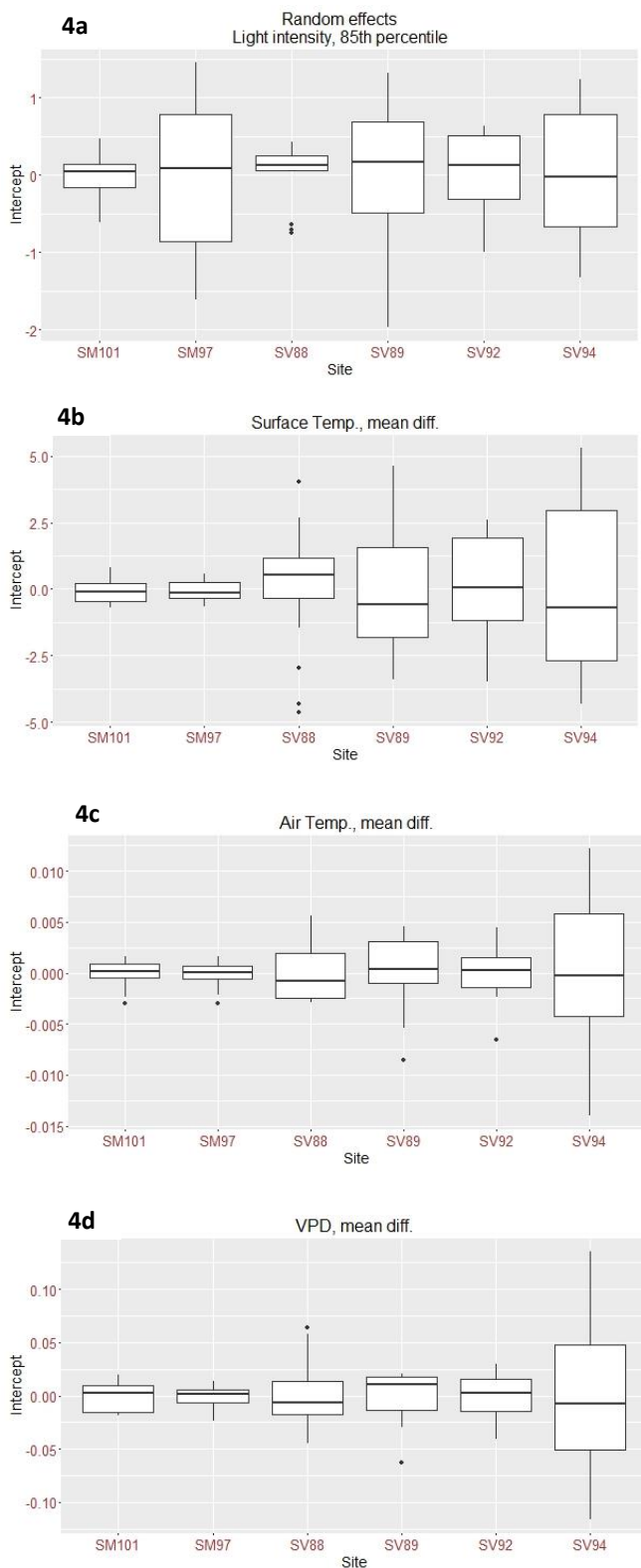


Figure 4a-d: Box plots showing the within-site variation in the estimated logger-intercepts for indices for the four microclimatic variables. For SM97 Suserup Skov, the box plot for light intensity and surface temperature is based on the intercept estimated for 14 data-loggers. The remaining box plots are based on the intercepts estimated for 16 data-loggers.

Figure 5a-d shows how the period-adjusted index-values (red dots) based on measurements from a single data logger, falls within the range of index-values found when using 16 (or 14) data loggers. The box plots are based on calculations of index-values for each data logger in each of the four 5-day periods – the same temporal scale for which the period-adjusted index values are predicted.

Except for two sites for surface temperature (Figure 5b), all the adjusted values are located below the median line. For light, the adjusted values for SM101, SV88 and SV92 are visibly located below the minimum value, while SV94 is located near, but below the minimum value. The adjusted value for SM101 is also located near, but below the minimum value for surface temperature and VPD, while SV88 is located close to, but below the minimum value for air temperature.

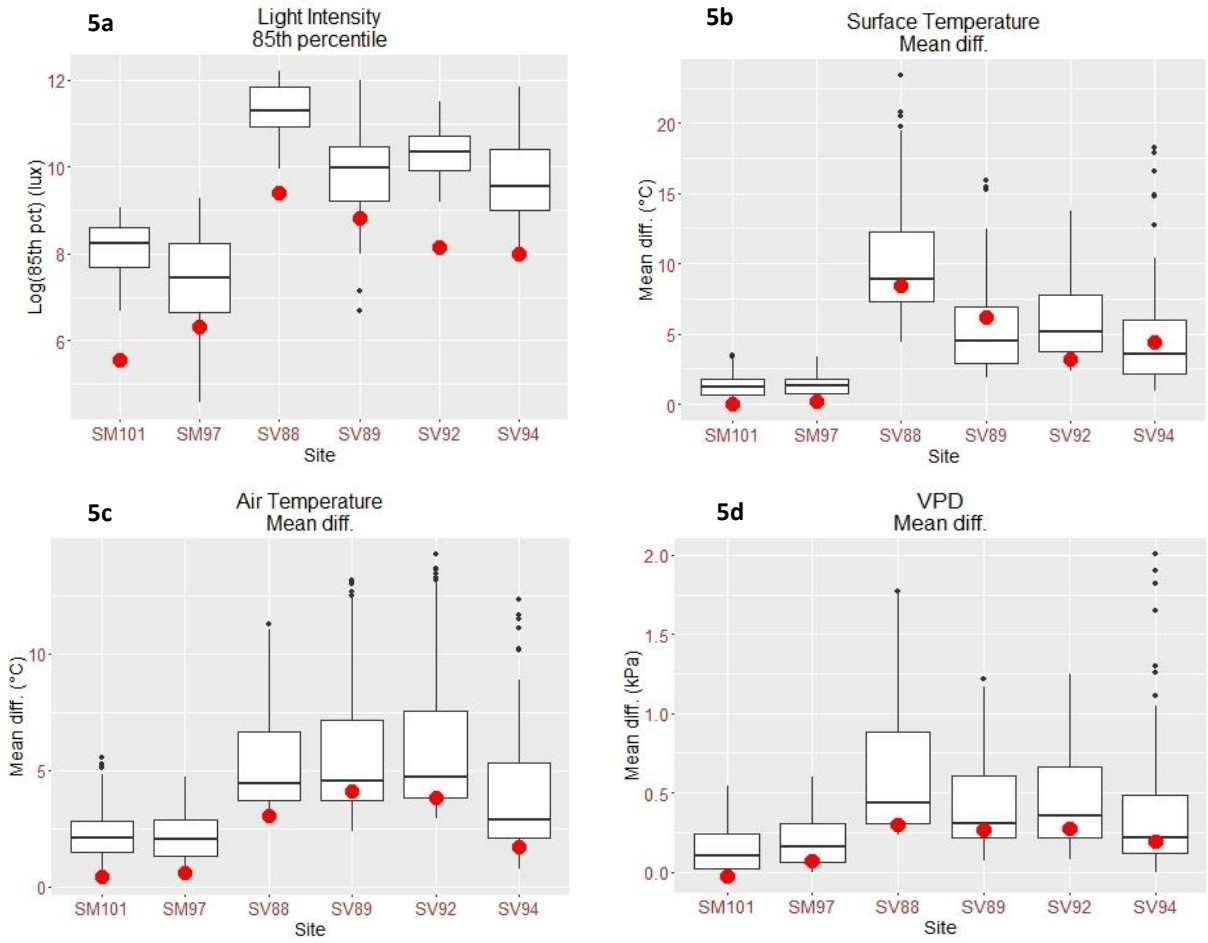


Figure 5a-d: Box plots based on calculations of index-values for each logger in each of four 5-day periods (14-18/8, 19-23/8, 24-28/8 and 29/8-2/9). For SM97 Suserup Skov, 14 loggers are included in 4a-b, while 16 loggers are included in the remaining box plots. The red dot denotes the adjusted index value estimated by the mixed effects models for the period 30/5-3/6.

3.3.1 Changes in rank

Figure 6a-d illustrates what spatially different placements of data loggers within a site, potentially can mean to a site's rank-position along gradients of microclimate.

The red dot indicates the mean rank and the black lines indicate the range of rank-positions the individual sites could potentially have had if represented by only a single data logger.

The mean rank among the six sites has been determined by looking at the index-values calculated for the entire site in the period 14/8 – 2/9, 2015. The minimum and maximum rank have been determined by looking at the data-logger showing the lowest and highest value within each site and comparing those values with each other. Rank 1 → 6 indicates highest index value → lowest index value.

Depending on the placement of the 16 data loggers, SV94 Røsnæs Krat can have index-values for all four microclimatic indices assigning it to all possible rank-positions (figure 6a-d).

For the light index, SV89 Frederikskilde Skov, like SV94 Røsnæs Krat, can possess all rank-positions, while the sites having the two highest mean rank-positions can hold the four highest rank-positions and the sites having the two lowest mean rank-positions, the four lowest rank-positions (Figure 6a). For the remaining three microclimatic indices, the sites having the three highest mean rank-positions can hold the four highest rank-positions, while the sites having the two lowest mean rank-positions can hold the three lowest rank-positions (figure 6b-d).

For all four microclimatic indices, SV88 Diesbjerg, SV89 Eskebjerg Vesterlyng and SV92 Kaldred Kær have a mean rank between 1 and 3; SV94 Røsnæs Krat is ranked as number 4; and the two forests SM97 Suserup Skov and SM101 Frederikskilde Skov are ranked 5th or 6th.

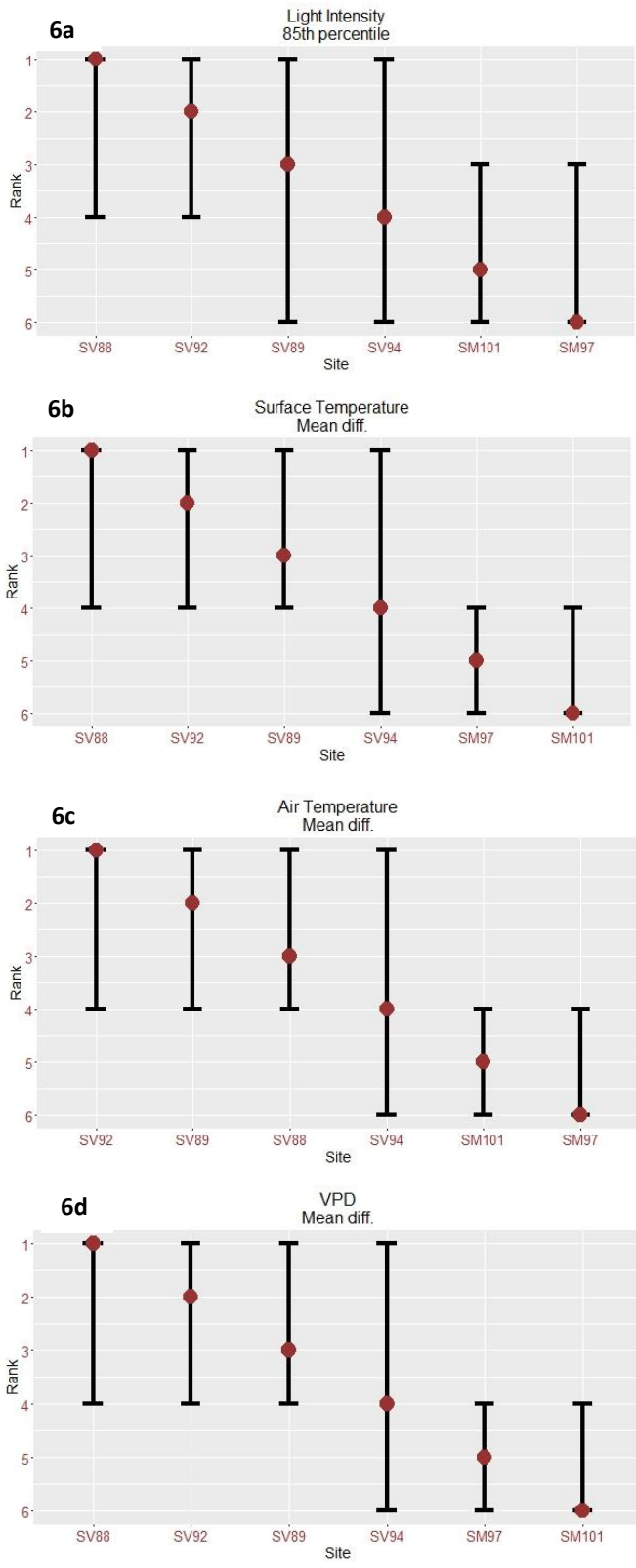


Figure 6a-d: Rank diagrams showing the mean rank (red dot) for each site and the potentially minimum and maximum rank (black lines) if the index value is calculated for one data-logger only. Rank 1 → 6 indicates highest index value → lowest index value. Rank of each site is based on data from 16 data-loggers, except for SM97 Suserup Skov in 6a-b, where rank is based on data from 14 data-loggers.

4. Discussion

Mantel tests between indices of five microclimatic factors and species composition of vascular plants, spiders and epiphytes, showed that the variation in species composition of spiders was better explained by light intensity, surface temperature and air temperature than any of the other organism groups. Vascular plants was the organism group for which the variation in species composition was best explained by soil moisture and finally, epiphytes was the organism group for which species composition was best explained by VPD.

The light index best describing variation in species composition was the 85th percentile calculated for daytime, explaining 44.1 % of spider species composition, while the best index for both surface – and air temperature was the difference between mean daytime – and mean nighttime temperature, explaining 41.9 % and 32.6 % of the variation in spider species composition respectively. Likewise, the difference between mean daytime – and mean nighttime was the best VPD-index, explaining 24.3 % of epiphyte composition, whereas the mean was the best measure of soil moisture, explaining 32.8 % of the variation in plant species composition.

For the light, temperature and VPD indices, where index-values were based on just a single data logger located in a 40 x 40 m site, results from linear mixed effects models incorporating measurements from additional data loggers in six of the 130 Biowide-sites, showed that the within-site variation accounted for 17.9 % of the total variation in light intensity, 8.8 % of the total variation in surface temperature, 2.2 % of the total variation in VPD, and a mere 0.01 % of the total variation in air temperature. The within-site variation however, differed substantially between sites of different vegetation cover and soil moisture content, but was high enough for all six sites to jump several rank positions depending on the placement of the data logger within the site.

4.1 Microclimate and vegetation cover

From Figure 3a-d, it is clear, that indices of light, temperature and VPD all express differences in vegetation cover. That they show the same pattern is no surprise, since both the raw

measurements (Table 2) and especially the index-values of the four variables (Table 10) correlate well with each other.

All of the light indices created, overall did similarly well when correlated with each of the three organism groups (Table 3). In all three cases, maximum light intensity did the poorest and especially for spiders and epiphytes, do maximum light intensity stand out as significantly poorer than the other indices. The 85th and 90th percentiles showed the highest correlations with all three organism groups, with the exception being mean light intensity doing marginally better for plants. The upper percentile values of light intensity are likely best at distinguishing biotopes of differential light conditions from each other, because they integrate the entire day's light conditions. On a sunny day, an open, flat site with more or less bare ground or low vegetation will receive high light intensities for a longer period throughout the day than a more vegetated site, where the vegetation blocks out some of the light at specific times of the day, depending on the position of the sun. Both can have the same maximum light intensity. The more vegetated site can even have a higher maximum, if for example a cloud happened to pass over the bare site during the hour of highest intensity. The upper percentiles on the other hand, are able to distinguish the sites receiving high amounts of light throughout the day – a condition that is highly influential for plant and animal life.

In this study, the 85th percentile happened to be the index showing the highest correlation with variation in species composition. It could just as well have been the 90th percentile, the mean or the median, as they did not do much worse. It could also have been the 87th percentile, but I did not test that. Point is, there is no universally correct index, but indices like the mean and the upper percentiles are great candidates, because they incorporate both intensity (lux) and duration of solar radiation.

As seen in Figure 3a, the 85th percentile of light intensity is a good descriptor of overall vegetation cover, expressed as succession stage. There is obviously some overlapping, because succession is a continuous gradient that we have tried categorizing into three boxes of late, mid and early.

Furthermore, slope and aspect of a site greatly influences the amount of light received. An open site located on a steep northern slope will receive far less radiation during the day than an open site on a steep southern slope (Suggitt et al. 2011). Two sites in early succession can thus have very different 85th percentiles of light intensity depending on topography and orientation. It would

therefore have been interesting to see how the light intensity index – and the indices of the other microclimate variables for that matter, would be able to detect sites of different slope and aspect in combination with vegetation cover, but those data were not available to me.

The best index of both surface temperature, air temperature and VPD was the difference between mean daytime-values and mean nighttime-values. As seen from Figure 3b-d, they too express the level of vegetation cover. This is because vegetation cover buffers the daily variation in temperature and humidity through shading and insolation.

Under forest canopies, temperatures were generally lower during the day and higher during the night compared to open sites. The mean difference in day and night temperatures is therefore lower below the canopy than below the open sky. That it is the ability of a site to dampen temperature-increases during the day and temperature-decreases during the night, that separates sites of differential vegetation cover, is also visible from the correlations between species composition and percentile-values (Table 4 and 5). When percentiles were calculated for daytime, the upper percentiles showed the highest correlations with species composition, separating bright and warm sites from shaded and cooler sites. When percentiles were calculated for nighttime, the lower percentiles on the contrary, showed the highest correlations with species composition, separating insulated sites able to reduce heat loss, from open sites less able to do so. This pattern is evident for both air temperature and surface temperature, but more distinct for the latter. For air humidity, VPD was 0 kPa (RH = 100 %) or close to, for most hours of the night, irrespective of vegetation cover. It is therefore a site's ability to keep a high humidity during a warm and sunny day, which says something about its vegetation cover. Because VPD is calculated from air temperature and relative humidity, and relative humidity decreases as temperature increases, the cooler shaded sites will generally have a higher relative humidity and thus a lower VPD during the day, than the warmer open sites.

Surface temperature is able to predict the variation in species composition better than air temperature (Table 9). Looking at the correlations between the indices in Table 10, surface temperature is highly correlated with light intensity ($r = 0.90$, $P < 0.001$), and the two indices thus

have similar correlations with variation in species composition (Table 9). Conversely, air temperature only has a correlation of $r = 0.68$ ($P < 0.001$) with the light intensity index. An explanation for the higher correlations of light and surface temperature with species composition compared to air temperature, may be evident in Figure 3c, which indicates that air temperature is good at distinguishing the late-successional sites from early – and mid-successional sites, but visibly poorer than light intensity and surface temperature at differentiating between the latter two. Chen et al. (1999) studied the differences in microclimate between the interior of a Douglas-fir forest and adjacent clear-cut, partial cut and aggregated harvesting sites. They found light intensity to be unique for all four sites, while air temperature, measured at a height of 2 m, was lower during the day in the forest interior, but did not differ between the remaining sites. In a study of the same Douglas-fir forest, depth of edge influence (DEI) was measured for a range of microclimatic variables along 240 m transects (Chen et al. 1995). Relative humidity and wind had $DEI > 240$ m, while air temperature reached an equilibrium around 180 – 240 m. Wind drives air circulation and greatly affects both air temperature and relative humidity, so when conditions result in wind-effects penetrating deep into the forest, the edge effect of air temperature and relative humidity is likely to do so as well.

How deep an edge effect is, depends – among other things – on vegetation structure and wind speed, and was in the study by Chen et al. (1995) also found to depend on aspect.

This may explain why air temperature in this study seems to be poorer at separating sites with a more open vegetation structure (Figure 3c) compared to light intensity and surface temperature (Figure 3a-b). Wind has a relative higher effect in more open structures, resulting in a higher degree of air mixing and evening out of air temperatures. That we in this study actually do see a difference (Figure 3c), with early-successional sites having a higher median difference between mean day and mean night temperatures, can likely be attributed to the fact that our loggers were placed at a height of just 15 cm. Even relatively low vegetation can therefore have had a moderating effect on air temperatures.

4.2 Microclimate and soil moisture

Soil moisture seems to be largely uncoupled from vegetation structure (Figure 3e) although the box plot indicates that late successional sites generally have a higher minimum VWC. This would make sense, since the lower daytime temperatures and lower VPD associated with forests, usually prevents dry-outs of the size possible in open environments.

Whereas the indices of light intensity, VPD, air – and surface temperature all were significantly correlated with each other, none of them were significantly correlated with soil moisture (Table 10), although the correlation with VPD was close to being significant ($r = 0.172$, $P = 0.055$). Looking at Figure 3f-i, there is not any clear patterns between the microclimate variables and soil moisture, as it was the case for vegetation cover. Wet sites however, generally seem to have a slightly lower index value. This pattern is most noticeable for surface temperature (Figure 3g) and because wet soils take longer to both warm up and cool down, it is not surprising that wet soils would show smaller differences between mean daytime and mean nighttime surface temperatures.

Whatever patterns may be derived from the box plots in Figure 3f-i, correlations between indices of light intensity, VPD, air – and surface temperature and the soil moisture index, are still small and non-significant (Table 10). However, the soil moisture content as indicated in the box plots by “dry”, “moist” and “wet” (Figure 3f-j), is not based on the soil moisture measurements, but estimated before sites were even chosen to be part of the Biowide project. From Figure 3j, it is evident though, that the soil moisture index is consistent with this categorization.

4.3 Variation in species composition as a function of microclimate

Temperature is known to greatly influence the choice of habitat for many spider species (Barghusen et al. 1997; Petcharad et al. 2016), and the distribution of spiders was therefore expected to be well correlated with especially surface temperature – which was also the case. It was however, somewhat unexpected that variation in spider species composition was better explained by variation in light than plant species composition. Spider composition did not only

show a marginally higher correlation with a single light index, but was, aside from maximum light intensity, substantially better described by all indices.

Because of the obvious correlation between surface temperature and light intensity, it is not surprising that spider species distribution is also well-explained by light levels, but vascular plants are directly affected by light, due to its main role in photosynthesis, and was therefore expected to be distributed more narrowly along the light gradient than spiders.

A possible explanation of why spider species composition is better explained by variation in light could be that many spider species have a narrow distribution and were found in only a single – or a few sites compared to species of vascular plants. This is not the case however. Whereas approximately 18 % of spider species were found in just a single site and 49 % found in five or less sites, the same percentages for plant species are 21 % and 59 % respectively. It therefore seems more likely that spiders have more defined microhabitat requirements, while a higher fraction of plant species have a broader range and can be found in biotopes of more differential light conditions.

Because being shade-tolerant is not the same as being light-intolerant, plant species adapted to shaded environments can also be found in light environments. Where the presence of shade-intolerant species in shaded environments is limited by low-light conditions, the presence of shade-tolerant species in higher light environments is usually limited by competition (Smith and Smith 2009). Many plant species are therefore physiologically able to survive in light conditions spanning broad parts of the light gradient, but are often displaced to narrower parts of it by competition.

Several studies have found light level to be a primary factor influencing the distribution of spider species (Bultman et al. 1982; Entling et al. 2007; Fuller et al. 2014). Studying how composition of cursorial spiders changes along a successional gradient, Bultman et al. (1982) found clear patterns between succession and guild composition; the presence of wolf spiders declined sharply when moving from early to late successional sites, whereas the presence of vagrant web-builders and crab spiders increased. Additionally, there was very little overlap in species composition between the different plant communities and no species overlap occurred between the old-field and the climax forest included in the study. This supports our observation that variation in spider species

composition is closely related to variation in light levels (which is related to succession, Figure 3a) and indicate that this tight relation partly stems from different spider guilds being associated with different biotopes.

Had I had more time, it would therefore have been interesting to study how variation in spider guild composition, rather than species composition, relates to variation in light levels.

Whether or not it is the microclimatic conditions resulting from shading or the vegetation structure creating the shaded conditions that generate the distributional pattern observed for spiders, is however unclear. Vegetation and litter structure is both important for web attachment, retreat sites and refuges from predators, but also affect important microclimatic conditions such as temperature, soil moisture and wind speeds (Wise 1993).

A Mantel test between spider species composition and plant species composition shows that plant species composition is able to explain 52.7 % ($P < 0.001$) of the variation in spider species composition, which is a higher percentage than any of the microclimatic variables. This indicates that vegetation composition is important for the distribution of spiders, although whether or not this is due to the architecture of the vegetation, the resulting microclimatic conditions, or a combination of both, is still not evident.

In a study by Hore and Uniyal (2008), Mantel tests showed that microclimate (a mixture of physiochemical variables) was able to explain 40.7 % of the variation in spider species composition between 20 study sites in India. Using a partial Mantel test, which is essentially the same as a regular Mantel test, but where the correlation between two matrices are made while controlling for the effect of a third (Smouse et al. 1986), Hore and Uniyal (2008) found that microclimate was only able to explain 13.9 % of the variation in species composition, when the effect of vegetation structure was controlled for. In contrast, vegetation structure explained 48.8 % of the variation when the effect of microclimate was eliminated. Vegetation structure thus influenced the distribution of spiders considerably more than microclimate did.

If I partial out the effect of plant species composition, surface temperature (SurfaceTemp_mean_diff) for example explains 31.4 % ($P < 0.001$) of the variation in spider species composition, which is a significantly lower percentage than the 41.9 % explained when plant composition is not taken into account (Table 9). The difference between the two percentages is

not nearly as great as that found by Hore and Uniyal (2008) though. This may be because species composition is not exactly the same as vegetation structure; different communities can have a similar structure and some species can be found in biotopes of very different vegetation structure. The 31.4 % is therefore not necessarily the percentage of variation in species composition explained solely by surface temperature, but compared to the 41.9 % (Table 9), it shows that the correlations found between surface temperature and spider species composition in the Mantel tests (Table 4) to some degree are explained by properties of plant species composition unrelated to surface temperature. I know that both LIDAR data and a variety of structural measurements such as vegetation height, tree density, percentage of bare soil etc. are available for the 130 study sites, and given more time, it would be interesting to investigate to what degree these structure variables, individually or in combination, are able to explain the variation in spider species composition – or the composition of epiphytes for that matter, as this group obviously must be related to vegetation structure as well.

4.4 Within-site variation in microclimate

Investigation of microclimate at a wider spatial scale in six of the 130 Biowide sites, showed that the variation between 16 spots within 40 x 40 m sites was highest for light intensity, followed by surface temperature, VPD and lastly air temperature (Table 11). Even though the light index showed the highest within-site variation (17.9 % of total variation), it also had the highest between-site variation (74 % of total variation) and the lowest between-period variation (4.8 % of total variation). This pattern was also evident among the remaining three microclimatic variables; as the within-variation decreased, so did the between-site variation, while the between-period variation increased. Only the within-site variations of air temperature and VPD deviated slightly from this pattern (Table 11).

This pattern tells us, that differences in site characteristics do not affect the index-values of air temperature and VPD to the same degree as for surface temperature and, in particular, light. Differences in weather conditions on the other hand, are the main source of variation in measured index-values of air temperature and VPD, explaining more than 50 % of the total variation.

Furthermore, the mixed effects model accounts for 96.7 % of the total variation in light intensity, whereas conditional R^2 for the remaining microclimatic variables ranges from 83.1 % - 86.5 % (Table 11). There is thus substantially more variation unaccounted for by the explanatory variables for the temperature and VPD indices, and I suspect within-period variation may account for a significant part of this.

Looking at the within-site variation of the estimated logger-intercepts in Figure 4a-d, there is an obvious difference between sites in the size of their within-site variation.

For light (Figure 4a) the smallest variation is found for SV88 Diesbjerg and SM101 Frederikskilde Skov, while especially SM97 Suserup Skov and SV94 Røsnæs Krat, show high variations.

That SV94 Røsnæs has a high variation in light levels is not surprising, as it is the only site of the six categorized as being in a mid-successional stage and contains a mixture of both trees, scrubs and a diverse understory and is moreover located on a slope. Conversely, SV88 Diesbjerg, which is also located on a slope, had a low and far more homogenous vegetation structure.

What I find most surprising, is the high variation in light found for SM97 Suserup Skov – especially compared to SM101 Frederikskilde Skov, which subjectively viewed, seemed more heterogeneous with a big opening in the canopy and a more varied understory. Strikingly, when looking at Figure 4b, the within-site variation in surface temperature is similarly small for SM97 Suserup Skov compared to SM101 Frederikskilde Skov.

An explanation for this “mismatch” in within-site variation must be that some data loggers in SM97 Suserup Skov were placed in exceptionally dark places – below giant fallen trees for example, and that it does not have a major influence on surface temperature whether it is dark or *very* dark.

Apart from SM97 Suserup Skov, the remaining sites all show a similar pattern of within-site variation for light and surface temperature. For air temperature and VPD, the differences in within-site variation between the sites is not as pronounced and only SV97 Røsnæs Krat stands out as having a noticeably higher within-site variation.

Whereas, the within-site variation in most of the six sites, likely stem from differences in vegetation cover or topography, I believe a major part of the variation within SV92 Kaldred Kær is due to differences in soil moisture. This site is very flat and very homogeneous vegetation wise,

but some of the surface loggers were covered in up to several cm of clear water, while others were not. In SV89 Eskebjerg Vesterlyng, a few surface loggers were also under a couple of cm of clear water at some point, but placement of loggers was also visibly different in relation to vegetation cover.

The effect of weather on microclimate differed between the six sites as well. Figure 5a-d shows the within-site variation of index-values calculated for each logger in each of the four periods. In contrast to Figure 4a-d, the variation between periods is thus included here.

Comparing the box plots in Figure 4a-d and 5a-d, the most obvious differences are found for air temperature and VPD – the variables for which between-period variation explained the highest proportion of the total variation (Table 11). Overall, the early-successional sites SV88 Diesbjerg, SV89 Eskebjerg Vesterlyng and SV92 Kaldred Kær show a variation equal to or higher than SV94 Røsnæs Krat for both surface temperature, air temperature and VPD (Figure 5b-d) compared to the box plots in Figure 4b-d, where SV94 Røsnæs Krat shows the largest variation and is markedly larger for air temperature and VPD.

The two forests SM97 Suserup Skov and SM101 Frederikskilde Skov, have the lowest amount of variation in temperature and VPD, irrespective of between-period variation is included or not; nonetheless, variation in period seems so have a small effect on especially air temperature and VPD.

When looking at light intensity, there is not much of a difference between Figure 4a and 5a, but period did not contribute substantially to the total variation in light index values (Table 11), so that is to be expected. Whatever effect of weather-variation that is present though, mainly seems to stem from SV88 Diesbjerg and SM101 Frederikskilde Skov, which have the smallest variations in Figure 4a, but variations slightly larger than that of SV92 Kaldred Kær in Figure 5a.

Generally, the microclimate in early-successional sites therefore seems to be more affected by weather, than the mid – and late-successional sites – likely because they are more open and exposed.

4.5 Spatial and temporal variation in microclimate

In this study, I have only been focusing on the effect of a wider spatial scale; how much variables of microclimate vary within a 40 x 40 m site, when 16 loggers are spread out evenly in six different sites of differential vegetation structure and soil moisture content.

For light, this variation was substantial, while the within-site variation for air temperature turned out to be practically zero. Nevertheless, if wanting to compare sites by ranking them along microclimatic gradients, even the small within-site variation found for air temperature and VPD is sufficient for sites to potentially jump several rank-positions (Figure 6a-d), because the between-site variation is low as well.

How well the single data logger placed in the 130 Biowide sites actually represents the average microclimatic conditions in the sites, is likely close to the site-mean, as loggers were placed in spots that subjectively seemed to be characteristic of the overall site-conditions. Looking at Figure 5a-d showing how the period-adjusted index values for the six sites falls within the range of index values found when using 16 data loggers, the adjusted values are generally within the range, but below the median. However, the very consistent pattern below the median – especially for air temperature and VPD (Figure 5c-d), indicates that this placement is caused mainly by differences in period. For surface temperature, where the adjusted values can be found both above and below the median line, placement of logger seems to have had an influence as well.

Measuring microclimate at a wider spatial scale will logically enough increase the accuracy of placement along a gradient, but exactly how wide this scale should be is difficult to say, and depend on both the microclimatic factor measured, the spatial characteristics of the site and the scale of your study. When investigating the between-site variation in microclimatic variables showing high variability over small spatial scales, several measurements would be sensible, to adequately cover the within-site variation. Not only because a wider spatial scale will result in a mean index-value that is more telling of the overall microclimatic environment in the site, but also because the within-site variation in itself is an interesting measure.

Because the presence or absence of species in a biotope generally reflect long-term environmental conditions, and not just the conditions during a few weeks over the summer, studying the variation in microclimate on a wider temporal scale might reveal important insights into the distribution of species.

During the winter, soils under forest cover are generally warmer than soils in open biotopes (Aussenac 2000). So just as the cooler temperatures in summer are important for some species, the insulating effect during winter is likely important for the same - or other species as well. I also imagine that the difference in e.g. light intensity between deciduous forests and coniferous forest are also somewhat different during winter and autumn than during spring and summer.

Furthermore, when I visited SV89 Eskebjerg Vesterlyng in the first part of August, it was painfully hot and the soil was dry. Just a little over a month later though, a considerable part of the site was under clear water; a condition that clearly has a huge say in what species – especially plant species, are able to grow there. These are just a few examples of temporal variability in microclimate. Generally, the Danish landscape looks very different depending on the time of year, so it would be relevant for the understanding of species distribution as a function of microclimate, to conduct measurements over a wide temporal scale. That being said, microclimatic differences between different biotopes will be more pronounced during sunny summer days (Morecroft et al. 1998), so measurements during this period is most likely sufficient to adequately say something meaningful about the general distribution of species as a function of microclimate.

4.6 Microclimate as predictor of species distribution

Variation in the five microclimatic variables was individually able to explain between 24.3 % - 44.1 % of the variation in species composition of one of tree organism groups, with light being the best descriptor of species distribution and VPD the worst. Keeping in mind, that numerous both abiotic and biotic environmental factors, species interactions such as competition, facilitation, predation etc., and countless stochastic processes and events, influence the species composition at a particular site and thereby the distribution of species, I think these are reasonably high percentages. In comparison, Hore and Uniyal (2008) got a Mantel $r = 0.407$ ($P < 0.001$) when

correlating distance matrices incorporating several microclimatic variables with dissimilarity matrices of spider species composition in 20 sites across 10 vegetation types in India.

Of course, the resulting correlations with species composition stems from the microclimate variables expressing something more than just an abiotic condition. Variables such as light, temperature and VPD to a high degree reflect the biological environment in the form of vegetation structure. Soil moisture on the contrary, is largely independent of vegetation structure (Figure 3e). Furthermore, strong correlations between the microclimatic variables (Table 2) and in particular between indices of variables (Table 10), means that incorporated in a light index is also surface temperature, air temperature, VPD and likely other microclimatic variables not investigated in this study. From just a single microclimate variable, several both abiotic and biotic conditions important for species composition can thus be deduced.

To achieve a more precise prediction of the composition and the landscape-scale distribution of species, factors more or less independent of a specific microclimatic variable can be added in a species distribution model. The light intensity index could for example be combined with indices of air temperature and soil moisture, nutrient richness, topographical measures such as aspect and slope, and measures of biotic expansion that is not readily detected by light availability – e.g. amount of deadwood, rocks and dung.

Dispersal limitation has also been mentioned as a factor affecting species distribution. Unlike the effect of biotic interactions, the effect of dispersal limitation is fairly easy to examine when knowing the distances between study-sites.

In a small, uniform and connected country like Denmark, a few rare species might be dispersal limited (Sand-Jensen et al. 2008), but it should not be a major limiting factor when looking at entire organism groups. To make sure, that this is actually the case, I did a partial Mantel test between the light intensity indices and species composition of the three organism groups, where the effect of geographical distance was removed. As expected, there was barely any difference between the resulting Mantel statistics when distance was accounted for and the ones in Table 3, where it is not.

5. Conclusion

The indices of microclimate that individually best describe the landscape-scale distribution of vascular plants, spiders or epiphytes in Denmark, is the 85th percentile of daytime light intensity, mean soil moisture and the difference between mean daytime and mean nighttime values for both surface temperature, air temperature and VPD.

Apart from mean soil moisture, all indices seem to mainly reflect differences in vegetation cover; comparing the microclimatic environment of an open site with that below a forest canopy, the below canopy environment generally experiences lower light levels and lower differences between mean daytime and mean nighttime surface temperature, air temperature and VPD. Supplementary measurements taken at a wider spatial scale in six sites of differential vegetation structure and soil moisture content, showed that the within-site variation for the light index explained close to 18 % of the total variation, while that of surface temperature explained close to 9 %. How high the within-site variation was for the individual site, varied substantially though, but was high enough for all sites to potentially jump several rank positions when sites were ranked according to their index-values. To better cover the light levels and surface temperatures experienced in the Biowide sites, it would therefore make sense to widen the spatial scale using additional loggers.

For the air temperature and VPD indices, the within-site variation was substantially lower, explaining just around 2 % of the total variation in VPD and showing practically no variation for air temperature. Despite the low within-site variation, all sites were able to jump several rank positions depending on placement of the logger, because the between-site variation was low as well. For air temperature and VPD, between-period variation explained more than 50 % of the observed variation. When trying to distinguish different biotopes from each other using the indices of these microclimate variables, it would therefore make more sense to collect data in very stable weather conditions or collect simultaneous data on weather-related variables (e.g. wind speed and direction) than to add additional loggers.

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Appendix 1

The number, ID and name of each of the 130 sites, the region and cluster in which they are located, and their stratum. Early, mid and late refers to the succession stage. Wet, moist and dry refers to the level of moisture. Rich and poor refers to the nutrient content.

Site nr.	Site ID	Site name	Region	Cluster	Stratum
1	NV1	Råbjerg Kirke	Nordjylland	Vendsyssel	Early, Dry, Poor
2	NV2	Uggerby Strand	Nordjylland	Vendsyssel	Early, Wet, Rich
3	NV3	Råbjerg Mile	Nordjylland	Vendsyssel	Early, Wet, Poor
4	NV4	Kjærsgård	Nordjylland	Vendsyssel	Field
5	NV5	Vandplasken	Nordjylland	Vendsyssel	Hotspot
6	NV6	Uggerby Skovvej	Nordjylland	Vendsyssel	Ley
7	NV7	Kjul Strand	Nordjylland	Vendsyssel	Mid, Moist, Rich
8	NV8	Bunken	Nordjylland	Vendsyssel	Mid, Wet, Poor
9	NV9	Tversted Plantage	Nordjylland	Vendsyssel	Plantation
10	NT10	Kællingdal	Nordjylland	Thy	Early, Dry, Rich
11	NT11	Lild Strand	Nordjylland	Thy	Early, Moist, Poor
12	NT12	Raspkær	Nordjylland	Thy	Late, Moist, Poor
13	NT13	Tømmerby Fjord	Nordjylland	Thy	Late, Wet, Poor
14	NT14	Febbersted	Nordjylland	Thy	Mid, Dry, Poor
15	NT15	Kokkærvand	Nordjylland	Thy	Mid, Moist, Poor
16	NT16	Tjenestejorden	Nordjylland	Thy	Oldfield
17	NT17	Tovsigvej	Nordjylland	Thy	Plantation
18	NT18	Østerild	Nordjylland	Thy	Early, Moist, Rich
19	NH19	Buderupholm	Nordjylland	Himmerland	Hotspot
20	NH20	Urskoven	Nordjylland	Himmerland	Late, Dry, Poor
21	NH21	Skindbjerglund	Nordjylland	Himmerland	Late, Dry, Rich
22	NH22	Høstemark Engskov	Nordjylland	Himmerland	Late, Moist, Rich
23	NH23	Høstemark Sumpskov	Nordjylland	Himmerland	Late, Wet, Rich
24	NH24	Regan Vest	Nordjylland	Himmerland	Mid, Dry, Rich
25	NH25	Gravlev Kær	Nordjylland	Himmerland	Mid, Wet, Rich
26	NH26	Rold	Nordjylland	Himmerland	Plantation
27	VU27	Husby Klit	Vestjylland	Ulfborg	Early, Dry, Poor
28	VU28	Ejstrup Mose	Vestjylland	Ulfborg	Early, Wet, Poor

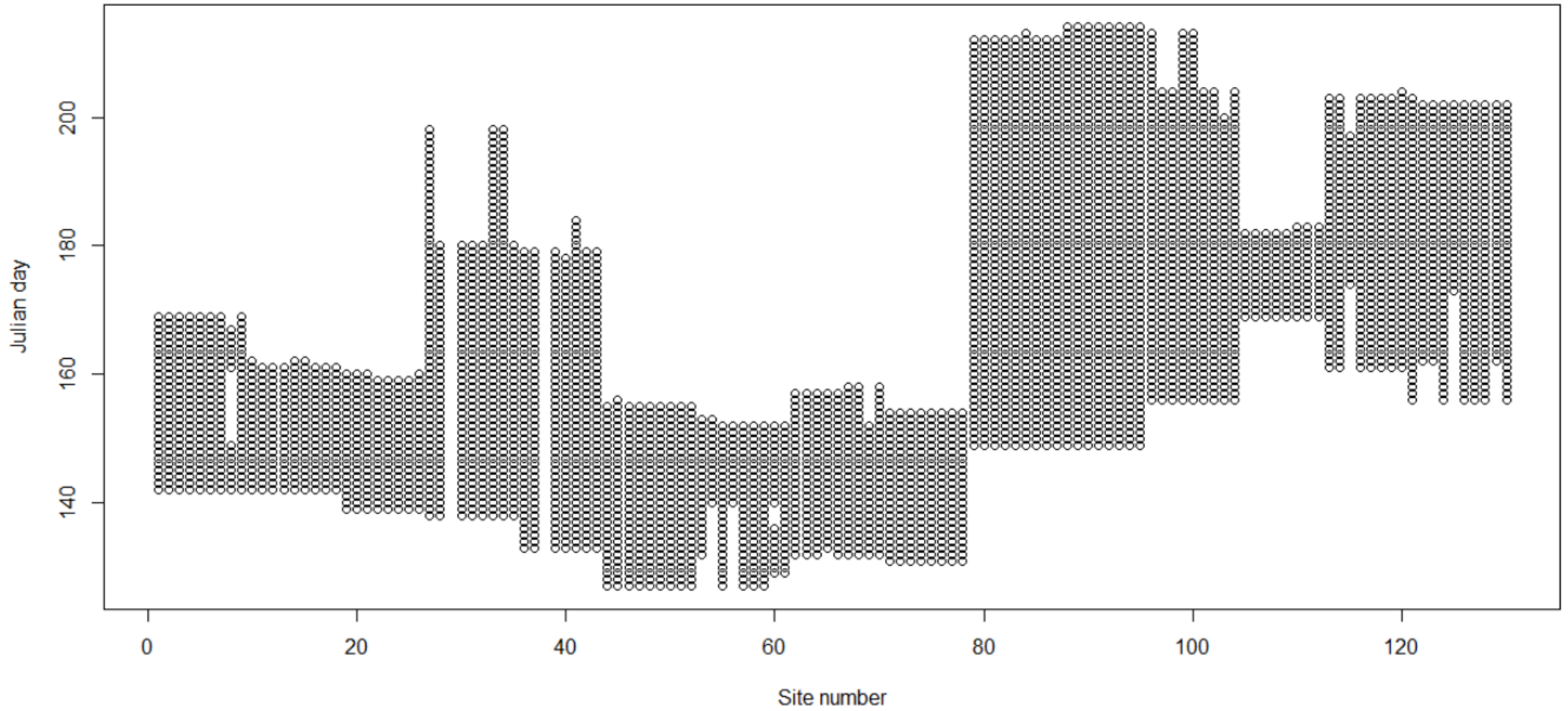
29	VU29	Sønderbyvej	Vestjylland	Ulfborg	Field
30	VU30	Lilleå	Vestjylland	Ulfborg	Mid, Dry, Poor
31	VU31	Ejstrup Eng	Vestjylland	Ulfborg	Mid, Moist, Rich
32	VU32	Ejstrup Krat	Vestjylland	Ulfborg	Mid, Wet, Poor
33	VU33	Nissum	Vestjylland	Ulfborg	Mid, Wet, Rich
34	VU34	Klitvej	Vestjylland	Ulfborg	Oldfield
35	VU35	Stråsø Plantage	Vestjylland	Ulfborg	Plantation
36	VO36	Nymindegab	Vestjylland	Oksbøl	Early, Moist, Rich
37	VO37	Houstrup Strand	Vestjylland	Oksbøl	Early, Wet, Rich
38	VO38	Vrøgum Kær	Vestjylland	Oksbøl	Hotspot
39	VO39	Kjærgård Løvklitte	Vestjylland	Oksbøl	Late, Moist, Poor
40	VO40	Lønne	Vestjylland	Oksbøl	Ley
41	VO41	Blåvand	Vestjylland	Oksbøl	Mid, Dry, Rich
42	VO42	Breddal	Vestjylland	Oksbøl	Mid, Moist, Poor
43	VO43	Filsøvej	Vestjylland	Oksbøl	Plantation
44	VD44	Lovrup	Vestjylland	Draved	Early, Dry, Rich
45	VD45	Helm Hede	Vestjylland	Draved	Early, Moist, Poor
46	VD46	Lindestykket	Vestjylland	Draved	Hotspot
47	VD47	Lindet	Vestjylland	Draved	Late, Dry, Poor
48	VD48	Gram Slot	Vestjylland	Draved	Late, Dry, Rich
49	VD49	Grønnevej	Vestjylland	Draved	Late, Moist, Rich
50	VD50	Gråbjerg Mose	Vestjylland	Draved	Late, Wet, Poor
51	VD51	Gram å	Vestjylland	Draved	Late, Wet, Rich
52	VD52	Damvej	Vestjylland	Draved	Plantation
53	EM53	Elbjerg	Østjylland	Mols	Early, Dry, Rich
54	EM54	Kalø	Østjylland	Mols	Field
55	EM55	Glatved	Østjylland	Mols	Hotspot
56	EM56	Hestehaven	Østjylland	Mols	Late, Dry, Rich
57	EM57	Helligkilde	Østjylland	Mols	Mid, Dry, Poor
58	EM58	Tyskertårnet	Østjylland	Mols	Mid, Dry, Rich
59	EM59	Sletterhage	Østjylland	Mols	Mid, Moist, Poor
60	EM60	Strandkær	Østjylland	Mols	Mid, Moist, Rich
61	EM61	Langemose	Østjylland	Mols	Early, Wet, Poor
62	ES62	Urfuglebakken	Østjylland	Silkeborg	Early, Dry, Poor

63	ES63	Letmose	Østjylland	Silkeborg	Mid, Wet, Poor
64	ES64	Mossø	Østjylland	Silkeborg	Early, Moist, Rich
65	ES65	Tørvefladen	Østjylland	Silkeborg	Early, Moist, Poor
66	ES66	Odderholm	Østjylland	Silkeborg	Early, Wet, Rich
67	ES67	Ry Sønderskov	Østjylland	Silkeborg	Hotspot
68	ES68	Hårup Sande	Østjylland	Silkeborg	Late, Dry, Poor
69	ES69	Knagerne	Østjylland	Silkeborg	Late, Moist, Poor
70	ES70	Gjessøvej	Østjylland	Silkeborg	Late, Wet, Poor
71	EV71	Bjergfald	Østjylland	Vejle	Late, Moist, Rich
72	EV72	Vejle Fjord	Østjylland	Vejle	Late, Wet, Rich
73	EV73	Brøndsted Fælled	Østjylland	Vejle	Ley
74	EV74	Rands Fjord	Østjylland	Vejle	Mid, Wet, Rich
75	EV75	Svinholt	Østjylland	Vejle	Oldfield
76	EV76	Vesterskov	Østjylland	Vejle	Plantation
77	EV77	Rand Skov	Østjylland	Vejle	Plantation
78	EV78	Grund Skov	Østjylland	Vejle	Plantation
79	SN79	Melby Hede	Sjælland	Nordsjælland	Early, Dry, Poor
80	SN80	Melby Overdrev	Sjælland	Nordsjælland	Hotspot
81	SN81	Strødam	Sjælland	Nordsjælland	Late, Dry, Poor
82	SN82	Birkemose	Sjælland	Nordsjælland	Late, Moist, Rich
83	SN83	Maglemose	Sjælland	Nordsjælland	Late, Wet, Poor
84	SN84	Toggerup Tørvemose	Sjælland	Nordsjælland	Mid, Wet, Poor
85	SN85	Ellemose	Sjælland	Nordsjælland	Mid, Wet, Rich
86	SN86	Tisvilde Hegn	Sjælland	Nordsjælland	Plantation
87	SN87	Tibberup Holme	Sjælland	Nordsjælland	Plantation
88	SV88	Diesbjerg	Sjælland	Vestsjælland	Early, Dry, Rich
89	SV89	Eskebjerg Vesterlyng	Sjælland	Vestsjælland	Early, Moist, Poor
90	SV90	Eskebjerg Enghave	Sjælland	Vestsjælland	Early, Wet, Poor
91	SV91	Mallesnæs	Sjælland	Vestsjælland	Early, Moist, Rich
92	SV92	Kaldred Kær	Sjælland	Vestsjælland	Early, Wet, Rich
93	SV93	Skamlebæk	Sjælland	Vestsjælland	Mid, Dry, Poor
94	SV94	Røsnæs Krat	Sjælland	Vestsjælland	Mid, Dry, Rich
95	SV95	Røsnæs	Sjælland	Vestsjælland	Oldfield
96	SM96	Allindelille Fredskov	Sjælland	Midtsjælland	Hotspot

97	SM97	Suserup Skov	Sjælland	Midtsjælland	Late, Dry, Rich
98	SM98	Broby Vesterskov	Sjælland	Midtsjælland	Plantation
99	SM99	Avnsø	Sjælland	Midtsjælland	Late, Moist, Poor
100	SM100	Smuldmosen	Sjælland	Midtsjælland	Mid, Moist, Poor
101	SM101	Frederikskilde Skov	Sjælland	Midtsjælland	Late, Wet, Rich
102	SM102	Kongskilde Friluftsgård	Sjælland	Midtsjælland	Ley
103	SM103	Fuglebjerg	Sjælland	Midtsjælland	Field
104	SM104	Bimosen	Sjælland	Fyn	Mid, Moist, Rich
105	FF105	Svanninge Bakker	Fyn, Lolland, Møn	Fyn	Late, Dry, Poor
106	FF106	Hestebakke	Fyn, Lolland, Møn	Fyn	Early, Dry, Rich
107	FF107	Dalkildegård	Fyn, Lolland, Møn	Fyn	Plantation
108	FF108	Iglesø	Fyn, Lolland, Møn	Fyn	Early, Wet, Poor
109	FF109	Rødme Svinehaver	Fyn, Lolland, Møn	Fyn	Mid, Dry, Poor
110	FF110	Skyttegård	Fyn, Lolland, Møn	Fyn	Late, Moist, Poor
111	FF111	Nybo Mose	Fyn, Lolland, Møn	Fyn	Mid, Moist, Poor
112	FF112	Stævningen	Fyn, Lolland, Møn	Fyn	Mid, Wet, Poor
113	FL113	Fuglsang Storskov	Fyn, Lolland, Møn	Lolland	Plantation
114	FL114	Løgnor	Fyn, Lolland, Møn	Lolland	Hotspot
115	FL115	Bursø	Fyn, Lolland, Møn	Lolland	Field
116	FL116	Fuglse Mose	Fyn, Lolland, Møn	Lolland	Late, Wet, Poor
117	FL117	Skelsnæs	Fyn, Lolland, Møn	Lolland	Late, Wet, Rich
118	FL118	Søholt	Fyn, Lolland, Møn	Lolland	Mid, Wet, Rich
119	FL119	Musse Mose	Fyn, Lolland, Møn	Lolland	Mid, Moist, Rich
120	FL120	Hejrede Sø	Fyn, Lolland, Møn	Lolland	Oldfield
121	FM121	Klinteskov	Fyn, Lolland, Møn	Møn	Late, Moist, Rich
122	FM122	Ulvshale Klit	Fyn, Lolland, Møn	Møn	Early, Dry, Poor
123	FM123	Ulvshale Hede	Fyn, Lolland, Møn	Møn	Early, Moist, Poor
124	FM124	Busemark Mose	Fyn, Lolland, Møn	Møn	Early, Moist, Rich
125	FM125	Busemark Sø	Fyn, Lolland, Møn	Møn	Early, Wet, Rich
126	FM126	Høvblege	Fyn, Lolland, Møn	Møn	Mid, Dry, Rich
127	FM127	Timesø Bjerg	Fyn, Lolland, Møn	Møn	Late, Dry, Rich
128	FM128	Jydelejet	Fyn, Lolland, Møn	Møn	Hotspot
129	FM129	Hegnede Bakke	Fyn, Lolland, Møn	Møn	Ley
130	FM130	Lindebakker	Fyn, Lolland, Møn	Møn	Plantation

Appendix 2

Graph showing in Julian days when the light intensity, air temperature, surface temperature and relative humidity was measured at each of the 130 sites.



Appendix 3

Overview of which sites are not included in the analyses.

Missing sites in analyses involving:

Light intensity and surface temperature

VU29 Sønderbyvej
VO38 Vrøggum kær
VO40 Lønne
VD48 Gram slot
FL119 Musse mose

Air temperature and vapour pressure deficit

NT 15 Kokkær vand
VU29 Sønderbyvej
VO38 Vrøggum kær
EV77 Rand skov
FM123 Ulvshale hede

Vascular plants

NV4 Kjærsgård (field)
NV6 Uggerby skovvej (ley)
VU29 Sønderbyvej (field)
VO40 Lønne (ley)
EM54 Kalø (field)
EV73 Brøndsted fælled (ley)
SM102 Kongskilde friluftsgård (ley)
SM103 Fuglebjerg (field)
FL115 Bursø (field)
FM129 Hegnede bakke (ley)

Epiphytic/eplithic mosses and lichens

Sites not examined:

NH19 Buderupholm
NH20 Urskoven
NH21 Skindbjerglund
NH24 Regan Vest
NH25 Gravlev kær
NH26 Rold
VD46 Lindestykket

Sites with no mosses/lichens:

NV3 Råbjerg mile
NV4 Kjærsgård
NV6 Uggerby skovvej
NT16 Tjenestejorden
VU29 Sønderbyvej
VU34 Klitvej
VO40 Lønne
EM54 Kalø
ES64 Mossø
ES65 Tørvefladen
EV73 Brøndsted fælled
SM103 Fuglebjerg
FL115 Bursø
FL120 Hejrede sø
FM124 Busemarke mose
FM125 Busemarke Sø
FM129 Hegnede bakke

Appendix 4

Overview of changes made to the original species data. → means "changed to".

Vascular plants

Deleted:

Chenopodium sp.
Carex demissa x lepidocarpa
Carex flava x lepidocarpa
Salix sp.

Changes:

Calystegia sepium ssp. Sepium → Calystegia sepium
Crataegus laevigata and Crataegus monogyna → Crataegus sp.
Dactylis glomerata → Dactylis glomerata ssp. glomerata
Euphrasia sp. → Euphrasia stricta
Larix x marschlinsii → Larix sp.
Medicago sativa → Medicago sativa ssp. Sativa
Mentha sp. → Mentha aquatica
Plantago major ssp. Major → Plantago major s. lat
Rhinanthus minor and Rhinanthus serotinus → Rhinanthus sp.
Salix repens ssp. repens var. repens → Salix repens
Stellaria nemorum ssp. Montana → Stellaria nemorum
Urtica dioica var. dioica → Urtica dioica
Veronica scutellata var. scutellata and Veronica scutellata var. villosa → Veronica scutellata

Mosses and lichens

Deleted:

Cladonia L spp

Spiders

Deleted:

Trochosa sp
Xysticus sp

Changes:

Dolomedes fimbriatus → Dolomedes sp.

Appendix 5

Explanation of the different index abbreviations. *All day* refers to the entire 24 hour period. *Daytime* refers to the hours 5–21 and *nighttime* refers to the hours 22–4.

Light Intensity

MaxLight_all	Maximum light intensity calculated for all day
MeanLight_all	Mean light intensity calculated for all day
MedianLight_all	Median light intensity calculated for all day
sdLight_all	Standard deviation of light intensity calculated for all day
MedianLight_day	Median daytime light intensity
sdLight_day	Standard deviation of daytime light intensity
Light_5pct_day	5th percentile of daytime light intensity
Light_10pct_day	10th percentile of daytime light intensity
Light_15pct_day	15th percentile of daytime light intensity
Light_85pct_day	85th percentile of daytime light intensity
Light_90pct_day	90th percentile of daytime light intensity
Light_95pct_day	95th percentile of daytime light intensity

Surface Temperature

MaxSurfaceTemp_all	Maximum surface temperature calculated for all day
MinSurfaceTemp_all	Minimum surface temperature calculated for all day
MeanSurfaceTemp_all	Mean surface temperature calculated for all day
MedianSurfaceTemp_all	Median surface temperature calculated for all day
sdSurfaceTemp_all	Standard deviation of surface temperature calculated for all day
MinSurfaceTemp_day	Minimum daytime surface temperature
MeanSurfaceTemp_day	Mean daytime surface temperature
MedianSurfaceTemp_day	Median daytime surface temperature
sdSurfaceTemp_day	Standard deviation of daytime surface temperature
MeanSurfaceTemp_night	Mean nighttime surface temperature
MedianSurfaceTemp_night	Median nighttime surface temperature
sdSurfaceTemp_night	Standard deviation of nighttime surface temperature
SurfaceTemp_mean_diff	Difference between mean daytime and mean nighttime surface temperature
SurfaceTemp_median_diff	Difference between median daytime and median nighttime surface temperature
SurfaceTemp_max_diff	Difference between maximum daytime and maximum nighttime surface temperature
SurfaceTemp_sd_diff	Difference between standard deviation of daytime and standard deviation of nighttime surface temperature
SurfaceTemp_5pct_day	5th percentile of daytime surface temperature
SurfaceTemp_10pct_day	10th percentile of daytime surface temperature
SurfaceTemp_15pct_day	15th percentile of daytime surface temperature
SurfaceTemp_85pct_day	85th percentile of daytime surface temperature
SurfaceTemp_90pct_day	90th percentile of daytime surface temperature
SurfaceTemp_95pct_day	95th percentile of daytime surface temperature
SurfaceTemp_5/95_day	5th percentile of daytime surface temperature divided by the 95th percentile of daytime surface temperature
SurfaceTemp_10/90_day	10th percentile of daytime surface temperature divided by the 90th percentile of daytime surface temperature

SurfaceTemp_15/85_day	15th percentile of daytime surface temperature divided by the 85th percentile of daytime surface temperature
SurfaceTemp_5pct_night	5th percentile of nighttime surface temperature
SurfaceTemp_10pct_night	10th percentile of nighttime surface temperature
SurfaceTemp_15pct_night	15th percentile of nighttime surface temperature
SurfaceTemp_85pct_night	85th percentile of nighttime surface temperature
SurfaceTemp_90pct_night	90th percentile of nighttime surface temperature
SurfaceTemp_95pct_night	95th percentile of nighttime surface temperature
SurfaceTemp_5/95_night	5th percentile of nighttime surface temperature divided by the 95th percentile of nighttime surface temperature
SurfaceTemp_10/90_night	10th percentile of nighttime surface temperature divided by the 90th percentile of nighttime surface temperature
SurfaceTemp_15/85_night	15th percentile of nighttime surface temperature divided by the 85th percentile of nighttime surface temperature

Air Temperature

MaxAirTemp_all	Maximum air temperature calculated for all day
MinAirTemp_all	Minimum air temperature calculated for all day
MeanAirTemp_all	Mean air temperature calculated for all day
MedianAirTemp_all	Median air temperature calculated for all day
sdAirTemp_all	Standard deviation of air temperature calculated for all day
MinAirTemp_day	Minimum daytime air temperature
MeanAirTemp_day	Mean daytime air temperature
MedianAirTemp_day	Median daytime air temperature
sdAirTemp_day	Standard deviation of daytime air temperature
MeanAirTemp_night	Mean nighttime air temperature
MedianAirTemp_night	Median nighttime air temperature
sdAirTemp_night	Standard deviation of nighttime air temperature
AirTemp_mean_diff	Difference between mean daytime and mean nighttime air temperature
AirTemp_median_diff	Difference between median daytime and median nighttime air temperature
AirTemp_max_diff	Difference between maximum daytime and maximum nighttime air temperature
AirTemp_sd_diff	Difference between standard deviation of daytime and standard deviation of nighttime air temperature
AirTemp_5pct_day	5th percentile of daytime air temperature
AirTemp_10pct_day	10th percentile of daytime air temperature
AirTemp_15pct_day	15th percentile of daytime air temperature
AirTemp_85pct_day	85th percentile of daytime air temperature
AirTemp_90pct_day	90th percentile of daytime air temperature
AirTemp_95pct_day	95th percentile of daytime air temperature
AirTemp_5/95_day	5th percentile of daytime air temperature divided by the 95th percentile of daytime air temperature
AirTemp_10/90_day	10th percentile of daytime air temperature divided by the 90th percentile of daytime air temperature
AirTemp_15/85_day	15th percentile of daytime air temperature divided by the 85th percentile of daytime air temperature
AirTemp_5pct_night	5th percentile of nighttime air temperature
AirTemp_10pct_night	10th percentile of nighttime air temperature

AirTemp_15pct_night	15th percentile of nighttime air temperature
AirTemp_85pct_night	85th percentile of nighttime air temperature
AirTemp_90pct_night	90th percentile of nighttime air temperature
AirTemp_95pct_night	95th percentile of nighttime air temperature
AirTemp_5/95_night	5th percentile of nighttime air temperature divided by the 95th percentile of nighttime air temperature
AirTemp_10/90_night	10th percentile of nighttime air temperature divided by the 90th percentile of nighttime air temperature
AirTemp_15/85_night	15th percentile of nighttime air temperature divided by the 85th percentile of nighttime air temperature

VPD

MaxVPD_all	Maximum vapour pressure deficit calculated for all day
MeanVPD_all	Mean vapour pressure deficit calculated for all day
MedianVPD_all	Median vapour pressure deficit calculated for all day
sdVPD_all	Standard deviation of vapour pressure deficit calculated for all day
MeanVPD_day	Mean daytime vapour pressure deficit
MedianVPD_day	Median daytime vapour pressure deficit
sdVPD_day	Standard deviation of daytime vapour pressure deficit
MaxVPD_night	Maximum nighttime vapour pressure deficit
MeanVPD_night	Mean nighttime vapour pressure deficit
MedianVPD_night	Median nighttime vapour pressure deficit
sdVPD_night	Standard deviation of nighttime vapour pressure deficit
VPD_mean_diff	Difference between mean daytime and mean nighttime vapour pressure deficit
VPD_median_diff	Difference between median daytime and median nighttime vapour pressure deficit
VPD_max_diff	Difference between maximum daytime and maximum nighttime vapour pressure deficit
VPD_sd_diff	Difference between standard deviation of daytime and standard deviation of nighttime vapour pressure deficit
VPD_5pct_day	5th percentile of daytime vapour pressure deficit
VPD_10pct_day	10th percentile of daytime vapour pressure deficit
VPD_15pct_day	15th percentile of daytime vapour pressure deficit
VPD_85pct_day	85th percentile of daytime vapour pressure deficit
VPD_90pct_day	90th percentile of daytime vapour pressure deficit
VPD_95pct_day	95th percentile of daytime vapour pressure deficit
VPD_10pct_night	10th percentile of nighttime vapour pressure deficit
VPD_15pct_night	15th percentile of nighttime vapour pressure deficit
VPD_85pct_night	85th percentile of nighttime vapour pressure deficit
VPD_90pct_night	90th percentile of nighttime vapour pressure deficit
VPD_95pct_night	95th percentile of nighttime vapour pressure deficit

Soil moisture

MaxSoilM	Maximum soil moisture
MinSoilM	Minimum soil moisture
MeanSoilM	Mean soil moisture
MedianSoilM	Median soil moisture
sdSoilM	Standard deviation of soil moisture