Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt

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Studies on changes in phytosociological and animal species composition in beech forests under global warming in Bavaria, Germany

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1. Introduction

Forests in central Europe have been affected by anthropogenic disturbances for centuries. The extension of these disturbances has been rising since the last century under the aspect of global change (Sala et al. 2000; Matesanz et al. 2010). Mainly forest management was completely changed: by the abandonment of traditional uses like forest pasture and litter removal (Glatzel 1991; Gimmi et al. 2008); by use of highly modern engineered forest machines for timber harvesting methods; by the preference of natural regeneration by foresters instead of planting trees. Apart from management nitrogen input into forest ecosystems has increased worldwide due to human activities like an increased production and use of artificial fertilizers, a risen combustion of fossil fuels, an intensified livestock breeding and an enhanced cultivation of nitrogen fixing plants in agriculture (Holland et al. 1999). Mean nitrogen input into forests in Bavaria amounted approx. 15 kg N/ha per year for the period from 1991 to 2007. But it differed dependent from region to region and from year to year between 5 kg/N ha and 32 kg/N ha (StMELF 2008). One main effect of increased nitrogen input, which was already observed in former studies in central Europe, was an increase of nitrophilous species in the forest understorey vegetation (Röder et al. 1996; Diekmann and Dupré 1997; Walther 1997; Carraro et al. 1999; Fischer 1999; Bernhardt-Römermann et al. 2009). Spread of non-native plant species is a further disturbance aspect. This fact had been reported from different countries of the northern hemispere (USA: Rooney et al. 2004; Netherlands: Vanhellemont et al. 2010; Lithuania: Dobravolskaité and Gudžinskas 2011; Austria: Essl et al. 2011; temperate zone of the northern hemisphere: Fischer et al. 2013) and seems to be induced (i) by globale trade (ii) by climatic change (Masters and Norgrove 2010; Shi et al. 2010; Huang et al. 2011; Zhang et al. 2011) and (iii) by better road construction in the forests (Mortensen et al. 2009).

Since the last report of the IPCC (IPCC 2007) it has been generally approved that the earth climate changes and mainly temperature increases. In the time period from 1901 to 2000 global average surface temperature has risen by 0.6 K, in the time period 1906 to 2005 by 0.74 K (IPCC 2007). It is assumed that temperatures will rise even more in this century. Compared to the average of 1980 to 1999 an increase of the global mean temperature between 1.1 and 6.1 K is expected up to the end of the 21st century (Moomaw et al. 2011). Temperature increase is also the most dominant ongoing trend in climate change in Germany, especially during winter time (Schönwiese et al. 2006). In Bavaria, a federal state of Germany, the mean annual temperature rose by 0.6 to 1.2 K, and December mean temperature by 1.8 to 2.5 K from 1931 to 2000 depending on the region (KLIWA 2005). For Germany an increase of the annual mean temperature between 2.5 and 3.5 K is expected

for 2100, compared to the average of 1961 to 1999 (UBA 2006). For the south and south eastern part of Germany winter temperatures are even expected to increase up to 4 K (UBA 2006).
First effects of global warming on plant and animal species have been proved:

- phenological activity period of woody plants has been extended from 1959 to 1993 by 10.8 days (Menzel and Fabian 1999) and starts around six days earlier;
- migratory birds arrive earlier in their breeding ground and start breeding earlier;
- butterflies appear earlier and also amphibians start breeding earlier (Walther et al. 2002);
- In northern Europe *Ilex aquifolium* migrates northwards with the shift of the January isotherm (Berger et al. 2007).
- Species richness is enhanced in higher altitudes in the Alps (Grabherr et al. 1994; Parolo and Rossi 2008), but typical mountain plants might be threatened as their migration is limited by the height of the mountains (Dullinger et al. 2012).
- For the range of terrestrial plants and animals in the northern hemisphere an average northward shift by 6.1 km per decade or an upward shift of 6.1 m per decade has been reported for the last 50 years (Thuiller 2007). In mountain areas treeline advances to higher altitudes (Walther et al. 2002).
- In the north mediterranean mountains European beech *Fagus sylvatica* shifts to higher altitudes and is replaced by holm oak *Quercus ilex* at lower altitudes (Peñuelas and Boada 2003).
- An increase of evergreen thermophilous species (Walther 1997; Carrao et al. 1999) and a decrease in frequency of mountain species (Walther 1997) had been determined in beech forests in Switzerland.
- A reduction of the present average size of the ranges of 150 high mountain plant species in the Alps by 44 to 50% is predicted by Dullinger et al. (2012) for the end of the 21st century.
- A change of the present distribution of 1,350 plant species in Europe was analysed by Thuiller et al. (2005) for different climate change models and the result revealed that more than half of the species could be threatened or be vulnerable by 2080.
- A global meta-analysis on phenological shifts which includes 677 animal and plant species on a timescale from 16-132 years reveals that 9 % of the analysed species show a trend to a delay of spring advancement, 27 % no trend, but 62 % a trend to an earlier spring event (Parmesan and Yohe 2003).

Hence the ongoing global warming of the last decades is expected to have already consequences on the species composition in forests and that species composition will change even stronger in the future decades. It is assumed that plant as well as animal species will be affected by increasing temperatures.

Beech (*Fagus sylvatica*) forests are considered as the prevailing natural vegetation type in central Europe covering naturally most parts of Germany, and even of Bavaria. Due to its ecological modesty of soil base saturation many different site types ranging from acidic to base-rich soils can be occupied by this species (Walentowski et al. 2004; Knapp et al. al. 2008). Beech forests are relatively poor in other canopy tree species and many stands are naturally dominated only by this species. The understorey vegetation of vascular plant species may be species rich (Fig. 1), mostly on base-rich soils, or it may be poor in species on acidic soils (Fig. 2). Species richness also depends on light availability.

The influence of temperature increase of the last decades on a change in the species composition of beech forests in central Europe has not been clearly observed up to now and is in the focus of this thesis. Depending on the findings regarding changes in species composition mentioned above our main hypothesis is that thermophilous species have increased in the plant species composition of beech forests.

Furthermore the temperature preference of plant species and ground beetles along a temperature gradient was analysed and based on these results the regional shift of the location of potential suitable beech forest habitats in Bavaria under increasing temperatures was modelled for these two species groups.

Summing up in this thesis a change in plant species composition during the last decades (1950-2010) was analysed as well as a change of potential suitable habitats was modelled for the future (2071-2100) for plant species (including bryophytes) and for ground beetles (Carabidae). The modelling for the future is based on the recent habitats (1971-2000), assuming a temperature increase of 1.8 K up to the period 2071-2100.

Fig.1: Species rich beech forest on a base-rich calcareous soil (Chiemgauer Alps, 1,400 m a.s.l)

Fig.2: Species poor beech forest on an acidic gneiss soil (Oberpfälzer Forest, 790 m a.s.l)

2. Methods

This thesis consists of two different research parts:

- **time series** study: a repetition of old phytosociological relevés
- **temperature gradient** study: phytosociological relevés located along an altitudinal (temperature) gradient

2.1 Time series study

Phytosociological relevés are documents of the plant species composition in one specific location at the date of the relevé. Both single species and species composition are imprints of the environmental conditions and therefore a phytosociological relevé is also a document of the relevant environmental parameters. Old phytosociological relevés can be repeated if the exact locations are known. Such repetitions reveal occurred changes in the species composition between the different time periods which can be attributed to changed environmental conditions. For such a repetition we chose five phytosociological studies from different regions in Bavaria (Fig. 3).

- Sinngrund (30 relevés)
- Steigerwald (64 relevés)
- Franconian Alb (65 relevés)
- Lake Starnberg (30 relevés)
- Inn Glacier Moraine (38 relevés)

From these studies those relevés with beech dominating in the canopy tree layer (coverage > 50 %) were repeated. The old relevés were from different time periods dating back from 1949 to 1985 (in some cases old relevés had already been repeated in the 1990s). All relevés were repeated in 2010. We tried to repeat the old relevé as close to the original location as possible (Fig. 4). We used the historical maps of the former researchers where the positions of the relevés were marked and the descriptions in the relevé headers to relocate the plot positions. The same plot size was used for the new relevés as documented for the old ones. For all analyses we used presence/absence data of vascular plant species. Species growing in two or three layers were considered once.

The following climatic data were provided by the PIK (Potsdam Institute for Climate Impact Research):

- mean annual temperature (°C)
- absolute minimum temperature per year (°C)
- absolute maximum temperature per year (°C)
- annual temperature sum > 0°C per year (° days)
- annual temperature sum > 5°C per year (° days)
- annual temperature sum > 10°C per year (° days)
- annual temperature sum > 0°C of winter (° days)
- annual temperature sum > 5°C of winter (° days)
- annual temperature sum > 0°C of spring (° days)
- annual temperature sum > 5°C of spring (° days)
- annual temperature sum > 10°C of spring (° days)
- absolute number of frost days per year (days)
- absolute number of ice days per year (days)
- absolute number of days ≤-10°C per year (days)
- length of the latest frost period (days)
- last frost day of the year (date)
- first frost day of the year (date)
- annual precipitation sum
- precipitation sum winter (mm)
- precipitation sum spring (mm)
- precipitation sum summer (mm)
- precipitation sum autumn (mm)

The change of all these climatic parameters in the study areas was analysed for the time period 1951-2006 using Mann-Kendall test and Sen Slope (Mann 1945; Deo 2011; Jain and Kumar 2012). With the Mann-Kendall test significant changes over an analysed time period can be determined and distinguished from a random fluctuation. The trend of the change and its strength per year can be attained by the Sen Slope value over the analysed time period.

To distinguish the climatic components from other environmental influenced factors in the species composition we used a partial canonical correspondence analysis (pCCA, ter Braak 1988) with climatic data as explanatory variables and soil indicator values as covariables. In this case average values were used of the climatic values of the five years preceding the last year of the time period in which relevés were performed in each study area. In the pCCA only a selection of the climatic parameters was used. The selection was attained by using only the (i) significant variables from a

Monte-Carlo-significance test and (ii) by using the variables with the lowest variance inflation factor, avoiding problems with collinear factors.

The following climatic parameters met these requirements and were used in the pCCA:

- temperature sum of the winter (>5° C),
- number of frost days,
- date of the first frost day of the year and
- date of the last frost day of the year and
- annual precipitation sum

Soil indicator values were obtained by calculating mean unweighted Ellenberg (Ellenberg 2001) indicator values for nitrogen, moisture and reaction for each relevé.

The species ordination plot from the pCCA was compared with the percentage change in plant species frequency in the dataset. We had a closer look at the change in frequency of Ellenberg indicator values for temperature >6, which can be regarded as thermophilous species and at Ellenberg indicator values for nitrogen >6, which can be regarded as nitrophilous species. To evaluate the effect of forest management we used (i) the growth-form classification of the list of forest vascular plant species by Schmidt et al. (2011) and paid special attention to the change of tree species, considered changes in (ii) frequency of plant species indicating anthropogenic disturbances (Godefroid and Koedam 2008) in forests and (iii) in frequency of plant species tolerating high soil compaction (Godefroid and Koedam 2004), both indications for a highly engineered timber harvest. We also minded the change in frequency of non-native species, species which were introduced to central Europe after 1492 (Kowarik 2010).

For more details of the methods see **Publication 1**; Jantsch et al. (2013).

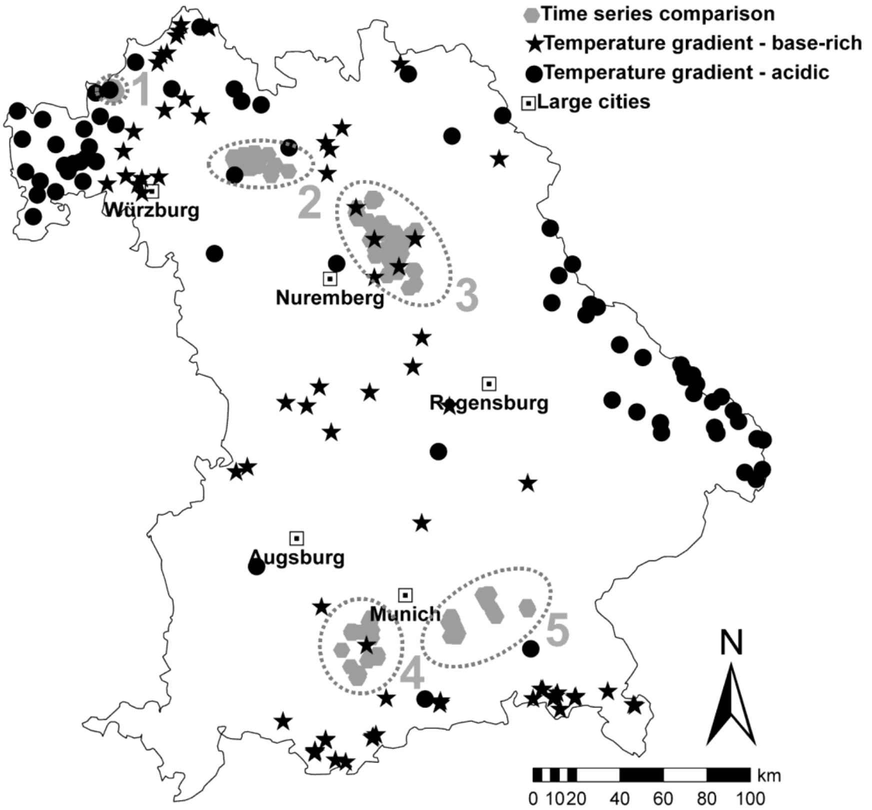

Fig.3: Location of the five study areas of the time series comparison (grey hexagons, encircled: 1 = Sinngrund, 2 = Steigerwald, 3 = Franconian Alb, 4 = Lake Starnberg, 5 = Inn Glacier Moraine) and of the plots of the temperature gradient study (black stars = plots on base-rich substrate, black dots = plots on acidic substrate). Borderline of Bavaria © Bundesamt für Kartographie und Geodäsie, Frankfurt am Main

Fig.4: Same plot at the Kleiner Knetzberg in the Steigerwald at the time of the original relevé on 3rd August, 1981 (left, photo taken by Walter Welß, used with friendly permission) and at the time of the repetition on 25th August, 2010 (right). The new occurence of *Impatiens parviflora* in the ground layer is visible.

2.2 Temperature gradient study

Along a continuous gradient of the annual average temperature 140 plots in beech forest stands in Bavaria were selected, 70 of them on acidic soils, 70 on base-rich soils (Fig. 3).

As the first step we preselected one plot in each suitable forest stand with the following criteria:

- exposition: south exposed slopes or slightly south exposed hilltops, varying maximum between east-southeast and west-southwest;
- size of the forest area: more than 200 ha;
- proportion of beech coverage: more than 50% on at least 10 ha;
- substrate: acidic or base-rich;
- buffer distance at least 1 km between each plot, except a temperature difference of at least 1°C was provided.

The preselection of the plots was performed in the geographical information system ArcGIS 9.3 on the basis of digital aerial photographs, geological, soil, topographic and climatic maps. Annual average temperature was obtained from a temperature map of Bavaria. The classification of the substrate type of the plots was based on the information of the geological map of Bavaria in the scale 1:500.000 and a map distinguishing five different types of base saturation in the soil (Kölling et al., 1996; Kölling, 2010). Base saturation types 1 and 2 was classified as base-rich, base saturation types 4 and 5 as acidic; base saturation type 3 regarded as intermediate was not considered to get two distinctive groups. By considering both substrate types most typical forest species should be included, but a classification of the substrate type was necessary because many species in central Europe only occur on base-rich substrate (Ewald, 2003). Southern exposition was selected to get the gradient as long as possible to the warm side. After this preselection we firstly chose all plots that provided a continuous mean annual temperature gradient respecting the maximum possible temperature range of beech forest stands in Bavaria: from 4.1 to 9.8 °C on acidic soils and from 4.2 to 9.1 °C on base-rich soils. This temperature range corresponds to an altitudinal gradient from 140 to 1,200 m a.s.l. on the acidic substrate and from 220 to 1,400 m a.s.l. on the base-rich substrate.

The selection of spatial homogenous distributed plots over Bavaria was the second objective, but small clustering could not be excluded, as beech forests, mountains and specific substrate types are clustered in the landscape.

Final selection of the plots was implemented in the field, using additional criteria for the plot:

- >50% cover of beech in the tree layer
- total coverage degree not less than 80%
- age of tree stand at least 80 years

- rock coverage of the plot less than 20%
- maximum 30° slope inclination

For sampling of the vegetation relevés in the selected forest stands two nested plots with the same center point were set up: the first of a size of 196 m² (14 m x 14 m) and the second of a size of 900 m² (30 m x 30 m).

All plant species from tree, shrub and herb layer were recorded on the 900 m² plot, bryophyte species only on the 196 m² plot (on soil as well as on rocks and dead wood). Ranging poles and tape measures were used for exactly defining the plot size.

A selection of 50 plots (25 on acidic and on base-rich substrate each) was chosen for the faunistic research. A dead wood proportion of at least 3 cbm/ha was used as criteria for the selection. Ground beetles were sampled on the 196 m² plot by digging seven 7x7 cm plastic cups in the soil surface along a 25 m line with 5 m distance between each, filled up to two thirds with a 10% solution sodium benzoate of neutral pH. These traps were emptied about every three weeks and active between the end of April to the beginning of October; in July and August was a break with no trapping (standard protocol, Trautner and Fritze 1999). This method considers both the catch of spring as of autumn breeding species.

Presence/absence data of the species were used for all analyses. All rare plant species which occurred less than seven times (59% of all species in total) were deleted from the matrix. Ground beetles with at least two occurences were used for the analyses. Rare species might present random occurrences that are not typical for beech forests; therefore modelling might be misleading for them.

Nomenclature for the scientific names of the vascular plant species indigenous to Bavaria follows Wisskirchen and Haeupler (1998), for all other plant species Erhardt et al. (2000), for bryophyte species Koperski et al. (2000) and for the ground beetles Müller-Motzfeld (2006).

2.2.1 Climatic data

Climatic parameters for our plots were obtained from a spatial interpolated climate model for the period 1971 to 2000 (Hera et al., 2012) as reference for the present climate. This climate model is based on daily measurements from around 80 climate stations for temperature and from around 570 stations for precipitation in Bavaria for the period 1971 to 2000 from the German Meteorological Service. The WETTREG B1 scenario (Spekat et al., 2007) was performed to calculate the climatic parameters for the time period 2071 to 2100. WETTREG B1 assumes an increase of 1.8 K of the mean annual temperature until 2100 and can be regarded hence as a moderate warming scenario. The spatial resolution of both models was 50 m x 50 m.

2.2.2 Creating maps

The mean annual temperature was calculated in a grid of 250 m x 250 m for Bavaria from the monthly averages of the climate model for the period 1971 to 2000 and for the period 2071-2100 based on the data of the available climate models. We had to respect the classification types "acidic" and "base-rich" also in modelling the potential suitable habitats, as we used the substrate as one criterion for our plot selection and for model building. On the basis of the geological map of Bavaria in the scale 1:500.000 and of the map distinguishing five different types of base saturation in the soil (Kölling et al., 1996; Kölling, 2010) a grid map with 250 m resolution with the classes acidic, base-rich and intermediate was set up. We applied the maptools-package (Lewin-Koh et al., 2012) in R statistics (R Development Core Team, 2012) for creating the raster files.

2.2.3 Statistical Analysis

Canonical correspondence analyses (CCA) were used to analyse the dependence of the species composition on environmental variables and to evaluate the importance of the temperature factor in the dataset by using the vegan-package (Oksanen et al., 2012) in R statistics.

We tested the following available environmental parameters: mean annual temperature and annual precipitation sum from the climate models; slope and aspect obtained from a digital elevation model (BVW, 2011); substrate and the exchangeable calcium and magnesium stock in the soil and the base-saturation type (BST on a scale 1 to 5) extracted from modelled maps (unpublished, version of 2007).

Significance of the environmental factors in the CCA was checked with an analysis of variance (ANOVA) with Monte-Carlo-significance test and insignificant factors were deleted from further analysis. The explained dispersion of the environmental parameters in the CCA was calculated respectively.

A correlation between species number per plot and mean annual temperature of the plot was tested using a linear regression.

Two different generalized linear models (GLM) were applied in R statistics (R Development Core Team, 2012) to analyse the response of individual plant species to mean annual temperature:

- a sigmoid model
- a unimodal model

First we tested for all plant species whether there was a significant interrelation between temperature and substrate (acidic or base-rich) in any of both GLM models. The occurrences of plant species with a significant interrelation between both parameters were separately analysed classified to the acidic and base-rich plots as well as for plant species which occurred only on one substrate type.
We calculated for all species both a sigmoid model and a unimodal model and selected the model that had a significant regression parameter of the second order polygon and as second option the model with the better explained deviance. An effect of temperature on the occurrence of all species with a significant regression parameter in anyone of both models was assumed.
The curve of a sigmoid model can rise to the left or right side. If the slope of the curve of the sigmoid model rose to the left side (colder climate range), we classified the species as adapted to lower temperatures, if the slope of the curve rose to the right side, we classified the species as adapted to higher temperatures (warmer climate range). The upper and lower ecological temperature bound is the intersection point of the modelled probability of occurrence with the a priori probability of occurrence of the individual species. In case of a sigmoid model there is only one (upper or lower) bound, in case of a unimodal model the lower and upper bound of the ecological amplitude is available. The whole ecological amplitude of a individual species can be described by a unimodal model, whereas only the warmer or colder end of the distribution of the species is captured in the Bavarian extend of temperatures in a sigmoid model. Species with a unimodal model were classified as adapted to intermediate temperatures. A significance level of 95% was applied for all decisions.

2.2.4 Modelling of the potential habitat suitability

The GLMs and climate models were applied in the dismo-package (Hijmans et al., 2012) in R statistics (R Development Core Team, 2012) for modelling the potential habitat suitability for the different plant species occurring in beech forests under the recent climate 1971-2000 and under the assumed climate of the years 2071-2100.
The threshold for the potential occurrence of the individual species was calculated as the logit-transformed prior probability:

$$threshold = log \frac{p_i/p_n}{1-(p_i/p_n)}$$

p_i=count of presences, p_n=count of plots

The values for the upper or lower ecological bound or amplitude were calculated by the intercept and slope of the GLM and the threshold (Fischer, 1994).
The accuracy of the generated models was evaluated by the AUC (area under the receiver operating curve) value which was calculated with the PresenceAbsence-package (Freeman and Moisen, 2008) in R statistics (R Development Core Team, 2012). The best models have an AUC near 1. An AUC around 0.5 reveals that the generated model is not better than a random model. For modelling the potential habitat suitability we only have selected species models with an AUC ≥0.80, which are considered as models with good performance (Hosmer and Lemeshow, 2000).
For more details of the methods see **Publication 2**; Jantsch et al. (accepted) and **Publication 3**; Müller-Kroehling et al. (resubmitted).

3. Summaries of single publications

3.1 Summary of Publication 1

Shift in plant species composition reveals environmental changes during the last decades: A long-term study in beech (Fagus sylvatica) forests in Bavaria, Germany

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The final publication is available at http://link.springer.com

This paper deals with the topic how far present found changes in phytosociological composition of beech forests in Bavaria can be attributed to the effects of climate change. Phytosociological relevés from the last six decades were repeated in five different regions in Bavaria.

Main climatic trend in the analysed beech forest in the study areas in Bavaria over the past decades is "warming". A clear shift of the new relevés compared to the old ones is visible in the partial canonical correspondence analysis (pCCA) along axis 2, which describes mainly the increase of temperature sum in the winter (TSUM_WIN in Fig. 5). But all five climatic parameters together explained only 6 % of the dispersion in the dataset; without precipitation only 5 %. The species which is best correlated with increase of temperature sum in the winter is the thermophilous tree species *Juglans regia* ("JugReg" close to the top in Fig. 6). This species was nearly not present in the old relevés and has increased in some study areas up to 23 % in frequency. *Juglans regia* was the only thermophilous plant species which raised significantly. On the first glance the increase of the thermophilous species *Juglans regia* fits very well with the increasing temperature; but there are, however, more factors which may explain the change: mainly a decreased nut harvest by humans and an increased dispersion by squirrels and birds. Apart from climate change effects other effects of global change were quite obvious.

We also found an increased frequency of nitrophilous species and a raise of the mean Ellenberg indicator value for nitrogen. This result was not really surprising, as this fact has already been described by different other studies in the past (Röder et al. 1996; Diekmann and Dupré 1997; Walther 1997; Carraro et al. 1999; Fischer 1999; Bernhardt-Römermann et al. 2009). But this effect seems to be weakened since the 1990s and is mainly reduced to changes decades before. The decrease of nitrogenoxides emissions and imissions since the 1990s (Builtjes et al. 2011) is probably one reason and a currently reached nitrogen saturation of forest soils (Mellert et al. 2005) another reason.

Tree species significantly increased and herb species significantly decreased in frequency.

Disturbance indicating plant species significantly increased as well as plant species tolerating high soil compaction. These changes can be best explained by the changes in forest management: a natural maturing of the forest stands leading to an increased timber harvest with highly modern engineered machines and better light conditions on the forest floor for young trees to grow up.

A trend towards thermophilization is statistically provable, however can hardly be related to individual species. *Juglans regia* seems to be one of the species whose increase can be referred to global warming, but other factors could be responsible for the spreading of this species, too.

Summing up the effects of temperature increase on changes in species composition in beech forests in Bavaria are still small up to now and are obscured by the reached nitrogen saturation of forest stands and changes in forest management. One reason could be the long life span of most forest species, even of herbaceous species. Species composition may also be conserved for a long time in old forests, whereas forests that grow up today under the recent climate may develop a different species composition. It can be assumed that the effects of climate change on beech forests will appear over a longer time period than the effects of disturbances like wind throw and management.

Candidate's own contributions

Idea of the paper, together with supervisor Anton Fischer

Selection of the study areas and plots

Performing of all field work (except study area Inn Glacier Moraine) and data collection

Analysing all data in MS Excel and R statistics, consulting with Hagen S. Fischer for statistical ideas

Writing and finalizing paper consulting with co-authors

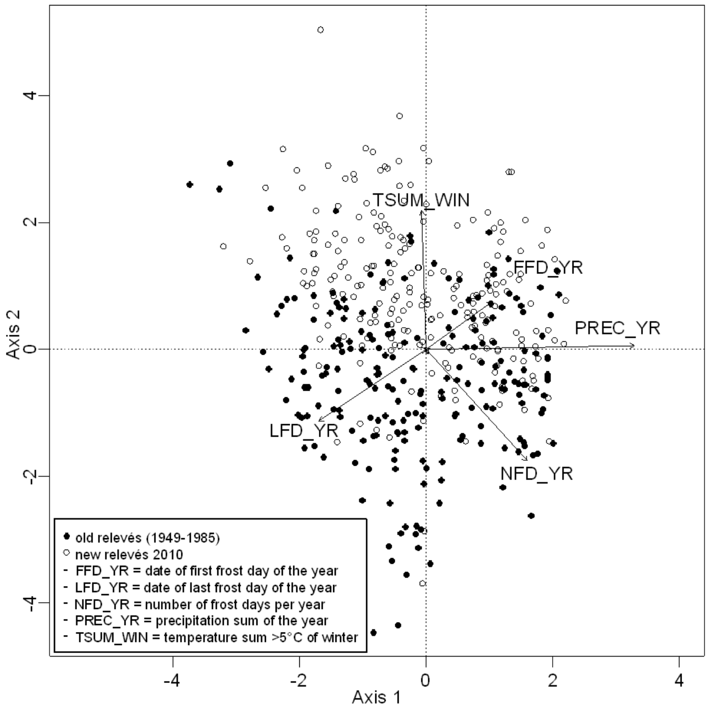

Fig. 5: Biplot of the old and new relevés and their environmental factors from the pCCA. According to Jantsch et al. (2013).

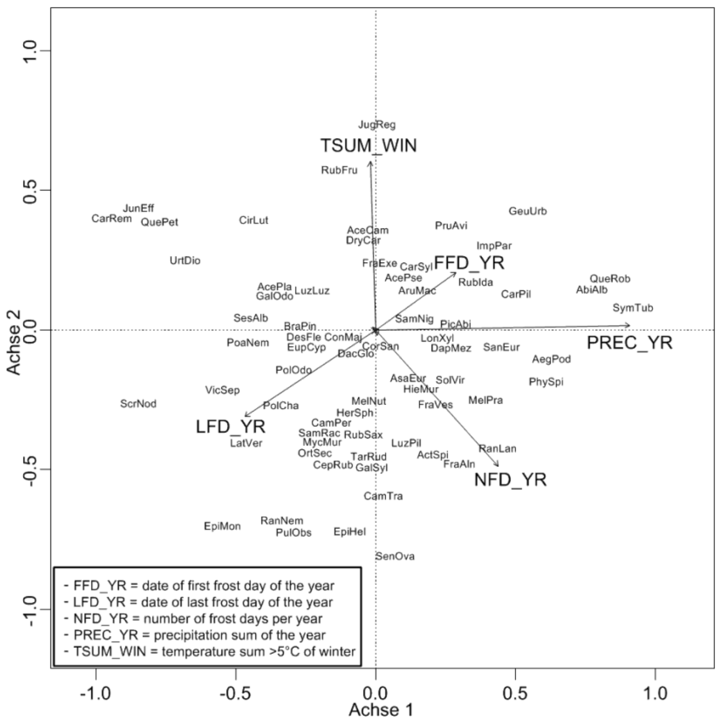

Fig. 6: Biplot of the plant species and the environmental factors from the pCCA. Only species with a significant change are shown. According to Jantsch et al. (2013).

3.2 Summary of Publication 2

How are plant species in central European beech forests (*Fagus sylvatica* L.) affected by temperature? - Shift of potential suitable habitats under global warming

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The final publication will be available at
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In this paper we analysed the effect of temperature on the occurrence of plant species (vascular plants and bryophytes) in beech forests in Bavaria along a temperature gradient. Based on these occurrences the change in the distribution of potential suitable habitats was modelled for the future (2071-2100) under global warming.

The majority of the analysed species with a temperature response was adapted to lower temperatures (36%), a smaller proportion was adapted to higher temperatures (18%), and the smallest proportion to intermediate temperatures (8%), having the optimum within the analysed gradient. The biggest group of species (38%) showed no temperature preference at all in our models.

Most plant species adapted to lower temperatures were herb species, whereas mostly tree species were adapted to higher temperatures.

Including the modelling of the shift of the location of potential suitable habitats, consequently cold adapted herbs like, *Prenanthes purpurea* (Fig. 7b compared to Fig. 7a), *Luzula sylvatica* and *Maianthemum bifolium* and showed a decreasing area of potential suitable beech forests habitats in the future. Indeed these species lose their suitable beech forest habitats outside the Alps and outside the Bavarian Forest completely in our models, meaning these species could be really threatened by global warming as elements of beech forests. We revealed the two tree species *Picea abies* and *Acer pseudoplatanus* also negatively affected by the temperature increase in the same way.

Impatiens parviflora is one herbal plant species which is positively affected by global warming and can gain new potential suitable habitats in beech forests in the future. New possibilities as admixed species in beech forests are given for the tree species: *Prunus avium* (Fig. 7d compared to Fig. 7c), *Acer campestre*, *Carpinus betulus*, *Juglans regia*, *Quercus petraea*, *Sorbus torminalis* which can extend their potential suitable habitats in the future.

Our modelled potential suitable habitats are different from the real distribution of the species. The models demonstrate only habitats, both recent and future, for south exposed beech forests in Bavaria with the selected criteria, where the species could occur with a high probability if (mixed) beech forests would exist there. Models might be different for the same species in another ecosystem or in the whole distribution range. Species migration, persistence and adaptation to increasing temperatures were not considered in our models. Nevertheless our models are useful, especially for forestry, because they show the spatial shift of the site potential of forest species in the future. Nature conservation will be faced with new tasks how to deal with shifting ranges in conservation areas and forestry will generally profit by the chance of using more species in the future in today colder areas.

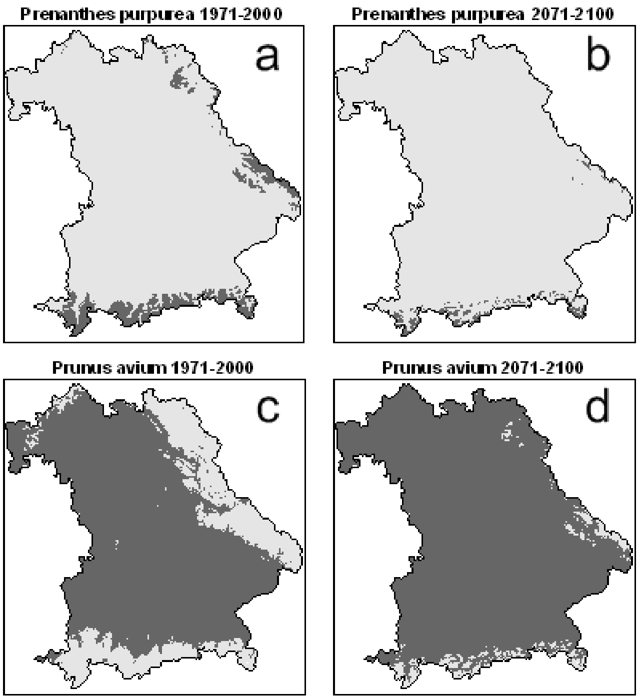

Fig.7: Maps of the modelled potential habitat suitability in south exposed beech forests for today (1971-2000) (left) and the future (2071-2100) (right) from the GLMs for the plant species *Prenantes purpurea* (a-b) and *Prunus avium* (c-d). Areas coloured in dark grey show where the conditional probability of the species occurrence is higher than the a priori probability in the data set.

Candidate's own contributions

Idea of the paper, together with supervisor Anton Fischer

Selection of the plots

Performing of all field work and data collection

Analysing all data in R statistics, consulting with Hagen S. Fischer for statistical ideas

Writing and finalizing paper consulting with co-authors

3.3 Summary of Publication 3

Modeling the effects of global warming on the ground beetle fauna of beech forests in Bavaria/Germany

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This manuscript has been resubmitted in revised form to

European Journal of Entomology

The final publication will be available at
http://www.eje.cz/scripts/content.php

This paper deals with the effect of temperature on the occurrence of ground beetles (Carabidae) in beech forests in Bavaria along a temperature gradient. Ground beetles were captured in traps at 50 plots distributed over Bavaria between April and October. The traps were emptied about every three weeks with a summer break from July to August. Generalized linear models were calculated for 34 species to analyse the temperature effect. For evaluating the models the results were compared with the occurrences of the same species in a regional gradient study in forests in Bavaria in general and in a bigger data set of forests not representing a gradient study. We found five ground beetle species adapted to intermediate temperatures by showing a unimodal response: *Abax parallelus, Carabus hortensis, Carabus linnei, Carabus nemoralis* and *Molops elatus*. All species except *Carabus linnei* will profit from slightly increasing temperatures. The six species *Pterostichus burmeisteri* (Fig. 8b compared to Fig. 8a), *Calathus micropterus*, *Carabus auronitens, Cychrus attenuatus, Pterostichus pumilio* and *Pterostichus unctulatus* are adapted to colder temperatures and their potential suitable habitats might be shrinking by increasing temperatures. Whereas *Notiophilus rufipes* (Fig. 8d compared to Fig. 8c) , *Carabus coriaceus, Harpalus latus, Limodromus assimilis* and *Pterostichus strennuus* are species adapted to warmer temperatures which might generally profit by global warming by enlarging their potential suitable habitats in beech forests. *Notiophilius rufipes* which was found on all of our three warmest plots is a species, which will profit by the temperature increase. The number of species affected positively as negatively by global warming seems to be equal, but *Abax parallelus, Carabus linnei, Molops elatus, Pterostichus burmeisteri* and *Pterostichus unctulatus* are species with a high responsibility for preservation in central Europe and none of the species adapted to higher temperatures can be attributed to this category. Out of all analysed species only *Pterostichus burmeisteri* is a ground beetle species typical for beech forests, all other ground beetle species are not linked to a specific forest type and occur in different forest types. But the models of these species are mostly plausible with the ecology of the species; however they can differ in other forest systems partly, because dead wood proportion, rock coverage and microclimate also play an important role for the species occurrence. Generally the models of the Bavarian wide gradient can be seen as more realistic on a broader scale than the models of the regional gradient. Habitat preference and distribution range should be considered for developing general predictions. One half of all found species is cold adapted and the other half warm adapted. Considering the temperature increase species number would stay nearly the same as warm adapted species spread in the areas where cold adapted species decrease. But among the cold adapted species are several species for which Germany bears a high responsibility for their preservation. Therefore mountain regions could be identified as most endangered by a change in species distribution through global warming.

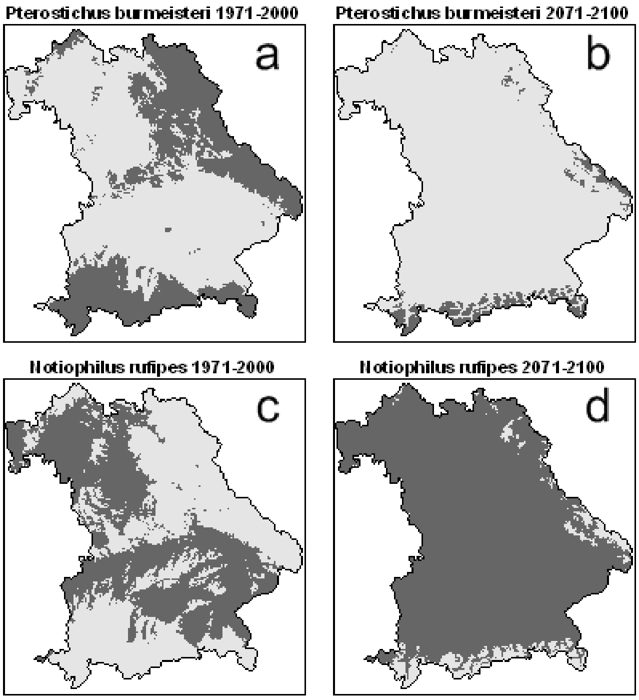

Fig.8: Maps of the modelled potential habitat suitability in south exposed beech forests for today (1971-2000) (left) and the future (2071-2100) (right) from the GLMs for the ground beetle species *Pterostichus burmeisteri* (a-b) and *Notiophilus rufipes* (c-d). Areas coloured in dark grey show where the conditional probability of the species occurrence is higher than the a priori probability in the data set.

Candidate's own contributions

Outline of the project, together with Stefan Müller-Kroehling and Anton Fischer

Selection of the plots

Analysing all data in R statistics, consulting with Hagen S. Fischer for statistical ideas

Arranging of figures and appendix

Complement of text, consulting with co-authors

4. Discussion

Contrary to our expectations the revealed influence of the temperature increase of the last decades on a change in plant species composition in beech forests in Bavaria was less with 5% explained dispersion. Up to now thermophilous plant species are not present, except the tree species *Juglans regia*. Global warming is supposed to have strong influence on the enhanced spreading of *Juglans regia* in central Europe (Loacker et al. 2007; Pompe et al. 2011; Hetzel 2012). We revealed an increased winter temperature sum as the main trigger for the increased occurrence in the time-series comparison and a preference for higher temperatures for *Juglans regia* in the temperature gradient. But apart from global warming also a reduced harvesting pressure on walnuts by man (Hetzel 2011) and an increased number of Eurasian red squirrels which are the main propagators (Hetzel 2011, 2012) might be reasons for the increased occurrence of this species in forests. The enhanced nitrogen level in forest soils through raised atmospheric nitrogen input over the last decades might be a further reason for the increase of this species as vitality of *J. regia* is strongly dependent on the nitrogen soil availability (Müller-Kroehling 2000). An increased spreading of *Juglans regia* into forests in central Europe was also found by Loacker et al. (2007) in an alpine valley close to Innsbruck in Austria and by Hetzel (2012) in the Ruhr-Basin. Therefore *J. regia* may also invade beech forests because of other reasons than the temperature increase.

In a long-term study in beech forests in the Rychlebské Mountains in the Czech Republic also no increase of thermophilous species was found (Hédl 2004). Apart from thermophilous plant species also no increase of evergreen-broad-leaved plant species like *Aucuba japonica* (Hetzel 2012), *Hedera helix* (Walther 1997; Dierschke 2005), *Ilex aquifolium* (Walther 1997; Huwer and Wittig 2012) or *Prunus laurocerasus* (Walther 1997; Hetzel 2012) was found. These species are indicator species for mild winter and spring temperatures in central Europe.

The most conspicuous revealed changes over the last decades like an increased number of tree species, of nitrophilous species, of disturbance indicating species and of non-native plant species could not be attributed to climate change, but to a change in forest management and an increased nitrogen input into forests over the last decades.

Contrary determining the temperature preferences of plant species in beech forests and modelling the shift of the potential suitable habitat showed a different picture concerning species sensitivity to temperature.

Most herb species, especially on the base-rich substrate had a preference for lower temperatures, whereas mostly tree species had a preference for higher temperatures. The revealed temperature preference of the species was mainly coincidental with the ecology of the species described in the literature (Oberdorfer 1994, Ellenberg 2001). For few plants a clear preference for temperature in beech forests was found which has not yet been described. Some species showing increasing or decreasing habitats in the future in Bavaria seem to respond already on increasing temperatures. Lenoir et al. (2010) determined in the Jura Mountains of France and Switzerland over the period 1989-2007 a decrease of the lower temperature adapted species *Prenanthes purpurea*, *Senecio ovatus* and *Solidago virgaurea* and an increase of the warmer temperature adapted species *Quercus petraea*. We revealed a certain change of the species *Senecio ovatus*, *Solidago virgaurea* and *Quercus petraea* also in our time-series study.

The cold adapted species composition of plants and ground beetles in the Alps seems to be most threatened by increasing temperatures, but it has to be kept in mind that the Alps represent a unique natural area which has a high diversity of habitat niches and soils which is one reason for the high species number (Ewald and Fischer 1993). The preference of species in the Alps for lower temperatures (<6.5°C) might also be induced by the higher altitude (>800 m) of the mountains. The temperature preference of bryophytes and their potential suitable habitats should be seen critically for such species, which do not actually fit with the previously described ecology (Nebel and Philippi 2001 a,b,c). The presence of rocks and dead wood is very important for some bryophytes, but these structures were not equally distributed along our gradient. High precipitation sums are also important for some bryophytes and in our dataset temperature and precipitation are strongly correlated. Therefore preference for lower temperatures can also be seen as preference for high precipitation sums. The models of potential suitable habitats should not be taken as the same as the distribution range of plants species (e.g. Schönfelder and Bresinsky 1990; BIB 2012) and of ground beetles (Lorenz 2004) in our study area. Our models are only valid for south exposed beech forests with the chosen criteria, but of course these criteria are not fulfilled in the whole study area in reality.

Cold adapted planted species are even supposed to maintain in their native growing areas for some time global warming (Thuiller et al. 2008), some populations might even adapt to increasing temperatures.

It is also assumed that new plant species will spread into beech forests within the next decades.

It is, however, hard to predict individual immigrating species, but such species might be found in the warmer parts of Europe which already represent the future temperatures of Bavaria (Bergmann et al. 2010). The plant species *Castanea sativa* and the ground beetle species *Notiophilus rufipes*, which were both present on our two warmest plots, are among the species which have recently been found only scattered but have a high potential to spread further in the forests under a warming climate.

5. Conclusions

Up to now, temperature increase seems not to have an effect on a fundamental change of plant species composition in beech forests. The response of the vegetation to changes in forest management and to the increased atmospheric nitrogen input into forests additionally obscures the climatic signal. Old beech forests conserve their species composition including many herb species having a long life span until dramatical climatic events take place. Such events can be periods with very high temperatures or very strong droughts. After such events species composition is expected to change more rapidly, so new species can spread easier in the forests, filling up locations becoming more suitable now for them. Our moderate 1,8 K scenario shows already strong changes of the potential suitable habitats for many species. Changes in the distribution of suitable habitats might even be stronger in a more realistic 3 K scenario at the ending 21st century compared to the current models. Therefore it is highly probable that strong changes will also take place in beech forests in the future. In case of the ground beetles such changes are expected to occur faster, because of shorter reproduction rates and larger movement ranges.

Forestry has to adapt to changes in the traditional cultivation of forest trees, but may generally profit because more native tree species can be admixed to beech forests especially in colder areas. Nature conservation will be faced with new tasks how to deal with changing species composition and shifting ranges in protected areas under global warming.

6. Summary

The objective of this work was to reveal first indications of the temperature increase of the last decades in a change of the vegetation in beech forests in Bavaria to thermophilous species, respectively, to show possible changes of the location of suitable beech forest habitats for individual plant and ground beetles species for the future. For that purpose 140 phytosociological relevés were performed along a temperature gradient (4-10 °C) in beech forests in Bavaria. On 50 of these plots additionally the ground beetles were determined. Phytosociological relevés are used to describe the environmental conditions of a forest stand by the occurring plant species. Additionally 227 phytosociological relevés, as documents of a former situation to compare with the recent situation, were repeated from the last decades (1949-1985) in five different areas (Sinngrund, Steigerwald, Franconian Alb, Lake Starnberg, Inn Glacier Moraine). The comparison of old and new relevés points out:

- Nitrophilous species, disturbance indicating species, and non-native species increased.
- A floristical conversion of the species combination driven by the temperature increase is statistical provable, but up to now it is hardly possible to identify species increasing or decreasing because of global warming.
- The first plants species apparently responding to the temperature increase maybe English Walnut *Juglans regia* (increase) and Wood Ragwort *Senecio ovatus* (decrease), but also other explanations are possible. Other floristically changes can be better explained by a change in forest management and an enhanced nitrogen input into forests than by global warming.

Modelling of the location of potential suitable beech forest habitats basing on the present lower and upper limits of the species in the temperature gradient reveals that under the assumption of a moderate temperature increase of 1,8 K

- Mainly herb species will decrease in beech forests.
- Woody species will be more favoured.
- Thus new options for forestry will arise in up to now colder regions or higher mountain areas.
- Total ground beetle species number will nearly stay the same through the similar numerical loss of cold adapted species as through the increase of warm adapted species. However, under the species adapted to lower temperatures are several species with a high responsibility for their protection in beech forests in central Europe.

The expected temperature affected conversion of the species composition in beech and mixed beech forests does not take place so clearly currently as suspected. This should be interpreted only as a delay to the reaction as in the forest not only trees can become very old but also many herb species. It is expected that the conversion will take place faster after disturbance events, like high temperatures and strong droughts.

7. Zusammenfassung

Ziel dieser Arbeit war es, erste Anzeichen des Temperaturanstiegs der letzten Jahrzehnte in einer Veränderung der Vegetation in Buchenwäldern in Bayern hin zu thermophileren Arten festzustellen, bzw. mögliche räumliche Veränderungen der Lage potenziell geeigneter Buchenwaldhabitate für einzelne Pflanzen und Laufkäferarten für die Zukunft aufzuzeigen. Dazu wurden entlang eines Temperaturgradienten (4-10° C) über Bayern 140 Vegetationsaufnahmen in Buchenwäldern durchgeführt. Auf 50 dieser Flächen wurden auch die vorkommenden Laufkäfer bestimmt. Zusätzlich wurden 227 historische Vegetationsaufnahmen aus zurückliegenden Jahrzehnten (1949-1985) in fünf unterschiedlichen Regionen Bayerns (Sinngrund, Steigerwald, Fränkische Alb, Starnberger See, Inngletscher-Moräne) wiederholt. Der Vergleich alter Aufnahmen und ihrer Wiederholungen zeigt:

- Stickstoffzeiger, Störzeiger und fremdländische Arten nahmen zu.
- Ein temperaturbedingter floristischer Umbau der Artenkombination ist statistisch nachweisbar, doch sind bisher temperaturbedingt zu- oder abnehmende Arten kaum eindeutig zu identifizieren.
- Die ersten Pflanzenarten, die anscheinend auf den Temperaturanstieg reagieren, sind die Walnuss *Juglans regia* (Zunahme) und das Fuchs‘ Greiskraut *Senecio ovatus* (Abnahme). Die bisher vorgefundenen anderen floristischen Veränderungen lassen sich bisher besser mit Veränderungen der Waldbewirtschaftung und einem angestiegenen Stickstoff-Eintrag erklären als mit gestiegenen Temperaturen.

Die Modellierung der Lage potenziell geeigneter Buchenwaldhabitate, basierend auf den heutigen Unter- bzw. Obergrenzen der Arten im Temperaturgradienten zeigt, dass unter Annahme einer moderaten Temperaturerhöhung von 1,8 K bis zum Jahre 2100

- Vorwiegend krautige Arten in Buchenwäldern zurückgehen werden.
- Gehölzarten eher profitieren werden.
- Sich dadurch in bisher kühleren Regionen bzw. höheren Gebirgslagen neue Optionen für die Forstbewirtschaftung ergeben.
- Für die Gesamtzahl der vorkommenden Laufkäfer ergibt sich ein Nullspiel durch den zahlenmäßigen gleichen Verlust kälteadaptierter Arten wie durch die Zunahme wärmeliebender Arten. Allerdings befinden sich unter den Arten, die an niedrigere Temperaturen angepasst sind, vier Arten mit hoher Verantwortung für deren Erhalt in Buchenwäldern in Zentraleuropa.

Der erwartete temperaturbedingte Umbau der Pflanzenartenzusammensetzung in Buchen(misch)wäldern läuft derzeit also noch nicht so deutlich ab wie vermutet. Da im Wald aber nicht nur die Bäume sehr alt werden können, sondern auch viele krautige Pflanzen, ist das wohl lediglich als Verzögerung der Reaktion zu interpretieren. Es ist zu erwarten, dass sich der Umbau nach Störungsereignissen (z.B. hohe Temperaturen und starke Trockenheit) dann umso schneller vollziehen wird.

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10. Eidesstattliche Erklärung

Ich erkläre an Eides statt, dass ich die bei der

Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der TUM

zur Promotionsprüfung vorgelegte Arbeit mit dem Titel:

Studies on changes in phytosociological and animal species composition in beech forests under global warming in Bavaria, Germany

am Fachgebiet Geobotanik

unter der Anleitung und Betreuung durch Prof. Dr. Anton Fischer ohne sonstige Hilfe erstellt und bei der Abfassung nur die gemäß § 6 Abs. 6 und 7 Satz 2 angegebenen Hilfsmittel benutzt habe.

[X] Ich habe keine Organisation eingeschaltet, die gegen Entgelt Betreuerinnen und Betreuer für die Anfertigung von Dissertationen sucht, oder die mir obliegenden Pflichten hinsichtlich der Prüfungsleistungen für mich ganz oder teilweise erledigt.

[X] Ich habe die Dissertation in dieser oder ähnlicher Form in keinem anderen Prüfungsverfahren als Prüfungsleistung vorgelegt.

[X] Ich habe den angestrebten Doktorgrad noch nicht erworben und bin nicht in einem früheren Promotionsverfahren für den angestrebten Doktorgrad endgültig gescheitert.

Die öffentlich zugängliche Promotionsordnung der TUM ist mir bekannt, insbesondere habe ich die Bedeutung von § 28 (Nichtigkeit der Promotion) und § 29 (Entzug des Doktorgrades) zur Kenntnis genommen. Ich bin mir der Konsequenzen einer falschen Eidesstattlichen Erklärung bewusst.

Mit der Aufnahme meiner personenbezogenen Daten in die Alumni-Datei bei der TUM bin ich

[X] einverstanden, [ ] nicht einverstanden.

....

(Ort, Datum, Unterschrift)

11. Attachment of single publications

Publication 1

Jantsch MC, Fischer A, Fischer HS, Winter S (2013) Shift in plant species composition reveals environmental changes during the last decades: A long-term study in beech (*Fagus sylvatica*) forests in Bavaria, Germany. Folia Geobotanica published online DOI 10.1007/s12224-012-9148-7

Publication 2

Jantsch MC, Fischer HS, Winter S, Fischer A (in editing process) How are plant species in central European beech (*Fagus sylvatica* L.) forests affected by temperature changes? - Shift of potential suitable habitats under global warming. Annali di Botanica

Publication 3

Müller-Kroehling S, Jantsch MC, Fischer HS, Fischer A (resubmitted) Modeling the effects of global warming on the ground beetle fauna of beech forests in Bavaria/Germany. European Journal of Entomology