Implications of Design and Data Quality for the Analysis of a Nationwide Biodiversity Monitoring Scheme

Inauguraldissertation

zur
Erlangung der Würde eines Doktors der Philosophie
vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

von

Matthias Plattner

aus Reigoldswil BL

Basel, 2016

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät

auf Antrag von

Fakultätsverantwortlicher und Dissertationsleiter: Prof. Dr. Andreas Erhardt

Korreferent: Prof. Dr. Bruno Baur

Basel, den 24. Mai 2016

Prof. Dr. Jörg Schibler
Dekan

Contents

1 Summary

Biodiversity monitoring schemes are designed to infer trends in biodiversity over long time periods. The value of a biodiversity monitoring program depends largely on its data quality. High quality data allow to estimate temporal trends without bias and with high precision. Data quality largely depends on the initial design of the monitoring scheme, on properly conducted fieldwork, on various aspects of quality control mechanisms, and on the methods to analyse the data. In my thesis I show and discuss implications of design and data quality presenting five case studies using data from the Swiss Biodiversity Monitoring Scheme (BDM). The BDM is a long-term programme of the Swiss Federal Office for the Environment and was initiated in 2001 to monitor Switzerland’s biodiversity. The programme focuses on changes in species richness and surveys selected species groups in a systematic sampling grid all over the country.

Defined and constant sampling methods are needed to allow for unbiased and precise estimations of biodiversity trends. In **Chapter I,** we analysed inter-observer variation of double-sampled vegetation plots. We could show that both systematic (directed) methodological errors and random variance of species counts were small. We concluded that BDM methods are adequate for detecting biodiversity trends. In the meantime this conclusion has been widely confirmed with recent data from quality control. **Chapter II** focuses on detectability of species that provides the link between a raw species count and true species richness. Variation in detectability between species or habitats may considerably bias trend estimates in biological studies. We therefore asked if capture-recapture methods were suitable to analyse differences in species detectability of butterflies and looked for underlying factors that may cause variation in detectability. Because the methods available at that time were not allowing the analysis of butterfly surveys over the whole season we had to restrict it to three mid-season surveys. We found that average detectability *per count* was 0.61 and was influenced by observer, transect and region. Individual species during one count were detected with a mean probability of 0.50. Since the study has been published in 2007 statistical methods have been substantially developed and nowadays enable detailed analyses of butterfly communities.

In the study in **Chapter III** we demonstrated how data from the systematic BDM surveys could be used in combination with environmental variables. We tested different sets of variables for modelling plant species richness and produced species richness maps for

Switzerland by predicting species richness for each kilometre square. We found that the final models performed similarly well. Average elevation was the best single variable for explaining plant species richness nationwide. Species richness maps typically showed belt-like patterns of highest richness at intermediate altitudes. We discussed different approaches for explaining such “mid-elevational peaks” of species richness.

In the frame of the BDM vascular plants, butterflies and birds are surveyed on the same sites during the same years. These simultaneous studies may be considered as a major advantage of the BDM compared to the monitoring programs in other countries. In the final two chapters we therefore inferred patterns between the species groups. **Chapter IV** is based on data of the first iteration of surveys. We looked at the *changes* that had happened in surveyed species communities of plants, birds and butterflies within the period of 5 years. As a response to climate warming we expected species to shift their distribution towards higher altitudes. We used the “Community Temperature Index” (CTI) to test for differences in reaction to climate change. As expected, in the lowlands birds and butterflies tracked climate warming with an average uphill shift of 42 and 38m respectively, while plants showed a shift of only 8m. At higher elevations there was no significant CTI change in plants and butterflies. In general our results supported the idea that reactions to climate change in alpine landscapes were lowest and alpine landscapes could be safer places because of their highly varied surfaces. In the study in **Chapter V** we examined to what extent distribution patterns of butterfly species are shaped by interactions with their individual host plants or, alternatively, by environmental factors. Our findings indicated that butterfly - host plant interactions were not relevant in benign environments. In contrast, at the cold distribution limits there was a strong coincidence between butterfly and plant ranges. We argued that this could be evidence for butterfly species being limited by the distribution of their host plants in harsh environments and discussed the implications of the findings under climate change conditions.

Finally I summarized the most important results and also included more recent experiences from other studies using BDM data and from unpublished analyses, e.g. from quality control. I concluded in discussing the strength and weaknesses of long-monitoring programmes and pointed out that they should be considered as a complementary data source and reference for experimentally orientated research.

2 General Introduction

In the last decades there has been growing evidence and rising public awareness of the **threats to biodiversity** by human activities. Biodiversity is the diversity of genes, populations, species, and landscapes, and of their interactions (Yoccoz et al., 2001). The importance of biodiversity and the negative impacts of biodiversity loss have been widely approved. Recent public discussion has often focused on benefits of biodiversity and the role of biodiversity for human welfare (De Groot et al. 2002, Maes et al. 2012). Amongst the influencing factors, **climate change** is likely to be a major driver on biodiversity on a global scale (Walther et al. 2002, Araújo and Rahbek 2006). Climate change can re-shape species distributional ranges and alter the composition of species communities (Walther et al. 2005, Parmesan 2006).

In the light of these developments reliable **biodiversity data** are a crucial basis for both effective conservation planning and political communication. In general our knowledge about biodiversity and its patterns increased considerably during the last years. This includes examples like data on species distributions and population sizes. Species inventories and samples of species provide baseline information for the analysis of biodiversity. For most vertebrates, plants, and some insects, networks of dedicated observers exist in many countries and enable large-scale assessments to be conducted at relatively low costs and partly on a volunteer basis (e.g. Oostermeijer and van Swaay 1998, Stefanescu et al. 2004). The value depends largely on the quality of the original data (Kier et al. 2005), the availability of environmental data, and the analytical methods used to combine them. However, there are huge differences in the amount, quality and profoundness of biodiversity information available depending on region, habitat type or taxonomic group.

Biodiversity monitoring schemes are designed to follow the state of biodiversity over a long time period. Schemes with strict methodological prescription and using a defined sampling grid can provide sound data on a regional, national or even continental scale, when data from different schemes are analysed in common (e.g. Inger et al. 2015). Therefore well defined and constant sampling methods are needed to compare data over larger time ranges. The detection of long-term changes is especially challenging, because trends may be small, occur with a delay or overlaying trends are confounded with each other.

Reproducible methods are the basis for high quality data, because they help to reduce, control and quantify ‘noise’ in the data, e.g. caused by imperfect detectability of species (Boulinier et al. 1998, Kéry and Schmid 2004).

2.1 Characteristics of the Swiss Biodiversity Monitoring Scheme

The Swiss Biodiversity Monitoring Programme (BDM) is a long-term monitoring scheme of the Swiss Federal Office for the Environment (FOEN) and was initiated in 2001. It was launched to monitor Switzerland’s biodiversity and to meet the Convention on Biological Diversity of Rio de Janeiro (Hintermann et al. 2000). The programme focuses on changes in species richness of selected taxa, measured at different spatial scales (Weber et al. 2004). In the Swiss BDM, species richness is assessed on two different scales. Biodiversity is represented by the main indicators ‘species diversity in habitats’ (for within-habitat diversity) and by the indicator ‘species diversity in landscapes’ (for within-habitat mosaic diversity) following the definitions of Whittaker et al. (2001). Species richness or the number of species present in a habitat over a certain time period, is the most widely used measure of biodiversity (Hintermann et al. 2000, but see e.g. Balmer 2002). There are a couple of reasons why species richness is used much more frequently than other biodiversity measurements: It is straightforward because species are fairly well-defined when compared with other kinds of diversity, e.g. landscape diversity and species are attractive and comprehensible making the results easy to communicate. Further the survey of most species does not require specialised technical equipment. In the Swiss BDM the following taxonomical groups are surveyed: mosses, vascular plants, molluscs (snails), breeding birds and day-flying butterflies and additionally aquatic invertebrates[1].

Sampling design and quality control

The surveying plots for both main indicators are distributed in a systematic, evenly spaced grid sample across Switzerland. Each year, 20% of sample squares were surveyed constituting a regularly spaced subsample of all sites (BDM Coordination Office 2014). Paired measures of all subsequent samples thus were available after 10 years for the first time. In an optimal case such a design allowed a real random sampling that is unbiased by effects of geographic and habitat properties or observer preferences. But even if the BDM

---

[1] Aquatic invertebrates are collected on a separate sampling grid, consisting of ca. 500 hundred watercourses.

field crew takes great efforts some of the sample plots were too dangerous to do field work because of their exposed alpine terrain. They had to be abolished in the regular scheme and were not substituted by alternative sampling plots. In the frame of the BDM indicators species groups are surveyed on the same sites during the same years. These simultaneous studies may be considered as a major advantage of the BDM compared to the monitoring programs in other countries. Several studies therefore inferred patterns between the species groups (e.g. Pearman and Weber 2007, Concepcion et al. 2015).

Vascular plants, birds and butterflies are assessed on approximately 470 squares of $1km^2$ and provide the data for the **indicator 'species diversity in landscapes'**. The size of the sample has been optimized to allow conclusions not only for Switzerland as a whole but also for five main biogeographic regions (Jura Mountains, Central Plateau, Northern Alps, Central Alps and Southern Alps). The regions of the Jura Mountains and the Southern Alps ("Ticino") were too small and could not be represented sufficiently with the original grid. In these regions therefore the original sampling grid was densified two fold by adding the same number of survey squares in a second grid. For the indicator **'species diversity in habitats'** data on molluscs, mosses and vascular plants are collected on roughly 1550 plots of $10m^2$. Each plot is allocated to a single type of land use or habitat respectively. Standard data analysis then focuses on species richness in main habitat types such as forest, or grassland of various altitudinal stages.

Quality control has to be seen as a comprehensive and long-lasting task. It ranges from first pilot surveys in the stage of method development over the evaluation of fieldworkers up to automated tests of plausibility for incoming data in the running programme. Variation related to the observer and the methods adopted can be controlled to a certain extent by a monitoring programme. Thus the BDM invested significantly in developing and testing appropriate methods and in training a field-crew. After regular fieldwork has started in 2001, the BDM has used approximately 10% of its annual field work budget on quality control. During the phase of method development and incorporation of new species groups into the programme the investment in improving data quality was substantially increased. To test data quality for all indicators and species groups, independent replicate surveys were performed in parts of the routine survey sample. This double sampling approach (Pollock et al. 2002) allows the quantification of inter-observer variation and other important measurements such as species detectability and generally an assessment of the reproducibility of indicator values.

Evaluation of methods

Prior to the start of the scheme a thorough evaluation and development of methods was needed. Method evaluation has to be seen as a learning process that is crucial for the later success of a monitoring scheme. Though for most species groups surveying methods already existed, they often were not optimised for reproducibility and therefore not suitable to monitoring programmes. One main reason was that methods are based solely on expert knowledge and proper description and testing of methods was missing. For some species groups, in particular birds and butterflies, proved and tested monitoring methods existed and were already widely applied (for citations see below). In these cases it was evident to rely on existing methods, not only for saving resources for method development but above all to allow the comparability of data and common analyses over larger regions. Good examples for the strength of pan-European analyses are the Grassland indicator for butterflies (Van Sway et al. 2015) and the Wild Bird Index for Europe (Gregory et al. 2010).

The BDM methods were evaluated and tested for reproducibility and efficiency prior to the initial routine survey in 2001. The methods for plants and molluscs in the indicator “species diversity in habitats” could be adopted from a running scheme in the Canton Argovia (Stapfer 1999) and for birds from the Common Bird Survey of the Swiss Ornithological Institute (Schmid et al. 2004). For butterflies the method of the British Butterfly Monitoring Scheme (Pollard and Yates, 1993) had been modified to meet the needs of the Swiss BDM. The adaptation of the original British transect method was necessary on the one hand to allow surveys in kilometre squares and to account for the different phenologies of species in Switzerland. On the other hand, the original method with about twenty surveys in a season was too costly. Based on intensive field tests we were optimizing the efficiency of the method and ended up with a number of seven surveys per season in the lowlands and four surveys in the higher Alps (Altermatt et al. 2008).

More detailed information about the organisation of the BDM, methodological description and exemplary results is given at www.biodiversitymonitoring.ch.

2.2 Outline of the thesis

In my thesis I will show and discuss implications of design and data quality for the use of biodiversity data coming from a national biodiversity monitoring scheme – the Swiss Biodiversity Monitoring (BDM). In **Chapter I** the importance of data quality to achieve an adequate precision for detecting changes in plant species richness is addressed. On the one hand, it is important that results of species counts are un-biased. We therefore examined systematic (directed) methodological errors caused by the observers. On the other hand, the undirected ("random") deviation must be addressed as well. Deviation can be seen as statistical noise that makes differences and changes more difficult to detect. So we examined the reproducibility of the measurements of species richness using the BDM methodology and estimated how precisely changes in species numbers could be predicted. For the analysis we used standard deviations of species counts from double sampling surveys to account for the variability between observers. With given BDM sample sizes the minimum detectable difference (Zar 1984) has been calculated for exemplary habitat types and biogeographic regions. Then differences were used to evaluate if BDM methods are sufficiently accurate to detect possible future changes in the state and trends of species numbers of vascular plants.

Chapter II focuses on detectability of species, linking between raw species counts and true species richness. Imperfect detectability can be caused by properties of the observer, the environment and the species itself (Buckland et al. 1993). Nevertheless, most monitoring programmes make the implicit assumption that all species are detected (detectability "p" equals 1) or that the expected proportion of species detected does not vary over dimensions of interest such as time, space or habitat (Boulinier et al. 1998). To learn more about the dimensions of species detectability in butterfly monitoring schemes we analysed BDM species counts from double samplings. Capture-recapture methods use the observed pattern of detection/non-detection among those species detected during repeated samples to infer the number of species that do not appear in those samples (Burnham and Overton 1979). We examined under what assumptions currently available capture - recapture models could be used to estimate species richness. We estimated both the total number of species during the BDM surveys as well as species detectability. Species detectability was already shown to vary by species, observer, region, year and season (Selmi and Boulinier, 2003, Kéry and Schmid 2006, Chen et al. 2013). We therefore integrated factors such as species, abundance, observer and biogeographic regions to identify influencing factors.

In the study in **Chapter III** we demonstrated how data from the systematic BDM surveys could be modelled in combination with environmental factors to predict fine-scale patterns of species richness and produce species richness maps for Switzerland. Model predictions and richness maps may not only add insight to general diversity patterns (Currie et al. 2004, Pimm and Brown 2004), but provide an appropriate basis for local and regional conservation planning (Ferrier et al. 2002). For predicting species richness over large areas information of environmental factors and the corresponding species richness are needed. The quality and the interpretability of models depend on the selection of variables and the predictor variables may not be evenly distributed over Switzerland. This lead us to base the study on three different sets of variables: land cover, environmental factors, e.g. climate and substrate, and topography. Former studies have shown that in regions with a limited altitudinal range, land use usually accounts for a high percentage of the variation in species richness (Heikkinen et al. 2004). This probably would be the case for the Swiss plateau. In contrast, in mountainous regions like the Alps, variations in radiation, temperature or other climate parameters and substrate play an important role (Grytnes et al. 1999, Wohlgemuth 2002, Moser et al. 2005). Topographical variables such as altitude or slope are known to be good proxies for some of the above mentioned parameters (Vetaas and Grytnes 2002). We correlated species numbers of vascular plants from the 1km^2 sampling squares of the indicator “species richness in landscapes” with the three sets of variables using generalized linear models (GLM). A fourth “synthetic model” was based on a combination of the best fitting variables from the three models. Finally we produced species richness maps for Switzerland by predicting species richness for each kilometre square.

All analyses in the former studies were based on data from regular or double surveys of the initial BDM phase describing the *state of species richness*. **Chapter IV** is based on data of the first iteration of surveys. Therefore we were able to look at the *changes* that had happened on the 1km^2 survey squares within the period of 5 years between the first and the second survey. As a response to climate warming we would expect that species shift their distribution towards higher latitudes or altitudes (Hickling et al. 2006, Gottfried et al. 2012). Some authors pointed out that alpine ecosystems are particularly threatened by climate warming (e.g. Franzen and Molander 2012), because a significant upward shift could lead to decreasing species ranges. Other studies proposed that the velocity of temperature change is lowest in alpine landscapes (Loarie et al. 2009) and alpine plant species could find suitable habitats within just a few metres because of the highly varied surface of alpine landscapes, creating thermal mosaics (Scherrer and Körner 2011). Switzerland is especially suitable as an exemplary object of investigation on altitudinal shifts because it has a large gradient ranging from 193 to 4634 m. Moreover, the BDM indicator "species richness in landscapes" provides data for plants, birds and butterflies that were sampled on the same squares in the same years. Due to different traits, e.g. differences in mobility, we expected taxonomic groups to differ in the rates they were tracking climate change. To test for differences in reaction to climate change we used the newly developed metrics "Species Temperature Index" (STI) and "Community Temperature Index" (CTI). For the STI, each species is given an indicator value reflecting its temperature niche. While for birds and butterflies we could rely on existing STI data from other European studies (Devictor et al. 2008, Schweiger et al. 2014), for plants we used Ellenberg temperature values (Landolt et al. 2010). To describe the CTI of a single survey square the mean of the individual STI from all species therein recorded were used. We analysed the temporal change in CTI for each sample square and each species group and standardized the values to compare between groups. To test whether standardized local changes in community average depended on altitude, we used linear mixed models and finally, to obtain p-values and confidence intervals for model predictions, we used bootstrap methods.

Another challenge is to include biotic interactions in model predictions of species distributions (Kissling et al. 2012), e.g. to asses the consequences of climate change. In the study in **Chapter V** we examined to what extent distribution patterns of butterfly species are shaped by interaction with their individual host plants or, alternatively, by environmental factors. The stress gradient hypothesis predicts that under physiologically stressful environmental conditions, e.g. at higher altitudes, abiotic factors shape range edges while in less stressful environments, e.g. at lower altitudes, negative biotic interactions, particularly competition, are more important (Bertness and Callaway 1994). We modelled the distribution of single species of butterflies and plants separately with species distribution models (SDMs) by correlating species presence/absence data in BDM samples with independent sets of variables. For species models we extracted variables that are ecologically relevant. We ended up with a set of environmental variables that were similar to those we used for modelling species richness distributions in Chapter III. We performed principal components analysis (PCA) on the environmental variables across all grid cells and found that the main environmental gradient strongly resembled the altitudinal gradient. The correlation between the modelled distribution of a given butterfly species and the modelled distribution of its host plant(s) was estimated using the relative proportion of modelled presences and absences along this main environmental gradient. The distribution of hosts and butterflies were plotted and the agreement of both distributional ranges at the upper and the lower limits of the gradient were checked visually. Cases in which modelled butterfly and plant distributions had joint limits or in which butterfly ranges even exceeded their host plant range, could be evidence for host-plant limitation of the butterfly species.

In the **General Discussion** I will consider current data analyses based on these experiences and highlight promising approaches for a better understanding of biodiversity patterns, changes of species richness and underlying processes in the future.

2.3 References

Altermatt, F., Birrer, S., Plattner, M., Ramseier, P., & Stalling, T., 2008: Erste Resultate zu den Tagfaltern im Biodiversitätsmonitoring Schweiz. Entomo Helvetica 1: 75-83.

Araújo, M. B., & Rahbek, C., 2006. How does climate change affect biodiversity? Science 313: 1396–1397.

Balmer, O., 2002. Species lists in ecology and conservation: abundances matter. Conservation Biology, 16(4), 1160-1161.

BDM Coordination Office 2014. Swiss Biodiversity Monitoring BDM. Description of Methods and Indicators. Federal Office for the Environment, Bern. Environmental studies no. 1410. 103 pp.

Bertness, M. D., & Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9: 191–193.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., & Pollock, K.H., 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology,79, 1018–1028.

Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J.L., 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London.

Burnham, K. P., & Overton, W.S., 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology, 60, 927–936.

Chen, G., Kéry, M., Plattner, M., Ma, K., Gardner, B., 2012: Imperfect detection is the rule rather than the exception in plant distribution studies. Journal of Ecology 101: 183–191.

Concepcion, E.D., Obrist, M.K., Moretti, M., Altermatt, F., Baur, B., & Nobis, M.P., 2015a. Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. Urban Ecosyst: DOI 10.1007/s11252-015-0474-4.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Turner, J.R.G., et al., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters, 7, 1121–1134.

Daleo, P., & Iribarne, O., 2009. Beyond competition: the stress-gradient hypothesis tested in plant-herbivore interactions. Ecology, 90(9), 2368-2374.

De Groot, R. S., Wilson, M. A., & Boumans, R. M., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecological economics, 41(3), 393-408.

Devictor, V., Julliard, R., Couvet, D., & Jiguet, F., 2008. Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B-Biological Sciences 275: 2743–2748.

Ferrier, S., Powell, G.V.N., Richardson, K.S., Manion, Van Rompaey, R., et al., 2004. Mapping more of terrestrial biodiversity for global conservation assessment. BioScience, 54, 1101–1109.

Franzen, M., & Molander, M., 2012. How threatened are alpine environments? A cross taxonomic study. Biodiversity and Conservation 21: 517–526.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barancok, P., et al., 2012. Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2: 111–115.

Gregory, R.D., & Strien, A.V., 2010. Wild bird indicators: using composite population trends of birds as measures of environmental health. Ornithological Science, 9(1), 3-22.

Grytnes, J.A., Birks, H.J.B., & Peglar, S.M., 1999. Plant species richness in Fennoscandia: evaluating the relative importance of climate and history. Nordic Journal of Botany, 19, 489–503.

Heikkinen, R.K., Luoto, M., Virkkala, R. & Rainio, K., 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural–forest mosaic. Journal of Applied Ecology, 41, 824–835.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global change biology, 12(3), 450-455.

Hintermann, U., Weber, D., & Zangger, A., 2000. Biodiversity monitoring in Switzerland. Schriftenreihe Landschaftspflege Naturschutz 62: 47–58.

Inger, R., Gregory, R., Duffy, J.P., Stott, I., Voříšek, P., & Gaston, K J., 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology letters, 18(1), 28-36.

Kéry , M., & Schmid, H., 2004. Monitoring programs need to take into account imperfect species detectability. Basic and Applied Ecology, 5, 65–73.

Kéry, M., & Schmid, H., 2006. Estimating species richness: calibrating a large avian monitoring programme. Journal of Applied Ecology 43: 101-110.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Kuper, W., Kreft, H., & Barthlott, W., 2005. Global patterns of plant diversity and floristic knowledge. Journal of Biogeography, 32, 1107–1116.

Kissling, W. D., Dormann, C. F., Groeneveld, J., Hickler, T., Singer, A., et al., 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography, 39(12), 2163-2178.

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., et al., 2010. Flora Indicativa, Ecological Indicator Values and Biological Attributes of the Flora of Switzerland and the Alps. Bern: Haupt-Verlag.

Loarie, S.R., Duffy P.B., Hamilton H., Asner G.P., Field C.B., et al., 2009. The velocity of climate change. Nature 462: 1052–1055.

Maes, J., Egoh, B., Willemen, L., Liquete, C., Bouraoui, F., et al. 2012. Mapping ecosystem services for policy support and decision making in the European Union. Ecosystem Services, 1(1), 31-39.

Moser, D., Dullinger, S., Englisch, T., Niklfeld, H., Grabherr, G., et al., 2005. Environmental determinants of vascular plant species richness in the Austrian Alps. Journal of Biogeography, 32, 1117–1127.

Oostermeijer, J.G.B., & van Swaay, C.A.M., 1998. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. Biological Conservation, 86, 271–280.

Parmesan, C. , 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37: 637–669.

Pateman, R. M., Hill, J. K., Roy, D. B., Fox, R., & Thomas, C. D., 2012. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. – Science 336: 1028–1030.

Pearman, P. B., & Weber, D., 2007. Common species determine richness patterns in biodiversity indicator taxa. Biological conservation, 138(1), 109-119.

Pimm, S.L., & Brown, J.H., 2004. Domains of diversity. Science, 304, 831–833.

Pollard, E., & Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation. Chapman & Hall, London.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L., & Sauer, J.R., 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics, 13, 105–119.

Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography 38: 406–416.

Schmid, H., Zbinden, N., & Keller, V., 2004. Überwachung der Bestandsentwicklung häufiger Brutvögel in der Schweiz. Schweizerische Vogelwarte, Sempach.

Schweiger, O., Heikkinen, R. K., Harpke, A., Hickler, T., Settele, J., et al., 2012. Increasing range mismatching of interacting species under global change is related to their ecological characteristics. Global Ecology and Biogeography, 21(1), 88-99.

Schweiger, O., Harpke, A., Wiemers, M., & Settele, J., 2014. CLIMBER: Climatic niche characteristics of the butterflies in Europe. ZooKeys, 367, 65.

Selmi , S., & Boulinier, T., 2003. Does time of season influence bird species number determined from point-count data? A capture – recapture approach . Journal of Field Ornithology, 74, 349–356.

Stapfer, A. 1999. Volkszählung in der Aargauischen Natur? Umwelt Aargau 6:5-60.

Stefanescu, C., Herrando, S., & Paramo, F., 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. Journal of Biogeography, 31, 905 – 915.

Van Swaay, C.A.M., Van Strien, A.J., Aghababyan, K., Åström, S., Warren, M. et al., 2015. The European Butterfly Indicator for Grassland species 1990-2013. Report VS2015.009, De Vlinderstichting, Wageningen.

Vetaas, O.R., & Grytnes, J.A., 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology and Biogeography, 11, 291–301.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C. et al., 2002. Ecological responses to recent climate change. Nature 416: 389–395.

Walther, G.R., Beissner, S., & Burga C.A., 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science 16: 541–548.

Weber, D., Hintermann, U., & Zangger, A., 2004. Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. Global Ecology and Biogeography, 13, 97–104.

Whittaker, R. J., Willis, K. J., & Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28(4), 453-470.

Wohlgemuth, T., 2002. Environmental determinants of vascular plant species richness in the Swiss Alpine zone. Mountain biodiversity: a global assessment (ed. by C. Körner and E.M. Spehn), pp. 103–116. Parthenon Publishing Group, Boca Raton.

Yoccoz, N.G., Nichols, J.D., & Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution, 16, 446–453.

Zar, H.J., 1984. Biostatistical Analysis. Prentice-Hall, New Jersey.

3 Chapter I: Data quality in monitoring plant species richness in Switzerland

COMMUNITY ECOLOGY 5(1): 135-143, 2004
1585-8553 © Akadémiai Kiadó, Budapest

Data quality in monitoring plant species richness in Switzerland

M. Plattner[1], S. Birrer and D. Weber

Hintermann & Weber AG, Ecological Consultancy, Planning & Research, Hauptstrasse 52, CH-4153 Reinach BL, Switzerland. Fax: +41 61 717 88 89
[1] Corresponding author. E-mail: plattner@hintermannweber.ch

Keywords: Baseline monitoring, Biodiversity, Data quality, Field methods, Reproducibility, Species richness, Switzerland, Vascular plants.

Abstract: The on-going Biodiversity Monitoring in Switzerland Programme (BDM) has monitored vascular-plant species richness since 2001. This long-term programme focuses on two indicators at different spatial scales. First, the local diversity indicator monitors changes of species richness within habitats or types of land use (within-habitat diversity). Second, the landscape diversity indicator is utilized to describe landscape diversity (i.e., within-habitat mosaic diversity). Here we examine if the reproducibility of the BDM methods is sufficiently precise to detect future changes in species richness. We demonstrate that systematic methodical errors are negligible. Random errors that make changes more difficult to detect are also small. We calculate the Minimum Detectable Difference (MDD) for selected BDM strata using the variance of measured values. Then we deduce the MDD values for paired samples using data from grasslands and forests in the Canton Argovia. With 2.4 and 1.6 species they are promisingly precise. We develop a simple scenario for possible changes in species richness and show that they surpass the deduced MDD values by a factor four to six. We conclude that the BDM methods are appropriate for detecting future changes in species richness.

Abbreviations: BDM – Biodiversity Monitoring in Switzerland Programme; SD – standard deviation; MDD – minimum detectable difference; SAEFL– Swiss Agency for the Environment, Forests and Landscape; Z9 – local diversity indicator; Z7 – landscape diversity indicator.

Introduction

The *Biodiversity Monitoring in Switzerland Programme* (BDM) is a long-term monitoring programme of the Swiss Agency for the Environment, Forests and Landscape (SAEFL) which monitors vascular-plant species richness over time. This on-going monitoring, initiated in 2001, focuses on changes in species richness of selected taxa (Hintermann et al. 2000) and at different spatial scales (Weber et al. 2004). Of central importance to the programme is species richness on a local scale (i.e., within-habitat diversity) and on a landscape scale (i.e., within-habitat mosaic diversity) following the definitions of Whittaker et al. (2001). Because local diversity is strongly influenced by land-use, the local diversity indicator (mean species richness on 10 m^2, Z9) is suitable to describe changes in species richness within different types of land-use in the cultural landscape. The landscape diversity indicator (mean species richness on 1 km^2, Z7) measures landscape diversity, which is the result of heterogeneity within patches, within habitat types (i.e., types of land-use), and between types of the land-use as shown, for example, by Wagner et al. (2000), Whittaker et al. (2001) and Zechmeister and Moser (2001). In addition to vascular plants, other taxa are surveyed (e.g., snails, butterflies). For details see the Interim Report on the BDM by Hintermann et al. (2002)[1].

Because a long-term monitoring programme such as the BDM must guarantee data set comparability when data are separated by large spans of time, highly reproducible methods are needed to reduce, control and quantify imperfect detectability of species (Anderson 2001, Boulinier et al. 1998, Pollock et al. 2002, Yoccoz et al. 2001, Kéry and Schmid 2004). Species detectability is the crucial variable influencing reproducibility of Z7 and Z9. It is affected by three classes of variables (Buckland et al. 1993): (1) variables related to the observer, (2) variables related to the environment and (3) variables related to the species. The species and their properties might stay the same across years, as also environmental properties, but the observers will change over time. It is therefore important to know, to what extent species detectability is influenced by the observer. The BDM therefore invests significantly in developing and testing appropriate methods.

---

[1] Further information on the BDM and actual datasets you will find under www.biodiversitymonitoring.ch.

Table 1. Summary of the BDM methodological characteristics for measuring vascular plant species richness.

Name Definitions follow Whittaker et al. 2001.	**Local diversity indicator Z9** Within-habitat diversity	**Landscape diversity indicator Z7** Within-habitat mosaic diversity
Methodological characteristic		
Sampling grid	Systematic, symmetrical	Systematic, symmetrical
Number of sampling units	1600	520
Sampling interval	Staggered survey over 5 years (each year a fifth of the entire sample)	Staggered survey over 5 years (each year a fifth of the entire sample)
Area surveyed per sampling unit	10m^2	12‘500m^2
Shape of sampling units	Circle	Transect of 2,500m, 5m wide, along paths and streets in a 1x1km grid unit
Locating sampling areas	Differential GPS (real-time)	Map 1: 25,000
Marking of sampling areas	With a buried magnet and 3 above-ground surveyed colour markings	None, (in some cases colour markings)
Relocation of sampling areas	Magnetic detector, report	Map 1: 25,000
Sampling frequency	Every plot is visited once in the alpine and subalpine zone and twice a year at lower elevations; zones following *Wärmegliederung der Schweiz* (Schreiber et al. 1977).	Every transect is visited once in the alpine zone and twice a year at lower elevations; zones following *Wärmegliederung der Schweiz* (Schreiber et al. 1977).
Type of records	Presence/absence	Presence/absence
Recorded species	Vascular plant species. Some subspecies and microspecies are summarized in aggregations. Currently 3041 taxa (including all 216 aggregations).	Vascular plant species (same as for Z9) exept planted or sewed species on private properties, parks or other settlements.
Strata for routine interpretation	Routine interpretation of 10 types of land use (habitats): colline, montane and subalpine grassland; colline, montane and subalpine forest; arable land; settlements; alpine meadows; alpine vegetation. Other strata are possible.	6 main biogeographic regions of Switzerland (Gonseth et al. 2001; Fig. 1.) Other strata are possible.
Additional taxa recorded	Mosses, snails.	Breeding birds, butterflies.
Percentage of field budget for quality control	Approximately 10 % of costs for field work	Approximately 10 % of costs for field work

Furthermore, data quality is examined continuously by methods which are detailed below.

The research presented here aims to test whether the BMD methodology is appropriate for detecting future changes in species richness. We analyze data from the ongoing survey, its quality control and some results of methodological tests. For both of the indicators Z9 and Z7 we examine the following questions:

- How reproducible are our species richness measurements?
- How precisely can changes in species richness be predicted?
- To what extent could mean species richness possibly change in the future?

Methods

Measuring changes in plant species richness

Since 2001 the BDM has routinely assessed vascular plant species richness on fixed surveying areas which are distributed systematically over Switzerland. The survey is staggered: each year one fifth of the entire sample for Z7 and Z9 is surveyed. Thus on the sixth year (2006) the first fifth of the areas will be re-assessed. Paired measures for all sampling units will be available after 10 years (2011).

Table 1 provides an overview of the most important methodological characteristics for Z9 and Z7. For more detailed information, see Hintermann et al. 2002.

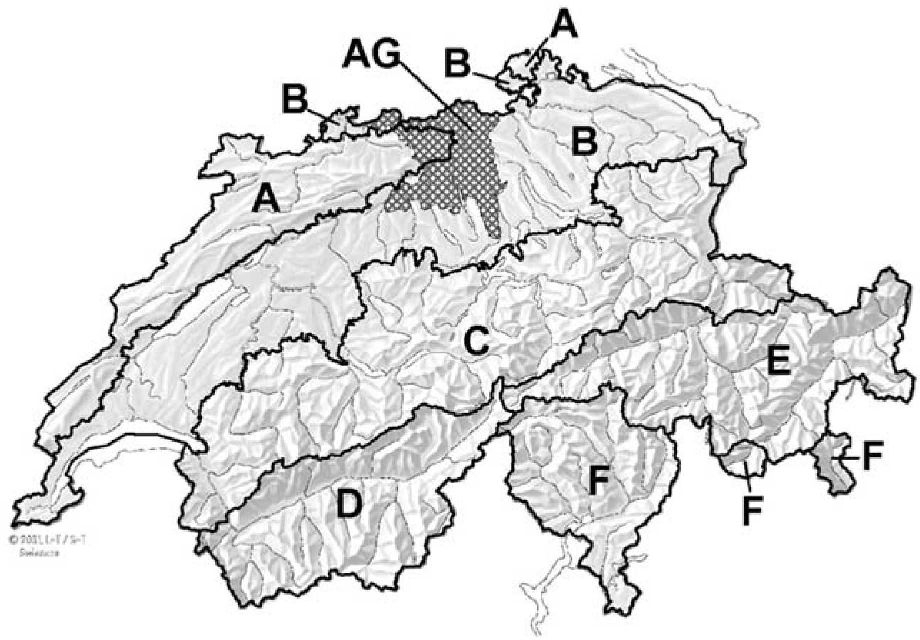


Figure 1. Study area. AG: Canton Argovia. The biogeographic regions of Switzerland (Gonseth et al. 2001) A: Jura, B: Central Plateau, C: Northern Alps, D: Western Central Alps, E: Eastern Central Alps, F: Southern Alps.

A fundamental methodological difference between Z7 and Z9 lies in the size and shape of the sampling plot. For Z9, the species richness in small circles of 10 m^2 is recorded. The exact centers of the circles that are defined by their coordinates are precisely located with a differential GPS. After the assessement, they are allocated to a single type of land use or habitat respectively. The landscape indicator Z7 is assessed along a 2.5 km transect with a total of 12,500 m^2 area. It represents a 1 km^2 grid unit with several different types of land use and habitats.

Evaluation of methods

Prior to the initial routine survey in 2001, methods were evaluated and tested for reproducibility and efficiency. Similar field data were previously assessed in the Canton Argovia (Fig. 1). Beginning in 1996, the Argovian survey consists of 517 Z9-sampling areas monitored with the same methods as the BDM (Weber 2002)[2]. A total of 73 paired measures were used to analyze the effects of paired samples (see below).

Routine survey

In 2001 and 2002, 13 botanists collected data from 493 Z9-sampling plots. The Z9 data are routinely interpreted for 10 types of land use (habitats) further differentiated by elevation. For Z7 in 2001 and 2002, a total of 184 transects were surveyed by 14 botanists. The Z7 data are routinely interpreted for the 6 main biogeographic regions of Switzerland (Gonseth et al. 2001, Fig. 1). In the Jura region and the Southern Alps, the sample size was doubled to allow more precise statements on the changes in species richness in these small regions.

Reproducibility of BDM-methods

The BDM invests approximately 10% of its annual field work budget on quality control. To test data quality, independent replicate surveys were performed on a part of the routine survey sample by 2 botanists who were not involved in the regular BDM survey. The regular BDM botanist team was unaware of which sample areas were replicated. This double sampling approach (Thompson et al. 1998, Pollock et al. 2002) allows not only a quantification of species detectability, but also of the reproducibility of Z7 and Z9 values.

Reproducibility is defined here as precision following Zar (1984). It is expressed by three indicators: (1) the difference of mean species richness between routine and control, (2) the mean of the absolute differences of species richness between routine and control and (3) the standard deviation (SD) of the differences of species richness be-

---

[2] See also www.ag.ch/natur2001/alg/pages/natur/programme/mehrjahresprogramm/kontrollprogramm/LANAG.

Table 2. Results of 28 replicated sample plots from the Canton Argovia survey.

	Species
Mean species richness on 10 m^2, Botanist A	**18.2**
Mean species richness on 10 m^2, Botanist B	**18.1**
Difference of mean species richness (Botanist A - Botanist B)	**0.1**
Mean of the absolute differences of species richness between botanists A and B	**2.5**
SD of the relative differences of species richness between botanists A and B	**3.3**

Table 3. Results from 23 replicated BDM transects.

	Species
Mean species richness on 2'500 x 5 m, routine survey	**250.1**
Mean species richness on 2'500 x 5 m, control	**255.1**
Difference of mean species richness (Control - Routine)	**5.0**
Mean of the absolute differences of species richness between routine and control	**19.7**
SD of the relative differences of species richness between routine and control	**23.4**

tween routine and control. These indicators express different sources of data variability such as bias between observers (indicator 1) or random variability (indicators 2 and 3). To distinguish different kinds of random variability (e.g., data vs. random observer variability) further analysis would be necessary.

Local diversity indicator. In 2001 and 2002 the methods used in the BDM replicate collections for Z9 differed slightly from those used in the routine collection. The data were therefore inappropriate for determining methodological reproducibility. Instead, data originating from the Canton Argovia survey (see above) were used. In the Canton Argovia in the years 1997, 1999 and 2000, 28 sample plots were re-assessed by a second botanist one or two days after the regular assessement.

Landscape diversity indicator. In 2001 and 2002, the BDM performed an independent control survey on 23 transects with indicator Z7 using the same methods as the routine survey.

Precision at detecting changes in species richness

Assuming a *t*-distribution, the precision in detecting changes in species richness using the *minimum detectable difference* (MDD) was determined by the following equation (Zar 1984, p. 111):

$$\delta = [\,(s^2/n)\,]^{0.5} * (t_{\alpha(2),n} + t_{\beta(1),n}) \tag{1}$$

δ: minimum detectable difference,

s^2: variance of measured values,

n: sample size,

t: critical value of the t-distribution,

α: probability of committing a Type I error, and

β: probability of committing a Type II error.

Let $\alpha = 0.05$ and $\beta = 0.10$.

For some of the strata that were routinely analyzed for Z9 and Z7, we calculated the MDD values. We set the variance of species richness values as s^2, assuming that the variance of changes in species richness over time never surpasses spatial variance. To estimate s^2 for the entire sample, we used the values of the subsamples from 2001 and 2002.

For the paired measures from Canton Argovia, Equation (2) was used as follows (Zar 1984, p. 153):

$$\delta = [\,(s_D{}^2/n)\,]^{0.5} * (t_{\alpha(2),n} + t_{\beta(1),n}) \tag{2}$$

$s_D{}^2$: variance of pairwise differences.

Comparing MDD values with possible changes in species richness

To determine if the calculated MDD values will be useful in detecting future changes in species richness, we contrived the following scenario for demonstrating possible changes in species richness: We assumed the vegetation on an average sample plot is drifting to species poor or species rich condition. Species richness of the 'poor' vegetation was defined as the mean for the third of samples with the lowest species richness and 'rich' vegetation by the mean value for the third of samples with the highest species richness.

We used species richness data from the BDM 2001 and 2002 survey for *montane grassland* (indicator Z9) and the *Central Plateau* (indicator Z7). For both strata, we calculated the mean of all sample areas, the mean for the

Table 4. Means and SD of species richness of BDM Z9 plots and calculation of the MDD for the entire BDM sample using Equation (1) (n= sample size).

Habitat type and elevations	n (2001-2002)	Mean species richness (2001-2002)	SD (2001-2002)	n (entire sample)	MDD (entire sample)
Forest all elevations	163	19.7	10.7	420	1.7
Subalpine forest	45	23.4	11.8	115	3.6
Montane forest	94	18.1	9.8	240	2.1
Colline forest	24	18.3	9.8	65	4.0
Grassland all elevations	120	36.6	15.7	316	2.9
Subalpine grassland	40	47.8	16.7	105	5.3
Montane grassland	63	31.7	13.8	163	3.5
Colline grassland	17	28.7	12.6	48	6.0

Table 5. Means and SD of species richness of BDM Z7 transects and calculation of the MDD for the entire BDM sample using Equation (1) (n= sample size).

Biogeographical regions	n (2001-2002)	Mean species richness (2001-2002)	SD (2001-2002)	n (entire sample)	MDD (entire sample)
Switzerland	153	223	73.9	383	12.3
Jura*	16 (31*)	242	30.5	39 (78*)	11.3
Central Plateau**	39	220	32.2	98	10.6
Northern Alps	49	250	65.4	123	19.3
Western Central Alps	14	207	82.8	35	46.7
Eastern Central Alps	22	195	89.2	55	39.7
Southern Alps*	13 (27*)	221	97.0	33 (68*)	38.7

*** region is sampled with doubled density**

**** only 1km^2 grid units with <50% water surface**

third of samples with the lowest species richness and the mean for the third of samples with the highest species richness. We compared the differences between the three mean values to the calculated MDD values to assess the utility of our survey techniques in detecting future changes in species richness.

Results

Reproducibility of data

Although there are considerable differences in the values produced for single plots, resulting mean species richness values were very similar for the local diversity indicator Z9 in the Canton Argovia survey (Table 2). The same statement can be made on the landscape diversity indicator Z7 in the replicated BDM transects (Table 3).

Distribution of values and precision

There are not yet paired measures for the BDM programme. Therefore, the BDM estimated the precision in detecting changes in species richness using the variance, or the SD, of species richness.

In the local diversity indicator, the SD of the stated species richness values for grassland (meadows and pastures) was higher than the forest samples (Table 4). The precision in detecting future changes in species richness (MDD) was calculated using Equation (1).

In the landscape diversity indicator, a high degree of variability was found for the SD of the stated species richness values between biogeographic regions (**Table 5**). The MDD values using Equation (1) ranged from 10.6 species for the Central Plateau to 46.7 species for the Western Central Alps.

The effect of paired samples

From the Z9 survey in the Canton Argovia, there were paired measures for 73 sample areas in grasslands and forests. We used these data to demonstrate the effect of paired samples on the MDD. First, we calculated the MDD using the SD of species richness analogous to Tables 4 and 5 (Table 6.a). By calculating the MDD with the differences of species richness of the paired measures using Equation (2), the variance in the actual data set was

Table 6. **a**. Unpaired Samples: Means, SD and variances of species richness of Z9 plots collected and re-collected in the Canton Argovia. Calculation of the MDD for the entire sample using Equation (1). **b.** Paired Samples: Means, SD and variances of differences of species richness of Z9 plots collected and re-collected in the Canton Argovia. Calculation of the MDD for the entire sample using Equation (2). n= sample size.

a

Habitat type	Year of collection	n (sub-sample)	Mean species richness	SD (sub-sample)	Variance (subsample)	n (entire sample)	MDD (entire sample)
Forest	1996-1997	37	13.5	7.2	52.3	93	2.4
Forest	2001-2002	37	14.7	7.3	53.4	93	2.4
Grassland	1996-1997	36	21.5	8.3	69.1	90	2.8
Grassland	2001-2002	36	23.4	10.2	104.7	90	3.4

b

habitat type	Years of collection	n (sub-sample)	Mean Δ of species richness	SD (sub-sample)	Variance (subsample)	n (entire sample)	MDD (entire sample)
Forest	96/97-01/02	37	1.1	4.9	24.0	93	1.6
Grassland	96/97-01/02	36	1.9	7.1	51.0	90	2.4

Table 7. Means and SD of species richness of BDM Z9 plots and Z7 transects. Calculation of the MDD for the entire BDM sample, assuming that the variances were halved by the effect of paired samples, using Equation (2) (n= sample size). **a.** Local diversity indicator (Z9). **b.** Landscape diversity indicator (Z7).

a

Habitat type and elevations	n (2001-2002)	Mean species richness (2001-2002)	SD (2001-2002)	n (entire sample)	MDD (entire sample)
Forest all elevations	163	19.7	7.6	420	1.2
Subalpine forest	45	23.4	8.4	115	2.6
Montane forest	94	18.1	6.9	240	1.5
Colline forest	24	18.3	6.9	65	2.8
Grassland all elevations	120	36.6	11.1	316	2.0
Subalpine grassland	40	47.8	11.8	105	3.8
Montane grassland	63	31.7	9.7	163	2.5
Colline grassland	17	28.7	8.9	48	4.2

b

Biogeographical regions	n (2001-2002)	Mean species richness (2001-2002)	SD (2001-2002)	n (entire sample)	MDD (entire sample)
Switzerland	153	223	52.3	383	8.7
Jura*	16 (31)	242	21.6	39 (78)	8.0
Central Plateau**	39	220	22.8	98	7.5
Northern Alps	49	250	46.2	123	13.6
Western Central Alps	14	207	58.5	35	33.0
Eastern Central Alps	22	195	63.1	55	28.1
Southern Alps*	13 (27)	221	68.6	33 (68)	27.4

* region is sampled with doubled density

** only 1km^2 grid units with <50% water surface

Table 8. Species richness of vascular plants from the BDM survey in 2001 and 2002. (n: number of sample areas, min: minimum value, max: maximum value, mean low 1/3: mean of the third of sample areas with the lowest species richness/ 'poor vegetation', mean high 1/3: mean of the third of sample areas with the highest species richness/ 'rich vegetation'). **a.** Local diversity indicator (Z9); 10 m^2 plots. **b.** Landscape diversity indicator (Z7); 12,500 m^2 transects.

a

Habitat type and elevation	n	Species richness min	Species richness max	Species richness mean low 1/3	Species richness mean all	Species richness mean high 1/3
montane grassland	62	11	75	18.6	31.7	49.1

b

Biogeographical region	n	Species richness min	Species richness max	Species richness mean low 1/3	Species richness mean all	Species richness mean high 1/3
Central Plateau	39	155	290	184.7	220.2	255.7

considerably smaller. Reductions of the MDD by almost one species resulted (Table 6.b).

Table 7 shows modifications of Tables 4 and 5. We assumed that for BDM strata the variances were halved by the effect of paired samples. This resulted in a reduction of the MDD from 0.5 to 1.8 species (Table 7.a) for the shown Z9 strata. For Z7 strata the MDD was reduced by 3.1 up to 13.7 species (Table 7.b).

Species richness from the BDM survey 2001/02

To determine if the calculated MDD values will be useful in detecting future changes in species richness, we defined 'poor' and 'rich' vegetation. Table 8 shows species richness values of the routinely analyzed strata montane grassland (Table 8.a) and Central Plateau (Table 8.b).

Discussion

Reproducibility of species richness

For routine and control collections of the local diversity indicator Z9, we achieved a nearly identical mean of the species richness of 18.2 species (regular) and 18.1 species (control). Similarly, for the landscape indicator Z7, the difference of the means of the species richness was only 5 species with a mean of species richness of more than 250 species. This indicates the stated differences –that must be understood as methodical errors– were nearly random (neither control nor regularly team worked better on an average). Although the methods do not allow a one hundred percent species detectability, detectability seems more influenced by random environmental and species-specific phenomena than by the observer.

When discussing reproducibility, it is important to address random deviation of differences. Deviation can be seen as statistical noise that makes changes more difficult to detect. The SD of the differences of species richness was 3.3 species for Z9 and 23.4 species for Z7 (Tables 2 and 3). By comparing these to the SD values of the analyzed strata for Z9 and Z7 (Tables 4 and 5), we observed that the former are much smaller than the latter, which is a basic requirement for methodological reproducibility.

The BMD focuses on detecting changes in species richness. For Z9, we compared the difference of mean species richness (Table 2) to the mean difference of changes in species richness in the Argovian survey (Table 6). The difference of the mean species richness values achieved in the replicate collections were lower by a factor of ten than the changes in species richness observed in the Argovian survey between 1996/97 and 2001/02. If these changes can be confirmed in 2005 when paired measures for the entire Argovian sample are available, some relevant changes in biodiversity can be demonstrated at a highly significant level. To what extent such statements will be possible for BDM Z9 data or even for Z7 (because of a lack of data) cannot yet be tested.

Detecting changes in mean species richness

We also would like to discuss how precisely the BDM will be able detect future changes in mean species richness. The MDD for some selected Z9 and Z7 strata was calculated (Tables 4 and 5). The MDD determines the minimum size of changes that can be detected for a given variance and sample size. The BDM has yet to obtain paired measures. Alternatively, we used the variance of species richness from the 2001/2002 BDM subsample for the calculation (Equation 1). Some of the MDD values are encouragingly precise, but for some of the strata the values are only within reach by large, improbable changes in richness. It has to be noted that these are strata with a naturally high degree of spatial heterogeneity with regards to species richness, such as the alpine regions for Z7. Here the gain of precision by using paired measures will be particularly above average as we will demonstrate in the following section.

The advantage of paired samples

Analysis of the Argovian data showed that the variances of differences of species richness of paired samples (Table 6.b, Equation 2) were only half of the species richness variances (Table 6.a, Equation 1). We postulate that when examining future changes in the whole of Switzerland the effects of paired samples will be even greater, because the Argovian data originate from a small, relatively homogeneous region. The benefit of analyzing paired samples increases with the spatial heterogeneity of species richness in a stratum because the MDD value is calculated by the differences of the pair-wise measures (Equation 2). We assume, therefore, that for the BDM, current variances of species richness will be reduced by fifty percent when paired measures are available. Comparison of Tables 4, 5 and 7 shows that for Z9 strata the MDD will be reduced by up to 2 species (colline grassland) and for Z7 up to 14 species in the Western Central Alps.

Comparing MDD values with possible changes in species richness

Differences in species richness between sample areas can be caused by multiple factors such as soil pH (Ewald 2003), and other site conditions (Ellenberg et al. 1991, Wohlgemuth 1993), disturbance (Tiegs et al. 2004), or natural hazards (e.g., windthrow, Palmer et al. 2000, Fischer et al. 2002). But the most important factor in a cultural landscape is the manner of land use, for example in different grassland types (Willems et al. 1993, Pauli 1998, Peintinger 1999, Fischer and Wipf 2002, Fischer et al., 2004) or in Middle European forests (Egloff 1991, Walther and Grundmann 2001, Dzwonko and Gawronski 2002).

The BDM is designed to detect changes in species richness over short periods, which are mainly caused by human interactions. In order to test and illustrate the precision that can be achieved, we assumed the vegetation on an average sample plot is drifting to species poor or species rich condition (Table 8). For montane grassland, with an overall mean of 32 species, this translated to a decrease of 13 species and an increase of 17 species. For Z7 Central Plateau, the differences between the mean values were about 35 species. Both strata montane grassland and Central Plateau are strongly influenced by human action. Therefore, 'poor', 'average' and 'rich' vegetation states can fluctuate between each other by changing the intensity and/or techniques of land use.

We compared the values in Table 8 to the MDD values in Table 7 and observed the expected MDD is approximately six times (Z9) and more than four times (Z7) smaller than the values from our scenario. This demonstrates that future changes for Z9 and Z7 will be detectable even if they are much smaller then our scenario values or if they only refer to a part of the sample areas.

Conclusions

These assumptions, based on the actual results, show that the reproducibility and the precision that can be achieved by BDM methods will be appropriate for detecting future changes in species richness.

Acknowledgements: We would like to thank Ch. Bühler and A. Zangger for discussion and assistance, the ALG (Baudepartement, Canton Argovia) for permission to use the Argovian survey data, Thomas Wohlgemuth, Scott Tiegs and an anonymous reviewer for their helpful comments on the manuscript. The research was supported by the Swiss Agency for the Environment, Forests and Landscape (SAEFL) and carried out by more than a dozen fearless botanists.

References

Anderson, D.R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29: 1294-1297.

Buckland, S.T., D.R. Anderson, K.P. Burnham and J.L. Laake. 1993. *Distance Sampling: Estimating Abundance of Biological Populations.* Chapman and Hall, London.

Boulinier, T., J.D. Nichols, J.R. Sauer, J.E. Hines and K.H. Pollok. 1998. Estimating species richness: The importance of heterogeneity in species detectability. *Ecology* 79: 1018-1028.

Dzwonko, Z. and S. Gawronski. 2002. Effect of litter removal on species richness and acidification of a mixed oak-pine woodland. *Biological Conservation* 106:389-398.

Egloff, F.G. 1991. Dauer und Wandel der Lägernflora. *Vierteljahrsschrift der Naturforschenden Gesellschaft Zürich* 136/4:207-270.

Ellenberg, H., H.E. Weber, R. Düll, V. Wirth, W. Werner and D. Paulissen. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* Volume 18. Verlag Erich Goltze KG, Göttingen.

Ewald, J. 2003. The calcareous riddle: Why are there so many calciphilous species in the Central European flora? *Folia Geobotanica* 38:357-366.

Fischer, A., M. Lindner, C. Abs and P. Lasch. 2002. Vegetation dynamics in Central European forest ecosystems (near-natural as well as managed) after storm events. *Folia Geobotanica* 37:17-32.

Fischer, M. and S. Wipf. 2002. Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biological Conservation* 104:1-11.

Fischer, M., J. Stöcklin, A. Weyand and K. Maurer. 2004 . Cultural and biological diversity of grasslands in the Swiss Alps. *Grassland Sciences in Europe*. In Press

Gonseth, Y., T. Wohlgemuth, B. Sansonnes and A. Butler. 2001. Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. Umwelt-Materialien Buwal 147:1-48.

Hintermann, U., D. Weber and A. Zangger. 2000. Biodiversity monitoring in Switzerland. *Schriftenr. Landschaftspflege Naturschutz* 62:47-58.

Hintermann, U., D. Weber, A. Zangger and J. Schmill. 2002. Biodiversity monitoring in Switzerland BDM – Interim Report. *Swiss Agency for the Environment, Forests and Landscape SAEFL.* Environmental Series No. 342.

Kéry, M. and H. Schmid. 2004. Monitoring programs need to take into account imperfect species detectability. *Basic and Applied Ecology* 5: 65-73.

Palmer, M.W., S.D. McAlister, J.R. Arévalo and J.K. DeCoster. 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. *Journal of Vegetation Science* 11:841-854.

Pauli, D. 1998. Plant species diversity and productivity in wetland communities. patterns and processes. PhD thesis. Institut für Umweltwissenschaften, Universität Zürich.

Peintinger, M. 1999. The effect of habitat area and management on species diversity in montane wetlands. PhD thesis. Institut für Umweltwissenschaften, Universität Zürich.

Pollock, K.H, J.D. Nichols, T.R. Simons, G.L. Farnsworth, L.L. Bailey and J.R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13: 105-119.

Schreiber, K.F., N. Kuhn, C. Hug, R. Häberli and C. Schreiber. 1977. Wärmegliederung der Schweiz. Eidg. Justiz- und Polizeidepartement, Bern.

Thompson, W.L., G.C. White and C. Gowan. 1998. *Monitoring Vertebrate Populations.* Academic Press, San Diego.

Tiegs, S.D., J.F. O'Leary, M.M. Pohl and C.L. Munill. 2004. Flood disturbance and riparian species diversity on the Colorado River Delta. *Biodiversity and Conservation.* In Press

Wagner, H.H., O. Wildi and K.C. Ewald. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* 15:219-227.

Walther, G.-R. and A. Grundmannn. 2001. Trends of vegetation change in colline and submontane climax forests in Switzerland. *Bulletin of the Geobotanical Institute ETH.* 67:3-12.

Weber, D. 2002. Langfristüberwachung der Artenvielfalt in den Nutzflächen des Kantons Aargau (LANAG). Die aktuellen Zahlen 2002. Unveröffentlicht, deponiert. Aarau, Baudepartement Kanton Aargau, Abteilung Landschaft und Gewässer.

Weber, D., U. Hintermann and A. Zangger. 2004. Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography* 13: 97-104.

Whittaker, R.J., K.J. Willis and R. Field. 2001. Scale and species richness: toward a general, hierarchical theory of species diversity. *Journal of Biogeography* 28:453-470.

Willems, J.H., R.K. Peet and L. Bik. 1993. Canges in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science* 4:203-212.

Wohlgemuth, T. 1993. Der Verbreitungsatlas der Farn- und Blütenpflanzen der Schweiz (Welten und Sutter 1982) auf EDV. Die Artenzahlen und ihre Abhängigkeit von verschiedenen Faktoren. *Botanica Helvetica* 103:55-71.

Yoccoz, N. G., J.D. Nichols and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16: 446-453.

Zar, H.J. 1984. *Biostatistical Analysis*. Prentice-Hall, New Jersey.

Zechmeister, H.G. and D. Moser. 2001. The influence of agricultural land-use intensity on bryophyte species richness. *Biodiversity and Conservation* 10: 1609-1625.

4 Chapter II: Species richness estimation and determinants of species detectability in butterfly monitoring programmes

Ecological Entomology (2007), **32**, 53–61

Species richness estimation and determinants of species detectability in butterfly monitoring programmes

MARC KÉRY[1] and MATTHIAS PLATTNER[2] [1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland and [2]Hintermann & Weber AG, Ecological Consultancy, Planning & Research, Reinach, Switzerland

Abstract. 1. Species richness is the most widely used biodiversity index, but can be hard to measure. Many species remain undetected, hence raw species counts will often underestimate true species richness. In contrast, capture–recapture methods estimate true species richness and correct for imperfect and varying detectability.

2. Detectability is a crucial quantity that provides the link between a species count and true species richness. For insects, it has hardly ever been estimated, although this is required for the interpretation of species counts.

3. In the Swiss butterfly monitoring programme about 100 transect routes are surveyed seven times a year using a highly standardised protocol. In July 2003, control observers made two additional surveys on 38 transects. Data from these 38 quadrats were analysed to see whether currently available capture–recapture models can provide quadrat-specific estimates of species richness, and to estimate species detectability in relation to transect, observer, survey, region, and abundance.

4. Species richness over the entire season cannot be estimated using current capture–recapture methods. The species pool was open, preventing use of closed population models, and detectability varied by species, preventing use of current open population models. Assuming a closed species pool during two mid-season (July) surveys, a Jackknife capture–recapture method was used that accounts for heterogeneity to estimate mean detectability and species richness.

5. In every case, more species were present than were counted. Mean species detectability was 0.61 (SE 0.01) with significant differences between observers (range 0.37–0.83). Species-specific detection at time $t + 1$ was then modelled for those species seen at t for three mid-season surveys. Detectability averaged 0.50 (range 0.17–0.81) for individual species and 0.65, 0.44, and 0.42 for surveys. Abundant species were detected more easily, although this relationship explained only 5% of variation in species detectability.

6. These are important, although not entirely unexpected, results for species richness estimation of short-lived animals. Raw counts of species may be misleading species richness indicators unless many surveys are conducted. Monitoring programmes should be calibrated, i.e. the assumption of constant detectability over dimensions of interest needs to be tested. The development of capture–recapture or similar models that can cope with both open populations and heterogeneous species detectability to estimate species richness should be a research priority.

Key words. Butterfly, capture–recapture, closed population models, detectability, monitoring, species richness.

Introduction

Increasing human pressure on natural resources requires a reliable accounting of biodiversity – the diversity of genes,

Correspondence: Marc Kéry, Swiss Ornithological Institute, CH-6204 Sempach, Switzerland. E-mail: marc.kery@vogelwarte.ch

populations, species, and landscapes, and of their interactions (Yoccoz *et al.*, 2001). By far the most widely used measure of biodiversity is species richness, the number of species present at one place and during a given period. Species richness is also an important criterion when selecting protected areas (e.g. Kerr, 1997) and is the central theme for biogeography (e.g. Jetz & Rahbek, 2002). The reasons why species richness is such an attractive measure of diversity are manifold; it is a straightforward measure because species are fairly well-defined when compared with other kinds of diversity, e.g. landscape diversity; its measurement does not require specialised technical equipment, such as other kinds of diversity, e.g. genetic diversity. For some taxonomic groups, such as most vertebrates, plants, and some insects, networks of dedicated observers exist in many countries and enable large-scale and yet detailed biodiversity assessments to be conducted at relatively low costs and partly on a volunteer basis (Pollard, 1977; Pollard & Yates, 1993; van Strien *et al.*, 1997; Oostermeijer & van Swaay, 1998; Rothery & Roy, 2001; Stefanescu *et al.*, 2004).

Species richness may be a simple concept, but its reliable measurement is not. Species richness is most often determined by enumeration, i.e. by counting all species detected at one place and time. However, some species present may not be detected in a survey. This will lead to a negative bias in a count estimate of species richness. Moreover, different proportions P_{it} of all species present may be overlooked at some places i and times t, than at others. Comparisons of species richness over time (e.g. trend estimates) or between places (e.g. regional comparisons) will then be distorted when based on raw counts of species. Hence, the count estimator of species richness may be fairly unreliable even when only used as an index ('relative species richness').

Most monitoring programmes make the implicit assumption that either all species are detected (i.e. $p_{it} = p = 1$) or, that the expected proportion of species detected does not vary over dimensions of interest such as time, space or habitat (i.e. $E(p_{it}) = p$, with $p < 1$). A third view is to assume that variation in p_{it} can be adequately explained by covariates, however, it is unlikely that all required covariates have been measured or are even known. These assumptions, the index assumptions (Conn *et al.*, 2004), are rarely stated explicitly or tested in studies that deal with species richness.

Detectability is important also in monitoring programmes that focus on trends of single species, because systematic changes of detectability over dimensions of interest (e.g. time) are confounded with abundance trends in raw counts of individuals. Only when average detectability is stationary over time do relative abundance comparisons reflect temporal trends in an unbiased fashion. Thus, the detectability thinking underlying the present study also has some relevance to single species studies, even if the particular estimation methods may differ.

Capture–recapture methods can be used to estimate the size of a 'population' of species as well as species detectability (e.g. Burnham & Overton, 1979; Boulinier *et al.*, 1998). These methods use the observed pattern of detection/non-detection among those species detected during repeated samples to infer the number of species that do not appear in those samples. They derive an estimate of the detectability of the average species in the community based on the species detected at least once. In the simplest case, species richness can then be estimated as the number of species counted divided by the estimated detectability (Williams *et al.*, 2002). Detectability is thus a crucial quantity, since it represents the direct link between observed species richness (raw species counts) and the unknown true number of species, as well as between observed counts of individuals and true abundance of a species (see above).

Recently, capture–recapture methods have been used to evaluate sources of variation in the detectability of bird species in large-scale monitoring programmes. Detectability was shown to vary by species, observer, region, year and season (Boulinier *et al.*, 1998; Selmi & Boulinier, 2003; Kéry & Schmid, 2004; Kéry *et al.*, 2005; Kéry & Schmid, 2006). Few such studies on such issues are available for invertebrate taxa (McCoy, 1999; King & Porter, 2005; Dorazio *et al.*, 2006). Butterflies are monitored in an increasing number of countries (e.g. Pollard, 1977; Pollard & Yates, 1993; van Strien *et al.*, 1997; Oostermeijer & van Swaay, 1998; Stefanescu *et al.*, 2004), but to the authors' knowledge, rigorous estimates of species detectability for a large number of species are lacking.

Species detectability is important, not only in an applied context, but also for ecological research. For example, in metapopulation studies, the presence of a species needs to be assessed reliably (Harrison *et al.*, 1988; Sutcliffe *et al.*, 1997; Saccheri *et al.*, 1998; Hanski & Singer, 2001; Krauss *et al.*, 2003). When modelling habitat relationships of butterflies (Bergman *et al.*, 2004; Cleary & Mooers, 2004; Hortal *et al.*, 2004) false absences will be induced when species detectability is less than 1. This will be particularly critical when false absence rates differ by habitat such as when detectability depends on habitat. Finally, detectability is important for range studies (Warren *et al.*, 2001; Crozier, 2004), where perceived range changes are actually the product of real distribution changes and changes in detectability. Imperfect detection will lead to incomplete registration of the distribution of a species, and to a time-lag in detecting range contractions or expansions. Hence, knowledge about detectability of butterfly species is desirable for both ecological and for management applications.

The Biodiversity Monitoring Program in Switzerland (BDM) is a long-term monitoring programme of the Swiss Federal Office for the Environment (FOEN). Part of the programme focuses on changes in species richness of selected taxa, in particular birds, butterflies, molluscs, and vascular plants, measured at different spatial scales (Hintermann *et al.*, 2002; Weber *et al.*, 2004). Indicators for biodiversity at a landscape scale are assessed in a total of 510 1-km^2 quadrats distributed as a systematic grid sample across Switzerland. The sampling scheme is based on a rotating panel with 20% of the total sample surveyed every year. Further information on the BDM and summarised actual data sets may be found on www.biodiversitymonitoring.ch.

Here, it is asked whether currently available capture–recapture models can be used to estimate species richness over an entire season. In an attempt at calibrating the measurements of species richness obtained from the Swiss butterfly monitoring scheme, detectability is then estimated for some 150 taxa surveyed in 2003 for a restricted time period during mid-season. Specifically, the following questions are dealt with: (1) Is the species pool sufficiently closed so that closed population capture–recapture models can be used for estimation of species richness? (2) Is species-specific detectability sufficiently homogeneous so that open population models can be used? (3) Can the entire survey season be restricted to a time window wherein the closure assumption is met? (4) How does species detectability in mid-season vary in response to factors such as species, observer, abundance, and biogeographic regions of Switzerland? (5) How could species richness in a scheme such as BDM be estimated rigorously? It is anticipated that these questions are of interest not only for butterfly monitoring programmes elsewhere, but also for other short-lived and particularly invertebrate groups such as dragonflies, orthopterans, or carabid beetles.

Methods

Butterfly monitoring in the Swiss BDM

The transect method used in the Swiss BDM is based on the British Butterfly Monitoring Scheme (BMS; see e.g. Douwes, 1976; Erhardt, 1985; Pollard & Yates, 1993). From 1996 to 2000, the method was tested and adapted to climatic and geographic conditions of Switzerland. The number of surveys per season is the most cost-relevant factor and had to be optimised for cost-effectiveness. BDM focuses on species richness rather than on population size of single species as does the BMS. This enables BDM to reduce the number of surveys from over 20 in the BMS to seven surveys, conducted between 21 April and 21 September, at lower elevations. Owing to the shorter growing season, fewer surveys are conducted at higher altitudes, with a minimum of four surveys conducted in July/August above 2000 m a.s.l. The surveys are conducted within defined time windows (‘periods’) of 2–3 weeks in a highly standardised fashion. An experienced observer walks a strictly defined transect of 2.5 km twice (back and then immediately forth) during very favourable weather conditions. Surveys are restricted to times when wind is less or equal to force 3 (Beaufort) and temperature exceeds 13 °C. In addition, BDM requires $< 20\%$ cloud cover on the transect route. For all day-flying butterfly species (including *Hesperiidae* and *Zygaenidae*), abundance (number of individuals seen) for each species detected is recorded along the transect in a distance of less than 5 m from the observer. Determination is usually made to the species level and only in some cases to taxon groups (e.g. *Pyrgus alveus* complex), so for simplicity we speak of species hereafter. The basic data yielded by the programme for each surveyed transect is a species by survey matrix that contains the number of individuals seen for each species for 4–7 surveys per year. A complete species list may be obtained on request.

Data used for analysis

Regular field work for the BDM butterfly monitoring started in 2003. In an attempt to calibrate the programme, 38 transects were chosen randomly among the 100 surveyed in 2003 for a double-observer study to assess variability in species detectability resulting from observers and other effects, such as weather. On every transect the standard observer conducted seven surveys as usual. In addition and unknown to him or her, an alternative observer conducted two surveys in mid-season (July) during periods 3 and 4. A total of 40 observers were involved in this study. Hence, for each of 38 transects, data from seven standard surveys plus two control surveys were available.

For different analyses, three subsets of these nine surveys were used. To test the closure assumption for time windows of varying lengths, the seven standard surveys only were used. To estimate mean detectability over all species present in the community and to compare capture–recapture estimates with counts of species richness, a closed species pool was assumed for the duration of the double-observer study and the two control and two standard surveys conducted in July were selected. To estimate species-specific detectability and its determinants, standard survey data from periods 4–6 were chosen and analysis was restricted to those species detected at least once.

Statistical analysis

Test of closure. To test if the species pool was sufficiently closed during time windows of varying lengths to permit use of closed population capture–recapture models for species richness estimation, the classical closure test described by Otis *et al.* (1978) was used. It compares the mean observed difference between first and last detection of each species to that expected under the assumption of closure. A negative value of the test statistic indicates a shorter than expected ‘time of residence’ of a species in the species pool and hence violation of closure.

Test for heterogeneity in species detectability. The model selection routine for capture–recapture models implemented in the CAPTURE program (Otis *et al.*, 1978) was first used for those temporally restricted parts of the season and for those transects where the closure assumption was not rejected. CAPTURE selects between eight models that make different assumptions about three possible sources of variation in detectability: temporal variation (t), behavioural variation (b), and individual heterogeneity (h) as well as any combination of these effects. Second, a generalised linear mixed model (GLMM) was used to test for heterogeneity between species (see *Determinants of species detectability*).

Capture–recapture estimation of species richness and detectability. Under the assumption of a closed species pool, the four July surveys from the double-observer study were used, and a capture–recapture model was used to estimate species richness for this restricted time window. With just two surveys per person it was impossible to compare models making different assumptions about the factors affecting species detectability, e.g. by using the model selection routine in CAPTURE or by conducting likelihood ratio tests in Program MARK (White & Burnham, 1999); at least three surveys would have been necessary. Therefore, model selection was guided by results from the analyses just described (see *Test for heterogeneity in species detectability*). Species heterogeneity in detectability was pervasive so the Burnham and Overton (1979) Jackknife estimator of the heterogeneity model was used to account for heterogeneous detectability when estimating species richness and the average detectability of all species on a transect during the July surveys.

This widely used estimator of species richness has performed well in comparisons (Otis *et al.*, 1978; Palmer, 1990; Baker, 2004).

Determinants of species detectability. Two approaches were used to test for factors associated with species detectability. First, mean species detectability based on the Jackknife estimate was modelled in a linear mixed model with a random transect effect. The mean estimated species detectability P_{ijkl} for observer i, biogeographical region j, and transect k may be written as

$$P_{ijkl} = a_1 + a_2 \times o_i + a_3 \times r_j + \tau_k + \varepsilon_l \qquad (1)$$

where a_1 is an intercept, a_2 is the fixed effect for observer o_i and a_3 that for region r_j. τ_k is a random effect for transect k and takes account of all unmodelled effects that vary among quadrats, while ε_l is an independent noise component for every transect–observer combination l. Both τ_k and ε_l are assumed to be drawn from independent normal distributions, the variances of which are to be estimated along with the parameters a_1, a_2, and a_3. Nine biogeographic regions of Switzerland and the 40 observers were compared. This analysis uses species-averaged estimates of the per-survey detectability for all species in a community. It does not provide estimates of species-specific detectability nor can it test for factors affecting detectability at the species level.

Therefore, a second approach was to use the standard data from the mid-season surveys in periods 4–6, to restrict analysis to those species seen during survey i, and to model the probability that a species was also seen during survey $i + 1$. A random effects logistic regression model was fit to the binary species sighting data, assuming that sighting S was a Bernoulli-distributed random variable, $S \sim B(p)$, governed by species-specific detectability p. For period i, region j, transect k and species l, it can be written

$$\begin{aligned}\mathrm{logit}(p_{ijkl}) = {} & a_1 + a_2 \times t_i + a_3 \times r_j + a_4 \\ & \times A_{(i-1)kl} + a_5 \times [A_{(i-1)kl} t_i] \\ & + a_6 \times [A_{(i-1)kl} r_j] + \tau_k + \sigma_l, \end{aligned} \qquad (2)$$

where a_1 is the intercept, and there are fixed effects a_2 for period t_i, a_3 for region r_j along with random effects τ_k for transect k and σ_l for species l. $A_{(i-1)kl}$ is the $\log_{10}$ of the number of individuals seen of species k on transect l at period $i - 1$, and $[A_{(i-1)kl} t_i]$ and $[A_{(i-1)kl} r_j]$ are the interactions between the number of individuals seen and period and region respectively. a_4 through a_6 are the fixed effects of the abundance covariate and its interactions with period and region. The random effects are again assumed to be drawn from two independent normal distributions, the variances of which are to be estimated along with the partly vector-valued parameters a_1 through a_6. The inclusion of these random effects in the analysis properly accounts for possible dependence of sightings induced by shared transects and species (Kéry, 2002). This model was fit as a GLMM (Littell *et al.*, 1996) with logit link and binomial distribution of errors for trial size 1 (i.e. a Bernoulli distribution).

For moving time windows of two successive surveys, the GLMM analysis assumes a closed species pool and no changes in abundance. The first assumption is probably true since surveys 4–6 were conducted during the main flight period of most species in July and early August, and successive surveys were only 2 weeks apart. The second assumption will not be strictly true. However, any change in abundance would make the test for abundance more conservative. This corresponds to the errors-in-variables problem that is well known to attenuate estimates of the regression coefficients.

The scope of the GLMM analysis is different from that of the mixed model for the Jackknife estimates. The latter analysis pertains to all species present in the community and thus includes those never detected. In contrast, the GLMM analysis pertains only to those species that were detected at least once during periods 4–6. It is likely that some rarer species with lower than average detectability may have been missed altogether. Therefore, estimates of detectability under the GLMM may be somewhat biased upwards with respect to the entire butterfly community. It was deemed insightful to conduct this analysis because any such bias was believed to be low and because it enabled species-specific estimates of detectability along with tests of effects of the number of individuals seen on the detectability of each individual species. The CAPTURE program (Otis *et al.*, 1978) was used for capture–recapture and GenStat (Payne *et al.*, 1993) for all other analyses.

Results

Timing of surveys and observed species richness

The average date of the seven standard surveys in 2003 was 12 May, 5 June, 2 July, 15 July, 31 July, 14 August, and 30 August. A total of 150 species were detected on the 38 transects, which represents 74% of the butterfly species surveyed in the BDM (S. Birrer, unpublished data). On average, 15.5 species (range 2–48) were counted per period and transect. There was a strong seasonal pattern in species counts (Fig. 1) with an increase from 9.7 species counted during the period of 12 May to a maximum of 21.5 and 21.8 species counted during the periods

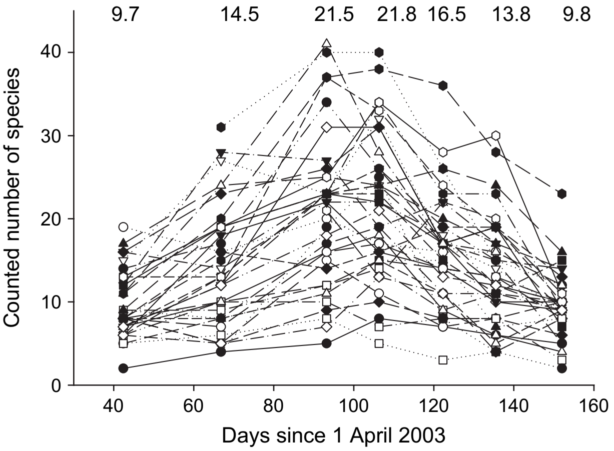


Fig. 1. Number of butterfly species counted on each of 38 transects for each of seven survey periods in the Swiss butterfly monitoring programme. Mean number of species counted for each survey period is shown above the graph. The mean timing of each survey is given as the mean Julian day since 1 April 2003.

of 2 July and 15 July, and followed again by a decline to 9.8 species counted during the last period of 30 August.

Closure of species pool

A test was conducted to establish whether the species pool could be assumed closed for the entire duration of the study or for parts of it for each of the 38 sampled butterfly communities. Among 35 communities for which a closure test could be calculated numerically, there was overwhelming evidence for a violation of the closure assumption (in the form of negative values of the test statistics; see Appendix). This means that when considering the entire season, species previously present left the community and/or that new species appeared. The closure assumption was most strongly violated for longer durations and when the periods over which the test was conducted included the beginning or the end of the season. Closure seemed least violated during periods 3–5, i.e. for the central surveys in July and August. Only for three out of 35 transects (nos 7, 18, and 31) could closure not be rejected in the majority of tested cases.

Heterogeneity of detectability among species

For these three transects (nos 7, 18, and 31) and those surveys where the closure assumption was not rejected, the model selection routine in the CAPTURE program was run. For surveys 1–6 on transect no. 7 the heterogeneity model M(h) was selected. For surveys 2–6 on transect no. 18, the model selected was M(0) with constant detectability, or M(bh), where detectability was heterogeneous and also differed for first detections and redetections. For surveys 2–5 on transect no. 31 model M(0) or M(h) was selected. Hence, for every case a model with heterogeneous species detectability was among those selected. The same conclusion was drawn from a GLMM for species detections in successive two surveys during periods 4–6 where the species variance component was highly significant (see below). Hence, detectability clearly varied among butterfly species and a model for butterfly species richness estimation needed to account for this.

Butterfly species detectability and its determinants

For the four July surveys during periods 3–4 (two surveys each by the standard and the control observer), more butterfly species were present than were counted. On all transects and for all observers, estimated species richness (Jackknife estimates) was higher than observed species richness (counts; Fig. 2). Mean species detectability based on Jackknife estimates averaged 0.61 (SE 0.01) per survey. Because most observers were specific to a region, observer and region effects were partly confounded. When added in a model singly, there were significant differences by region ($\chi^2_8 = 47.6$, $P < 0.001$) and also by observer ($\chi^2_{39} = 221.2$, $P < 0.001$). Detectability for different regions ranged from 0.52 to 0.71 and for individual observers from 0.37 to 0.83 (Fig. 3). When corrected for region, the effect of observer was still significant ($\chi^2_{38} = 88.8$, $P < 0.001$), but when corrected for observer, the effect of region was no longer significant ($\chi^2_7 = 8.5$, $P = 0.29$). This suggests that there were true differences among observers also within the same transect, but that regional differences may just be due to differences among the observers working in them.

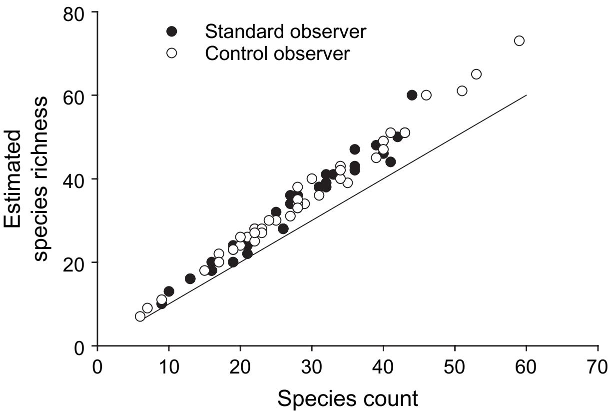


Fig. 2. Counts and Jackknife estimates of butterfly species richness for two summer surveys conducted by two different observers on 38 transects of the Swiss butterfly monitoring programme. If all species present were detected, the points would all lie on the line. Note that the species richness estimate refers to an approximately 2-week period, not the entire season.

Based on a GLMM for the standard survey data during periods 4–6, there was significant variation in detectability among transects as well as among species (Table 1). This confirms results obtained by the model selection routine of the CAPTURE program (see above). Furthermore, detectability varied significantly by survey and by the number of individuals seen during

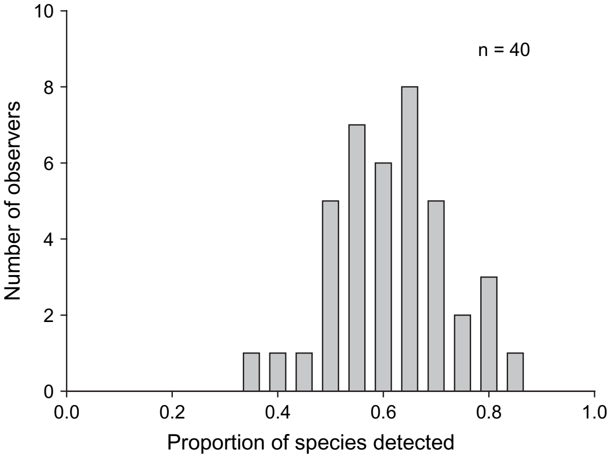


Fig. 3. Distribution of the average species detectability during a single survey for 40 observers in the Swiss butterfly monitoring programme based on Jackknife estimates. Note that observer effects are confounded with transect effects since most observers surveyed only one transect. Species detectability is the estimated proportion of species that are detected during one July survey.

Table 1. Effects on species-specific detectability of 150 butterfly species in 38 transects of the Swiss butterfly monitoring programme in 2003. The analysis is based on a generalised linear mixed model (GLMM) for sighting at survey $i + 1$ and is restricted to three mid-season surveys (nos 4–6) in July and August and to those species seen during survey i. It corresponds to the model given in equation 2.

Random effects	Estimate (SE)	d.f.	z	P
Transect	0.087 (0.044)	1	1.99	0.024
Species	0.728 (0.141)	1	5.16	<0.001
Fixed effects	**Estimate (SE)**	**d.f.**	**Wald χ^2**	**P**
Period	–	2	48.42	<0.001
Region	–	8	9.13	0.331
$\log_{10}$(number of individuals seen)	1.615 (0.273)	1	298.47	<0.001
Period × $\log_{10}$(number of individuals seen)	–	2	9.70	0.008
Region × $\log_{10}$(number of individuals seen)	–	8	1.53	0.141

the previous survey. Populations with a higher number of individuals seen were detected more easily, and this relationship changed over time. In contrast to the analysis of mean species detectability, the GLMM analysis showed no discernible difference between regions nor an interaction between region and the number of individuals seen (Table 1).

For individual species during periods 4–6, detectability per survey averaged 0.50 and ranged from 0.17 to 0.81 (Fig. 4). For periods 4, 5, and 6, it was estimated at 0.65, 0.44, and 0.42 respectively. Because the estimate for period 4 under the GLMM (0.64) and the corresponding Jackknife detectability estimate for periods 3–4 (0.61) were essentially the same, any bias of the GLMM approach owing to missed species appears to be low.

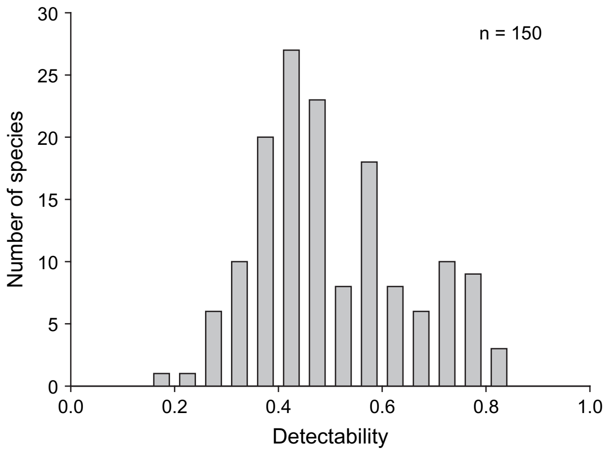


Fig. 4. Distribution of the mean detectability during a single survey for 150 observed butterfly species in the Swiss butterfly monitoring programme under the GLMM of Table 1. Detectability is expressed on a per-survey basis and refers to the average of three mid-season (July to early August) surveys.

Interestingly, the number of individuals seen explained only a surprisingly small amount of the total variation in detectability among species. A model without effects of the number of individuals seen (i.e. without the three last lines in Table 1) had a species variance component of 0.770 (SE 0.140). In an analysis accounting for the number of individuals seen effects (Table 1), the species variance was reduced by only 5.5%.

Discussion

Can capture–recapture be used to estimate insect species richness?

Use of currently available capture–recapture methods of estimating species richness requires making either of two assumptions: (1) if detectability varies by species, the species pool must be closed for the duration of all surveys, or (2), if the population is open, species must have homogeneous detectability. Unfortunately, in the Swiss programme, and probably for most larger multispecies insect surveys, neither assumption is tenable for the duration of all surveys. As expected, the butterfly species pool was not closed during the entire survey period. At the same time, species detectability was strongly heterogeneous. Therefore, at present, no rigorous analysis method is available to estimate species richness for the entire survey duration of the Swiss butterfly monitoring programme. To do this, either the survey design needs to be modified, or new capture–recapture methods need to be developed that can handle both open populations and heterogeneous detectability (see *Survey design considerations*). This would be a very welcome contribution to the ecology and management of short-lived species.

Detectability in butterfly communities

Detectability per survey of the average species at mid-season was estimated at 0.61 by the Jackknife estimator and ranged from 0.37 to 0.83 for 40 observers. Individual species during one July to August survey were detected with a mean probability of 0.50 (range 0.17–0.81) over 150 species. Thus, even for very well-trained field personnel, under highly standardised and suitable conditions and at mid-season, a large proportion of species may be missed when only a few surveys are conducted. It should be noted, though, that the combined species detection probability over all seven surveys in BDM will be much higher.

In addition, almost every tested factor had a significant effect on detectability: species, transect, observer, survey number, the number of individuals seen, and, perhaps, biogeographic region. Hence, care is needed in comparisons of raw counts of butterfly species unless surveys are much more frequent (e.g. $\approx$ 20 times per year, as in the British scheme), in which case the combined probability of detection for most species might approach 1.

For all other cases, arguably it is desirable to use an estimation scheme that formally includes a correction for any variation of detectability. Otherwise, one can not be sure if differences in counts result from genuine differences of species richness, differences in detectability, or both. In particular, monitoring programmes need to be calibrated, for example, the relationship between species count and true species richness must be evaluated. This is essentially an exercise in estimating detectability and may be carried out in a double-sampling scheme where detectability is estimated only in a subset of the total sample (Pollock *et al.*, 2002).

The detectability of a species is likely to be a combined effect of abundance, size, behaviour, observer, transect, survey number, and biogeographic region (see also Dennis *et al.*, 2006). Interestingly, abundance seemed to account for only a minor part of the species differences in detectability; only 5.5% of the species variance component was explained by the number of individuals seen 2 weeks before. However, only an indirect index of abundance was available. Errors in estimating abundance and changes in true abundance over a 2-week interval will both attenuate the slope of that relationship and reduce the statistical significance of its test (Neter *et al.*, 1990).

However, care is needed when interpreting detectability estimates in the present observational study, because factors that affect detectability may not strictly be separated. For instance, variation in mean butterfly detectability over biogeographical regions may be caused by any combination of the following factors: species composition, observer differences, and the interaction of species differences with a region. The first is the sum of effects of individual species. These species effects may also change over a region, hence the same species may have a different detectability in different regions, for instance due to different abundance or phenology. Observers arguably differ in their ability to detect any given species, but their ability may also differ by species, region, and the interaction between species and region. In this study, observer effects could not be estimated unconditionally because most of them only surveyed a single transect. Observer effects on mean species detectability were thus partly confounded with transect and regional effects. In the future, when an observer comparison is required, a crossed design with each observer surveying two or more transects is required.

Survey design considerations

Due to staggered phenology of individual species, the total species richness at a site represents a superpopulation of those species that are present at individual survey times during the entire activity season of butterflies. The size of this superpopulation could be estimated by sampling at two temporal scales. Several primary sampling periods during a season (e.g. seven, as currently in the Swiss survey) might be separated by 2–4 weeks. Within each primary period, at least two secondary surveys would have to be conducted within a short time period. The species pool could then be assumed closed within each primary period and open between primary periods. This design is called the robust design in the capture–recapture literature (Williams *et al.*, 2002), and might allow estimation of heterogeneous detectability within each primary sampling period, rates of change of the species pool between primary sampling periods, and the total size of the superpopulation of species present over the entire season. Indeed, a minor change of protocol in the Swiss programme would lead to robust design data without altering the current sampling scheme. Every transect is surveyed twice (back and forth), so if detections were recorded separately and if one assumes that an observer does not remember clearly observations from the first pass, a standard robust-design approach might be applicable for species-richness estimation. In addition, whether or not an observer has a tendency to remember the species he or she detected on the previous sampling occasion could be tested, similar to the so-called ‘behavioural response model’ in capture–recapture (Otis *et al.*, 1978).

It was also noted that capture–recapture estimation of species richness (or abundance) can be seen as a way of reducing the effort in a monitoring programme (e.g. Roy *et al.*, 2005). Instead of conducting a very large number of surveys (e.g. ≈ 20 as in the British scheme) to ensure that the overall detection probability of a species may be close to 1 so that virtually every species is *counted*, the information about detectability contained in much fewer surveys is used to *estimate* species richness.

Perspectives

Most monitoring programmes are focused on detecting changes, e.g. in population size, occupancy, or species richness, over space or time. If changes are detected, then the obvious next question is to ask what has caused these changes. In models for the investigation of community structure in closed populations, local species extinction and turnover rates can be estimated (Nichols *et al.*, 1998). These components of change can be important for diagnosing reasons for change and ought to be capable of being estimated using models similar to that of Dorazio *et al.* (2006).

Acknowledgements

We thank S. Birrer, P. Duelli, A. Erhard, S. Herrando, L. Jenni, S. Newson, P. Ramseier, P. Rothery, A. Tyre, D. Weber, and N. Zbinden for comments on drafts of this paper and M. Ercyes for illumination on the sampling design of the Swiss butterfly monitoring scheme. We also thank the Swiss Biodiversity Monitoring programme (BDM) of the Swiss Federal Office for the Environment (FOEN) for funding this study.

References

Baker, J.D. (2004) Evaluation of closed capture–recapture methods to estimate abundance of Hawaiian monk seals. *Ecological Applications*, **14**, 987–998.

Bergman, K.O., Askling, J., Ekberg, O., Ignell, H., Wahlman, H. & Milberg, P. (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography*, **27**, 619–628.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, **79**, 1018–1028.

Burnham, K.P. & Overton, W.S. (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology*, **60**, 927–936.

Cleary, D.F.R. & Mooers, A.O. (2004) Butterfly species richness and community composition in forests affected by ENSO-induced burning and habitat isolation in Borneo. *Journal of Tropical Ecology*, **20**, 359–367.

Conn, P.B., Bailey, L.L. & Sauer, J.R. (2004) Indexes as surrogates to abundance for low-abundance species. *Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters* (ed. by W. L. Thompson), pp. 59–74. Island Press, Washington, DC.

Crozier, L. (2004) Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, **85**, 231–241.

Dennis, R.L.H., Shreeve, T.G., Isaac, N.J.B., Roy, D.B., Hardy, P.B., Fox, R. *et al.* (2006) The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation*, **128**, 486–492.

Dorazio, R.M., Royle, J.A., Söderström, B. & Glimskär, A. (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, **87**, 842–254.

Douwes, P. (1976) An area census method for estimating butterfly population numbers. *Journal of Research on the Lepidoptera*, **15**, 146–152.

Erhardt, A. (1985) Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology*, **22**, 849–861.

Hanski, I. & Singer, M.C. (2001) Extinction–colonization dynamics and host-plant choice in butterfly metapopulations. *American Naturalist*, **158**, 341–353.

Harrison, S., Murphy, D.D. & Ehrlich, P.R. (1988) Distribution of the Bay checkerspot butterfly, *Euphydrias editha bayensis* – evidence for a metapopulation model. *American Naturalist*, **132**, 360–382.

Hintermann, U., Weber, D., Zangger, A. & Schmill, J. (2002) Biodiversity monitoring in Switzerland BDM – Interim Report. Swiss Agency for the Environment, Forests and Landscape SAEFL. Environmental Series no. 342.

Hortal, J., Garcia-Pereira, P. & Garcia-Barros, E. (2004) Butterfly species richness in mainland Portugal, predictive models of geographic distribution patterns. *Ecography*, **27**, 68–82.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Kerr, J.T. (1997) Species richness, endemism, and the choice of areas for conservation. *Conservation Biology*, **11**, 1094–1100.

Kéry, M. (2002) Inferring the absence of a species – a case study of snakes. *Journal of Wildlife Management*, **66**, 330–338.

Kéry, M., Royle, J.A. & Schmid, H. (2005) Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications*, **15**, 1450–1461.

Kéry, M. & Schmid, H. (2004) Monitoring programs need to take into account imperfect species detectability. *Basic and Applied Ecology*, **5**, 65–73.

Kéry, M. & Schmid, H. (2006) Estimating species richness: calibrating a large avian monitoring program. *Journal of Applied Ecology*, **43**, 101–110.

King, J.R. & Porter, S.D. (2005) Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. *Environmental Entomology*, **34**, 1566–1578.

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2003) Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia*, **137**, 591–602.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute Inc., Cary, North Carolina.

McCoy, K.D. (1999) Sampling terrestrial gastropod communities: using estimates of species richness and diversity to compare two methods. *Malacologia*, **41**, 271–281.

Neter, J., Wasserman, W. & Kutner, M.H. (1990) *Applied Linear Statistical Models*, 3rd edn. Irvin, Homewood, Illinois.

Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. & Sauer, J.R. (1998) Estimating rates of local species extinction, colonization, and turnover in animal communities. *Ecological Applications*, **8**, 1213–1225.

Oostermeijer, J.G.B. & van Swaay, C.A.M. (1998) The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. *Biological Conservation*, **86**, 271–280.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference for capture data on closed animal populations. *Wildlife Monographs*, **62**, 1–135.

Palmer, M.W. (1990) The estimation of species richness by extrapolation. *Ecology*, **71**, 1195–1198.

Payne, R.W., Lane, P.W., Digby, P.G.N., Harding, S.A., Leech, P.K., Morgan, G.W. et al. (1993) *Genstat 5, Release 3. Reference Manual*. Clarendon Press, Oxford.

Pollard, E. (1977) A method for assessing change in the abundance of butterflies. *Biological Conservation*, **12**, 115–132.

Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L. & Sauer, J.R. (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics*, **13**, 105–119.

Rothery, P. & Roy, D.B. (2001) Application of generalized additive models to butterfly transect count data. *Journal of Applied Statistics*, **28**, 897–909.

Roy, D.B., Rothery, P. & Brereton, T. (2005) The design of a systematic survey scheme to monitor butterflies in the United Kingdom. *Studies on the Ecology and Conservation of Butterflies in Europe, Vol. 1: General Concepts and Case Studies* (ed. by E. Kühn, R. Feldmann, J. A. Thomas, & J. Settele), pp. 102–105. Pensoft, Sofia.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature*, **392**, 491–494.

Selmi, S. & Boulinier, T. (2003) Does time of season influence bird species number determined from point-count data? A capture–recapture approach. *Journal of Field Ornithology*, **74**, 349–356.

Stefanescu, C., Herrando, S. & Paramo, F. (2004) Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *Journal of Biogeography*, **31**, 905–915.

van Strien, A.J., van de Pavert, R., Moss, D., Yates, T.J., van Swaay, C.A.M. & Vos, P. (1997) The statistical power of two butterfly monitoring schemes to detect trends. *Journal of Applied Ecology*, **34**, 817–828.

Sutcliffe, O.L., Thomas, C.D., Yates, T.J. & Greatorex-Davies, J.N. (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, **109**, 235–241.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B. *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Weber, D., Hintermann, U. & Zangger, A. (2004) Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography*, **13**, 97–104.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.), 120–139.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego.

Yoccoz, N.G., Nichols, J.D. & Boulinier, T. (2001) Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, **16**, 446–453.

Accepted 27 July 2006

Appendix 1. Tests of the closure assumption (z-values) of the butterfly community at each transect for different time windows (S 1–6 for instance denotes data from surveys 1–6). Transects are denoted by town and canton. The total number of species detected during seven surveys is also shown. The one-sided 95% critical value of the standard normal distribution is $z = 1.645$. Tests where the null hypothesis of closure cannot be rejected are shown in boldface. No test statistic could be obtained for the cases marked by an asterisk.

Quadrat no.	Town	Canton	Species	S 1–7	S 1–6	S 2–5	S 2–6	S 2–7	S 3–5	S 3–6
1	Oberems	VS	29	*	*	*	*	*	*	**−1.30**
2	Vernier	GE	14	*	*	*	*	*	*	*
3	Trélex	VD	50	−3.19	−2.60	−2.23	−2.40	−2.61	*	**−1.38**
4	Vallorbe	VD	48	−3.35	−2.65	−2.31	−2.31	−2.44	−1.71	−2.51
5	Grandvaux	VD	31	−4.18	−3.20	**−1.58**	−2.46	−3.71	−1.71	−2.49
6	Sonvilier	BE	27	−3.41	−2.08	**−1.59**	**−0.90**	−2.34	*	**−1.52**
7	Riaz	FR	24	**−0.61**	**−0.67**	**−1.15**	**−1.16**	**−1.33**	*	−1.89
8	Fully	VS	22	*	*	*	*	*	*	*
9	Ormont-Dessus	VD	53	*	*	−4.40	−5.72	−6.01	−2.74	−4.48
10	Wahlern	BE	24	−3.85	−2.93	**−0.44**	−2.09	−3.02	*	*
11	Kirchlindach	BE	21	−2.20	−2.78	*	−2.87	−2.41	*	−2.79
12	Vicques	JU	47	−6.76	−5.85	−2.96	−4.21	−5.85	−2.45	−3.19
13	Arni (BE)	BE	24	−4.43	−4.16	−2.85	−3.20	−3.53	*	*
14	Arisdorf	BL	24	**−1.10**	−1.96	*	*	**−0.49**	*	*
15	Eptingen	BL	38	−3.17	−3.24	**−1.49**	−2.20	−2.23	*	−1.71
16	Lungern	OW	57	−5.83	−4.07	−2.05	−3.10	−4.58	−2.40	−3.79
17	Mönthal	AG	36	−2.40	−2.68	**−1.01**	−2.34	−1.82	**−0.43**	−1.83
18	Schwarzenberg	LU	21	−2.14	**−1.26**	**0.62**	**−0.03**	**−1.56**	*	*
19	Geschinen	VS	56	−5.86	−5.83	−2.70	−3.95	−4.47	−2.92	−4.22
20	Hüttikon	ZH	22	−2.62	*	*	*	*	*	*
21	Beckenried	NW	50	−6.96	−5.86	−2.58	−3.05	−4.27	*	−2.64
22	Zug	ZG	24	−3.88	−2.54	−2.49	−2.84	−3.59	*	−2.60
23	Andermatt	UR	63	*	*	−3.48	−5.75	−7.08	−2.65	−4.72
24	Quinto	TI	59	−8.02	−6.93	−4.19	−5.74	−7.12	−2.30	−3.99
25	Bürglen (UR)	UR	52	−5.84	−5.56	−3.18	−4.43	−5.45	−2.19	−3.64
26	Adlikon	ZH	28	−3.72	−2.89	**−1.60**	−2.81	−3.35	*	−1.73
27	Sonogno	TI	58	−4.29	−4.21	−2.54	−2.77	−2.21	**−0.43**	−1.75
28	Mergoscia	TI	43	−4.18	−4.03	−3.09	−3.14	−3.83	−1.96	−1.75
29	Torricella-Taverne	TI	42	−4.27	−2.37	−1.93	−2.54	−3.98	**−1.10**	**−1.20**
30	Lago di Lugano	TI	22	*	*	*	*	*	*	*
31	Lodrino	TI	44	**−1.36**	**−1.23**	**−0.08**	**−0.54**	**−0.88**	*	**0.79**
32	Rieden	SG	36	−4.27	−4.43	−1.81	−2.90	−4.09	*	−2.42
33	Degen	GR	57	−4.52	−4.18	−2.12	−3.08	−3.58	**−1.22**	−2.56
34	Walenstadt	SG	54	−6.47	−5.91	−3.89	−3.84	−4.71	−1.89	**−1.53**
35	Mathon	GR	61	−8.41	−6.46	−3.34	−4.15	−6.13	*	−3.03
36	Soglio	GR	57	−5.97	−4.55	−2.42	−3.31	−4.90	−2.40	−3.24
37	St. Moritz	GR	29	*	*	−3.90	−3.37	−4.03	−2.74	−2.38
38	Brusio	GR	73	−8.99	−7.87	−4.27	−5.22	−6.77	−2.00	−2.97
Mean				−4.40	−3.83	−2.36	−3.08	−3.77	−1.96	−2.48

5 Chapter III: Modelling vascular plant diversity at the landscape scale using systematic samples

Journal of Biogeography (*J. Biogeogr.*) (2008) **35**, 1226–1240

ORIGINAL ARTICLE

Modelling vascular plant diversity at the landscape scale using systematic samples

Thomas Wohlgemuth[1]*, Michael P. Nobis[1], Felix Kienast[1] and Matthias Plattner[2]

[1]Swiss Federal Research Institute WSL, Birmensdorf and [2]Hintermann and Weber AG, Ecological Consultancy, Planning and Research, Reinach, Switzerland

ABSTRACT

Aim We predict fine-scale species richness patterns at large spatial extents by linking a systematic sample of vascular plants with a multitude of independent environmental descriptors.

Location Switzerland, covering 41,244 km^2 in central Europe.

Methods Vascular plant species data were collected along transects of 2500-m length within 1-km^2 quadrats on a systematic national grid (n = 354), using a standardized assessment method. Generalized linear models (GLM) were used to correlate species richness of vascular plants per transect (SR$_t$) with three sets of variables: topography, environment and land cover. Regression models were constructed by the following process: reduction of collinearity among variables, model selection based on Akaike's information criterion (AIC), and the percentage of deviance explained (D^2). A synthetic model was then built using the best variables from all three sets of variables. Finally, the best models were used in a predictive mode to generate maps of species richness (SR$_t$) at the landscape scale using the moving window approach based on 1-km^2 moving windows with a resolution of 1 ha.

Results The best explanatory model consisted of seven variables including 14 linear and quadratic parameters, and explained 74% of the deviance (D^2 = 0.742). Used in a predictive mode, the model generated maps with distinctive horizontal belts of highest species richness at intermediate altitudes along valley slopes. Belts of higher richness were also present along rivers and around large forest patches and larger villages, as well as on mountains.

Main conclusions The approach involved using consistent samples of species linked to information on the environment at a fine scale enabled landscapes to be compared in terms of predicted species richness. The results can therefore be applied to support the development of national nature conservation strategies. At the landscape scale, belts of high species richness correspond to steep environmental gradients and associated increases in local habitat diversity. In the mountains, the belts of increased species richness are at intermediate altitudes. These general belt-like patterns at mid-elevation are found in all model parameterizations. Other patterns, such as belts along rivers, are visible in specific parameterizations only. Thus we recommend using several sets of parameters in such modelling studies in order to capture the underlying spatial complexity of biodiversity.

Keywords

Biodiversity, conservation biogeography, generalized linear models, hotspots, land cover, landscape scale, model prediction, spatial patterns, Switzerland, topography.

*Correspondence: Thomas Wohlgemuth, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.
E-mail: thomas.wohlgemuth@wsl.ch

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2008.01884.x

INTRODUCTION

Species inventories and samples of species provide baseline information for the analysis of biodiversity. The value of the outputs depends largely on the quality of the original data (Kier *et al.*, 2005), the availability of environmental data, and the analytical methods used to combine them. Because vascular plants are an important component of terrestrial habitats, maps of species composition (vegetation maps) and of species richness (biodiversity maps) are valuable indicators for the derivation of spatially explicit conservation strategies.

Model predictions have proven valuable in the detection of biodiversity patterns (Engler *et al.*, 2004; Pimm & Brown, 2004). However, when the prediction of species richness is considered at the landscape scale, it is rare to have fine-grained information for large areas for both environmental factors and the corresponding species richness. For this reason, biodiversity maps that use a high extent/grain ratio are also rare (Zimmermann & Kienast, 1999; Araújo *et al.*, 2005). However, such fine-grained maps for large regions not only may provide an appropriate basis for local and regional conservation planning (Poiani *et al.*, 2000; Ferrier, 2002), but also may add insight to global diversity patterns (Currie *et al.*, 2004).

The ongoing refinement of spatial resolution of environmental factors (Pimm & Brown, 2004) will lead to an increase in the resolution of model predictions of variations in species abundances (Guisan *et al.*, 2002; Dullinger *et al.*, 2003; Lütolf *et al.*, 2006) as well as richness (Ferrier *et al.*, 2004). Refinement of the spatial resolution of species richness (response variable) follows two strands: one way to assess detailed species information at the landscape scale is to record species richness at a relatively fine grain, e.g. quadrats of 1 km^2 that are arranged contiguously (Heikkinen, 1996; Wyler, 2004). Another way – specifically suited to larger areas – is to use presence/absence data on single species rather than species richness. The latter are input into static models linking species occurrence with fine-grained environmental predictors. The models can be used to mimic potential fine-grain distributions of many species, leading to cumulative species richness assessment. Explanatory models of both approaches can then be used in a predictive mode to show fine-scale patterns of species richness, relevant to local planners.

Both the quality and the interpretability of models and the derived richness maps depend strongly on variable selection. In small regions with a limited altitudinal range, land use usually accounts for a high percentage of the variation in species richness (Heikkinen *et al.*, 2004; Kerr & Cihlar, 2004; Ortega *et al.*, 2004; Waldhardt *et al.*, 2004). In contrast, in mountainous regions, variations in energy or other climate parameters (Grytnes *et al.*, 1999; Vetaas & Grytnes, 2002; Bhattarai *et al.*, 2004; Hawkins & Pausas, 2004; Moser *et al.*, 2005), substrate (Wohlgemuth, 2002b; Bruun *et al.*, 2003) and topography (Heikkinen & Birks, 1996) are the main factors correlated with species richness. Patterns in the species composition and diversity of Switzerland reflect a wide range of the aforementioned ecological factors mainly influenced by topography as a proxy.

Environmental baseline information on Switzerland is available at a high level of resolution. Since 2001, presence–absence data on multiple taxa, including vascular plants, become available at various scales within the framework of the Swiss federal Biodiversity Monitoring programme (BDM, Plattner *et al.*, 2004; Weber *et al.*, 2004). Within this framework, vascular plant species richness has been collected on a systematic national grid of 1-km^2 plots (total $n = 520$). By the end of 2004, 68% ($n = 354$) of the sample quadrats were available for statistical analyses.

Here a predictive procedure is described that spatially quantifies the richness of plant species at the landscape scale, based on a systematic national sample and several sets of environmental variables at a fine grain. The procedure involves modelling species richness by regression techniques and predicting species richness by applying model predictors to a region using a moving window approach. In order to cope with the spatially unevenly distributed predictor variables, the study was based on three different sets of variables: topography, environmental factors (climate/substrate/water body) and land cover, and on a combination of the best fitting variables. The richness models and the subsequently derived maps are compared and used to discuss national landscape patterns of plant species richness. The suggested implications for biodiversity conservation are presented.

METHODS

Study area

The study area is Switzerland, which covers 41,244 km^2 in central Europe and ranges in altitude from 193 to 4634 m a.s.l. (45°49′–47°48′ N latitude, 5°57′–10°30′ E longitude; Fig. 1). Approximately 60% of the country is in the Alps and 10% in the Jura Mountains. The average elevation is 1300 m a.s.l. Almost 7% of the country is considered to consist of urban environments (indicated by land-cover types 16–24 in Table 1), including buildings, associated green areas, and road and rail networks (BFS, 1992/1997). The mean annual temperature ranges from −10.5 to 12.5°C, and annual precipitation from 438 to 2950 mm (Zimmermann & Kienast, 1999).

Plant species data

In the framework of the Swiss BDM, three types of indicators are monitored under the headings pressure, state and response. In total, 11 state indicators (Z, for German *Zustand*) are regularly assessed. The Z7 indicator monitors the diversity of vascular plants on a landscape scale using a systematic sample of 520 1-km^2 quadrats and minimum spacing ranging from 14.3 to 19.1 km (Hintermann *et al.*, 2000; Fig. 1). The grid is denser in the regions of the Jura Mountains and the Ticino. The BDM aims, among other objectives, to survey landscape

Figure 1 Swiss sample of vascular plant species richness on a landscape scale (1 km^2) within the framework of Switzerland's federal Biodiversity Monitoring programme.

biodiversity – from lowland to alpine zones – over a long period. By the end of 2004, 80% of the sample quadrats had been visited for a first assessment. Quality checks were made to exclude quadrats with incomplete species lists, and lists of quadrats adjacent to Switzerland's borders and < 1 km^2 in area. The resulting test data set for analysis was made up of species lists for 354 quadrats, 68% of the total sample (Fig. 1).

Data collection in the quadrats followed a strict procedure: for every sample quadrat, transect routes 2500 m long were defined by maintaining a close proximity to the quadrat diagonals. Wherever possible, transects followed existing paths or roads. Sample quadrats were each visited by one of 29 botanists. All vascular plant species growing in buffers of 2.5 m on both sides of the transect were registered electronically (Plattner *et al.*, 2004) and served as the measure of transect species richness of vascular plants (SR_t) in the following analyses. Quadrats will be reassessed every 5 years (Weber *et al.*, 2004), with 20% of the quadrats visited per year.

Environmental data

All the environmental predictors used in the study are available in digital form as 1-ha grids. They are derived from maps of various origins (Table 2). In order to predict species richness nationwide on a fine scale and with a 1-km^2 focal window, predictor maps were created with grain sizes of 1 ha by applying the focal functions mean, standard deviation, range, maximum and minimum on a 1-km^2 moving window with a 100-m increment. Three variable sets were included derived from the predictor maps: (1) topography, (2) environment consisting of climatic data, substrate and water bodies, and (3) land cover derived from an aerial assessment.

Topography set

Topography reflects the structure of the land surface. In mountainous regions, topography, as reflected by elevation, slope and aspect, greatly affects plant growth (Körner, 1999). Directly derived topographical variables often serve for modelling vegetation or plant species richness (Gottfried *et al.*, 1998; Guisan & Zimmermann, 2000). Elevation has served in many studies as a proxy for information on habitat diversity and species richness (Wohlgemuth, 1993; Pyšek *et al.*, 2002). Topographic heterogeneity also plays a role in the prediction of species richness at meso-scales (Fleishman & Mac Nally, 2002; Vormisto *et al.*, 2004; Sarr *et al.*, 2005). Because of the great variability in relief in Switzerland, topography was used as the first set of variables. Using a 100-m grid derived from the digital elevation model of 25-m resolution (DHM-25, Bundesamt für Landestopographie), the mean, minimum, maximum, range and standard deviation were derived (E.avg, E.min, E.max, E.ran, E.std) for each 1 km^2 (Table 2). In addition, variables were produced for the proportions of south- and north-facing slopes (N, S) and the relative amounts of different slope classes (FLAT, SLOPE, STEEP).

Environmental set

The definitions of the variables (Table 2) are based on earlier studies of the predictive power of both bioclimatic and habitat heterogeneity variables for total species richness of vascular plants in Switzerland (Wohlgemuth, 1998; Zimmermann & Kienast, 1999; Moser *et al.*, 2005).

The environmental variables temperature and precipitation refer to interpolations of measurements for the period 1961–1990 using DHM-25, 365 stations for precipitation sums, and 158 for average temperatures (Zimmermann & Kienast, 1999). Additional national data were acquired from the same source for the variables: potential direct solar radiation and monthly potential evapotranspiration (PET), using the formula of Turc (1961), which integrates cloudiness with corrected direct solar radiation. Water balance was calculated for July as the sum of precipitation minus PET.

The proportions of calcareous and siliceous substrate within quadrats were derived from the geotechnical map of

Table 1 Land-cover variables according to land-cover types in Switzerland 1992–1997 with 1-ha resolution (Bundesamt für Statistik, GEOSTAT, CH-2010 Neuchâtel).

Variables			Area of Switzerland		Sample plots (n = 353)		
Aggregation	Standard class	Cover type	km^2	%	Affected plots	Average area (ha)	Range used for simulation (ha)
Wooded areas							
L.forest[1]	1	Closed forest	10252.23	24.83	286	29.97	0–99
	2	Open forest	769.33	1.86	138	2.43	0–32
	3	Brush forest	605.14	1.47	72	2.08	0–63
	4	Woods	1089.75	2.64	256	3.12	0–20
L.tree[2]	2–4	Open woody formations	2464.22	5.97	275	7.64	0–67
Agricultural areas							
	5	Vineyards	154.36	0.37	15	0.27	0–54
	6	Orchards, fruit tree plantations	414.80	1.00	94	1.03	0–20
	7	Horticulture	40.36	0.10	16	0.10	0–70
	8	Arable land and grassland, lowlands	8373.55	20.28	201	19.66	0–97
	9	Farm pastures, lowlands	890.11	2.16	141	2.04	0–30
L.agrilow[3]	5–9	Agricultural lowlands	9873.18	23.91	208	23.11	0–97
	10	Mountain meadows	323.16	0.78	46	1.24	0–44
	11	Alpine pastures	5054.85	12.24	173	12.02	0–92
L.agrialp[4]	10–11	Agricultural alps	5378.01	13.02	181	13.26	0–92
Unproductive areas							
L.lake[5]	12	Lakes	1422.35	3.44	24	2.16	0–98
L.river[6]	13	Rivers and river shores	317.32	0.77	94	0.61	0–11
L.unprod[7]	14	Unproductive vegetation	2630.51	6.37	183	6.87	0–68
L.bare[8]	15	Bare areas: glaciers, rocks, sand, screes	6155.99	14.91	147	10.92	0–100
Urban areas							
	16	Buildings	385.08	0.93	107	0.77	0–10
	17	Surroundings of buildings	990.50	2.4	128	1.93	0–28
	18	Industrial buildings	72.92	0.18	21	0.10	0–50
	19	Industrial grounds	129.41	0.31	32	0.18	0–70
	20	Special urban areas	161.13	0.39	55	0.35	0–12
	21	Recreation areas and cemeteries	158.60	0.38	44	0.28	0–12
	22	Road areas	792.97	1.92	187	1.69	0–13
	23	Railway areas	84.49	0.2	27	0.14	0–60
	24	Airports and airfields	15.85	0.04	2	0.02	0–30
L.urban[9]	16–24	Urban areas	2790.95	6.75	221	5.46	0–50

Twenty-four standard classes and nine aggregated land-cover variables were used as a final set for modelling transect species richness (SR_t) per 1 km^2 (superscript numbers 1–9 refer to the legend of Fig. 2b).

Switzerland (De Quervain *et al.*, 1963–1967). Only two substrate types were distinguished because earlier studies have found these to be sufficient (Wohlgemuth, 1998, 2002a; Schmidtlein & Ewald, 2003; Wohlgemuth & Gigon, 2003). Lake and glacier surfaces in the geotechnical map were considered as additional substrate types. Water bodies that are indicated on the 1 : 25,000 topographic maps of Switzerland are available digitally (BFS GEOSTAT/Bundesamt für Landestopographie), with linear information on lakeshore length, river length and creek length.

Land-cover set

It was possible to distinguish between the environmental variables and a set of land-cover variables by concentrating on differences between ecological factors and those that are strongly influenced by human land use. Land-cover information was derived from aerial data and is available on a grid with a 100-m resolution in the land-use/land-cover data package GEOSTAT from the Swiss Federal Office of Statistics (Bundesamt für Statistik, 2001). The standard classification of 24 classes was used, as defined in Table 1. Each variable is indicated as a proportion with respect to a 1-km^2 quadrat. Using FRAGSTATS ver. 3.3 (http://www.umass.edu/landeco/research/fragstats/fragstats.html), landscape metrics were calculated, including Shannon's diversity index, Simpson's diversity index and the largest patch size index.

Numerical analyses

Alternative models were fitted using generalized linear models (GLM, McCullagh & Nelder, 1989) to analyse the relationship

Table 2 Variables used for regression models of transect species richness (SR_t) per 1 km^2

Variable root (1 ha)	Description	Derivation	Model variables (1-km^2 quadrats)
Topography set			
E	Elevation (m)	DEM-25 (Bundesamt	E. + avg, max, min, ran, std
Slope	0–3° = flat; 3–30° = slope; 30–100° = steep (%)	für Landestopographie)	FLAT, SLOPE, STEEP
Aspect	340–50° = north; 160–230° = south (%)		N, S
Environmental set			
TY	Temperature, annual average (°C)	Zimmermann & Kienast	TY. + avg, max, min, ran, std
T1	Temperature, January (°C)	(1999)	T1. + avg, max, min, ran, std
T7	Temperature, July (°C)		T7. + avg, max, min, ran, std
TR	Temperature, variation: T7–T1 (°C)		TR. + avg, max, min, ran, std
PY	Precipitation, year (mm)		Py. + avg, max, min, ran, std
P7	Precipitation, July (mm)		P7. + avg, max, min, ran, std
R3	Potential direct solar radiation, March		R3. + avg, max, min, ran, std
R7	Potential direct solar radiation, July		R7. + avg, max, min, ran, std
WB7	P7–PET7		WB7. + avg, max, min, ran, std
GEO	GLAC = glaciers, LAKE = lakes, CALC = calcareous substrate, SILI = siliceous substrate	De Quervain *et al.* (1963–1967)	GLAC, LAKE, CALC, SILI
LAK	Lake shores (m)	BFS GEOSTAT	LAK. + avg, max, ran, std
RIV	River length (m)	(Bundesamt für Landestopographie)	RIV. + avg, max, ran, std
CRE	Creek length (m)		CRE. + avg, max, ran, std

avg, mean; max, maximum; min, minimum; ran, range; std, standard deviation.

between vascular plant species richness and sets of variables. For all models, the response variable was the transect species richness of vascular plants (SR_t) per 1-km^2 quadrat. Because count data such as species richness can never be less than zero, the assumption of ordinary least-squares regression is likely to be broken (Nicholls, 1989; Crawley, 1993; Mittelbach *et al.*, 2001). We assumed SR_t to be a Poisson-distributed random variable and used a logarithmic link function in GLM (Crawley, 1993). All variables enter the models with linear and quadratic terms. In order to compare the influence of different factor types, the analysis focused on four models using variables from the topography set (topography model), the environmental set (environmental model), the land-cover set (land-cover model), and the synthetic model. All GLM analyses were performed using R ver. 2.1.1 (R Development Core Team, 2005).

For the land-cover set, the 24 standard land-cover classes were aggregated into four categories: wooded areas, agricultural areas, unproductive areas and urban areas (Table 1). An ecologically oriented variable selection was carried out (Luoto *et al.*, 2002), resulting in an aggregation of nine variables with realistic composition. Landscape metric variables were compared with aggregated land-cover classes using univariate correlation coefficients with SR_t, but they were not considered in the models because combinations of selected land-cover variables are easier to interpret.

In order to reduce the large number of initial variables in the environmental model ($n = 61$), the collinearity among the variables was first analysed. Groups of highly correlated variables were defined using a cut level of $R^2 = 0.9$ (corresponding to a variance inflation factor of 10). From each resulting group, only the one with the best GLM performance based on Akaike's information criterion (AIC, Venables & Ripley, 1999) was selected for further analysis, resulting in 30 remaining variables.

In a second step, GLM were built using the refined variable groups. Starting with the best performing single variable model based on AIC, the number of variables was increased until the change in explained deviance D^2 was less than 1% [D^2 = (null deviance – residual deviance)/null deviance, Schwarz & Zimmermann, 2005]. Each of the best *n*-variable models was determined by comparing all possible *n*-variable combinations. If the D^2 stop criterion had not been used, the final models would have included a large number of additional variables that would have accounted for a very small percentage of D^2.

Highly influential plots and outliers were detected in a third analytical step by examining regression diagnostics (residuals vs. fitted values, normal *Q*–*Q* plots, and Cook's distance plots). Reduced samples were reanalysed (step 2) until no influential plot or outlier remained. One outlier was detected and removed (final $n = 353$): the city of Geneva, of which 96% is urban.

For the final models, linear and quadratic terms were tested separately by backward elimination based on AIC, and nonsignificant parameters were excluded (*z*-statistic, R Development Core Team, 2005).

In order to characterize the models, we calculated the importance of the variables for the model performance. Accordingly, linear and quadratic terms were removed separately or together from the GLM models. Resulting changes in the explained deviance D^2 indicated the importance of the parameters and variables. Model robustness was evaluated with 10-fold cross-validations. For robust results, the mean of 100 internal cross-validations was used. The non-spatially explicit GLMs were tested for spatial autocorrelation using Moran's I correlograms on model residuals (R package ncf by O.N. Bjornstad, ver. 1.0–8). The significances of the autocorrelations ($P < 0.01$) were tested by resampling ($n = 1000$) based on adjusted P-values (Holm, 1979).

Species-richness maps were generated by applying the final models to the pixel values of the corresponding fine-grained factor maps. No predictions were calculated for quadrats with predictor values that exceeded the range of values in the model calibrations. For example, in the land-cover model, areas where > 50% is urban (Table 1) were out of the model range. Thus, cities were excluded from predictions and large lakes were also excluded from the simulations.

According to earlier studies on regional species richness in Switzerland, elevation is the best proxy variable for environmental variability when applied to the regions with areas ranging between 10 and 100 km^2 (Wohlgemuth, 1993). In preliminary analyses of richness at a 1-km^2 scale, average elevation rather than the relative range was found to be more highly correlated with the variability of plants throughout the altitudinal range of Switzerland (193 to 4634 m a.s.l.). Therefore, the predictive power of the four final models was evaluated by applying the models to a varying number of plots using average plot elevation as an upper threshold criterion.

RESULTS

The variable selection for the different models is listed in Table 3. For the topography model, a combination of elevation (average and range), slope (SLOPE) and aspect (N) showed a D^2 of 0.61. Using environmental variables, the best model with a D^2 of 0.69 combined temperature (annual average, range of annual variation), radiation (average in March), substrate (glaciers, calcareous substrate) and water bodies (standard deviation of creek length, maximum length lake shores). The land-cover model, using ecologically oriented aggregations in nine classes, had a D^2 of 0.70. The correlation coefficients between landscape metrics (e.g. patch richness) and SR_t were consistently high, often higher than correlation coefficients between SR_t and single or aggregated land-cover classes (Table 4). Nevertheless, for ease of interpretation of the model results and species richness maps, these landscape metrics were not included as variables in the models. The statistically most meaningful synthetic model had a D^2 of 0.74, and combined elevation (average), land-cover classes (bare areas, lowland agriculture, open woody formations), substrate (calcareous substrate), temperature (range of annual variation) and water body (standard deviation of creek length). If all the variables from the previous models were used, the full synthetic model yielded a D^2 of 0.78.

The relative importance of the parameters used in the models is shown in Table 5. For instance, if both the linear and the quadratic terms of the average elevation (E.avg) in the topography model were removed, the remaining model deviance D^2 would be decreased by 95.4%. The most important variables found were average elevation (topography model, synthetic model), average of mean annual temperature (environmental model) and bare areas (land-cover model). All models were quite robust after a 10-fold cross-validation (Table 6). The cross-validated mean absolute error (MAE) in species richness ranged between 28.5 (synthetic model) and 33.3 (topography model) species. The mean SR_t of the Swiss sample was 224 species (range two to 364 species).

The simulated richness map based on the synthetic model is presented in Fig. 2a. A clipped area is compared with selected environmental factors (Fig. 2b) and with the model predictions derived from the three single variable sets (Fig. 2c). In all maps, the coarse patterns of species-poor high-altitude land in the Alps, in comparison with the more species-rich valleys and lowlands, are readily apparent. At finer scales, patterns differ with respect to the model parameters used. The highest values for SR_t were simulated along steep altitudinal gradients in the mountains (topography and environmental model) and along rivers (land-cover model). In the lowlands of the Central Plateau, the features 'villages' and 'forest edges' corresponded best to locally increased SR_t (land-cover set). The prediction, generated by the synthetic model shows spatial features similar to the previous model predictions. In all maps predicted by the models, the patterns of increased species richness were often arranged distinctively along linear features: straight along mountain valleys, curved along rivers, and in belts around villages, large forests and isolated large mountains.

Mid-elevation peaks for the Swiss sample and for the predictive synthetic model are shown in Fig. 3. Peaks range from 1200 to 1300 m a.s.l. Model performance measured as the correlation (R^2) between modelled and sampled species richness (SR_t) declined (Fig. 4b) when high-elevation plots were successively excluded (Fig. 4a). For the topography, environmental and synthetic models, exclusion of plots below 2000 m does not result in a further loss of predictive power. In contrast, the performance of the land-cover model increased when only plots with an average elevation of < 1900 m a.s.l. were entered, and exceeded the synthetic model below 1400 m a.s.l. Average modelled richness (SR_t) as a function of systematically reduced high-elevation plots shows a clear bell-shaped curve (Fig. 4c). A maximum value is reached with a sample consisting of all plots ranging from 200 to 1800 m a.s.l.

The transect species richness SR_t of the Swiss sample and the residuals of the synthetic model were only moderately autocorrelated in space (absolute values of Moran's $I \leq 0.11$). Significant autocorrelations were found only at a lag distance of 40 km for both the response variable SR_t and residuals of the topography and land-cover models.

Table 3 Selection of model variables.

Variable					
n	Names or selection procedure	AIC	Residual deviance	D^2	Percentage change in D^2
Topography model					
1	E.avg	6082.0	3540.8	0.548	–
2	E.avg + E.ran	5755.3	3210.1	0.590	7.7
3	E.avg + E.ran + N	5677.0	3127.8	0.601	1.8
4	E.avg + E.ran + N + SLOPE	5613.8	3060.6	0.609	1.4
5	E.avg + E.ran + N + SLOPE + S	5586.2	3029.0	0.613	0.7
9	Stepwise regression (AIC; backward elimination & forward selection)	5541.9	2978.7	0.620	
10	All variables	5550.0	2976.8	0.620	–
Environmental model					
1	TY.avg	6615.9	4074.7	0.480	–
2	TY.avg + TR.ran	6051.7	3506.5	0.552	15.1
3	TY.max + R3.ran + GLAC	5561.7	3012.5	0.615	11.4
4	TY.avg + TR.ran + GLAC + CALC	5316.3	2763.1	0.647	5.2
5	TY.avg + TR.ran + GLAC + CALC + CRE.sd	5159.5	2602.3	0.668	3.2
6	TY.avg + TR.ran + GLAC + CALC + CRE.sd + R3.avg	5071.9	2510.7	0.679	1.8
7	TY.avg + TR.ran + GLAC + CALC + CRE.sd + R3.avg + RIV.max	5014.0	2448.8	0.687	1.2
8	TY.avg + TR.ran + CALC + CRE.sd + R3.avg + RIV.max + LAKE + SILI	4965.5	2396.3	0.694	0.97
29	Stepwise regression after reduction of collinearity (VIF>10)	4581.7	1952.6	0.751	–
30	All variables after reduction of collinearity (VIF>10)	4599.9	1948.7	0.751	–
61	All variables	4288.1	1540.9	0.803	–
Land-cover model					
9	L.forest + L.tree + L.agrilow + L.agrialp + L.lake + L.river + L.unprod + L.bare + L.urban	4953.3	2382.2	0.696	–
24	All variables (non-aggregated land-cover classes)	4760.7	2131.5	0.728	–
Synthetic model					
1	E.avg	6082.0	3540.8	0.548	
2	E.avg + L.bare	5618.7	3073.6	0.607	10.9
3	E.avg + L.bare + L.agrilow	5235.4	2686.2	0.657	8.1
4	E.avg + L.bare + L.agrilow + E.ran	5009.8	2456.6	0.686	4.5
5	E.avg + L.agrilow + E.ran + GLAC + L.agrialp	4827.1	2269.9	0.710	3.5
6	E.avg + L.agrilow + E.ran + GLAC + L.agrialp + L.tree	4703.0	2141.8	0.726	2.3
7	E.avg + L.bare + L.agrilow + L.tree + CALC + TR.ran + CRE.sd	4585.0	2019.8	0.742	2.1
8	E.avg + L.bare + L.agrilow + GLAC + L.tree + CALC + TR.ran + CRE.sd	4532.3	1963.1	0.749	0.98
17	Stepwise regression (AIC; backward elimination and forward selection)	4291.4	1694.2	0.784	–
20	All variables	4299.4	1692.3	0.784	–

A change in deviance $D^2 < 1\%$ was used as a stopping criterion. Null deviance = 7830.3; d.f. = 352.

DISCUSSION

A comparison of models and maps

The differences between the four final models (elevation, environment, land use, synthetic) are conspicuous, although some have low explained deviance. A surprisingly high amount of the variability in species richness is associated with topography; this is explained by the wide altitudinal range in Switzerland as well as the high degree of environmental heterogeneity in the quadrats, with flat areas in the lowlands, steep slopes in the mountains and exclusively alpine zones above the timberline. On the landscape scale (grain 1 km^2, extent Switzerland), average elevation was the best proxy variable to explain transect plant species richness nationwide. Elevation range and the corresponding temperature range were the second best variables in the topography set and the environmental models, respectively. This finding contrasts with earlier studies of floristic richness in landscape studies in Switzerland by Wohlgemuth (1993), where range was most important. In the latter study, however, the mapping units corresponded to topographically defined landscape entities such as valleys, and the average areas of the mapping units amounted to 84 and 49 km^2 below and above the timberline, respectively.

Areas with a high proportion of land with a northern aspect showed decreased SR_t in the topography model. The influence of aspect on species distribution and vegetation along mountain ranges is well established (Moor, 1952; Landolt, 1983; Forman, 1995). Nevertheless, only a few specific studies have confirmed an explicit influence of slope orientation on species richness (Harner & Harper, 1976; Nichols *et al.*, 1998; Searcy *et al.*, 2003). The results from the topography model suggest

Table 4 Pearson's correlation coefficients of land-cover and elevation variables (left) and landscape metrics variables (right) with transect species richness (SR_t).

Variables used for models	*r*	Landscape metrics	*r*
*L.bare	−0.627	Mean perimeter–area ratio	0.611
E.min (minimum elevation)	−0.469	Mean patch area	−0.609
*L.forest	0.442	Shannon diversity, 24 classes	0.595
*E.avg (average elevation)	−0.420	Patch richness	0.594
Woods (4)	0.414	Shannon diversity, 9 classes	0.592
E.max (maximum elevation)	−0.362	Simpson diversity	0.583
*L.lake	−0.284	Edge diversity	0.552
*L.tree	0.205	Number of patches	0.542
Mountain meadows (10)	0.205	Interspersion/juxtaposition index	0.514
		Largest patch index	−0.510
		Contagion	−0.429
		Mean Euclidian nearest distance	0.264

Only coefficients >0.2 are displayed. For definitions of land-cover variables see Table 1. Landscape metrics variables were not considered for modelling. *, Variables included in the final land-cover model or in the synthetic model.

that south-facing slopes are more species-rich than those on northern slopes. This result is consistent with the species–energy hypothesis (Currie, 1991; Moser *et al.*, 2005) and can be explained by radiation differences between the two aspects causing contrasting temperature regimes.

Compared with the topography model, the fit of the environmental model is only marginally improved. In this model, both the average and range of annual temperature replace elevation variables. Nevertheless, these temperature variables do not take into consideration local variations due to differences in slope and aspect because the relevant climate stations used for interpolation are always located on flat ground (international standard). Instead, slope and aspect are replaced by average radiation in the environmental model.

The addition of water bodies and calcareous substrate improves model performance. Calcareous substrate plays a significant role in geologically diverse regions and at the landscape scale (Wohlgemuth, 1998, 2002b; Ewald, 2003; Wohlgemuth & Gigon, 2003). If present, a calcareous substrate increases landscape species richness because of increased habitat diversity (Wohlgemuth & Gigon, 2003). Correspondingly, calcareous substrates in temperate zones support a richer flora than acid substrates (Pärtel, 2002; Ewald, 2003). The inclusion of glaciated areas further improved the model performance. This is due to the species–area effect because quadrats fully or partly covered by glaciers support only a few or no vascular plant species. Glaciers in Switzerland cover 2.7% of the surface. In a similar way, high-elevation zones with low species richness greatly improve the model performance. If these zones are excluded from prediction, the performance is significantly lower (Fig. 4b).

The fit of the land-cover model using the full sample was superior to those of both the topography and environmental models, having bare area as the best model predictor. With respect to the sample quadrats, the proportion of bare area is greater at high levels and reflects the steep gradient between the mountains and lowlands linked to plant species richness. In general, in Switzerland, landscape species richness below the timberline is twice as high as that above the trees (Wohlgemuth, 1993). The remaining variables in the land-cover model tended to be equally important for model performance. This supports both the habitat-diversity hypothesis that predicts higher species richness as a result of increased habitat diversity (Shmida & Wilson, 1985) and the species–area effect with decreasing vegetation area at higher elevations. The results were confirmed by the generally high correlation coefficients of landscape metric variables listed in Table 4. When using the land-cover model predictors for extrapolating species richness spatially, the belts along steep altitudinal gradients, such as along valley slopes, are less pronounced than in maps based on environmental model predictors. This is because there are only a few possible land-cover categories along valley slopes – such as forests, mountain meadows and unproductive vegetation – that correspond to the general unimodal response of species richness along the altitudinal gradient. In comparison, the diversity of land cover categories present in lowland landscapes results in a better correspondence to fine-scale differences in species richness.

A further increase in model fit resulted from the synthesis of all predictors from the previous models. Although clearly visible in the mountainous regions, the influence of the altitudinal gradient is less pronounced than in the models of topography and environment. By analogy to the land-cover model, the synthetic model results in more interpretable patterns of species richness in culturally rich landscapes such as the Central Plateau than those that result from models using topography or environmental variables.

The comparison of the four model-predicted maps revealed the importance of including different variables to improve the predictability of species richness over larger and variously structured regions. As many studies have shown (e.g. Francis & Currie, 2003; Currie & Francis, 2004), topographic variables or derived climate variables explain the majority of richness variation at coarse scales across a large geographical extent. If the climatic variation of a region is small, however, land-cover diversity correlates better with species richness, following the habitat-diversity hypothesis.

Table 5 Calibrated linear (l) and quadratic (q) parameters of variables for selected models and effects of parameter removals on model performance.

	Linear parameter (l)			Quadratic parameter (q)			Percentage change in D^2		
Variable	Estimate	SE	*P*-value	Estimate	SE	*P*-value	$-l$	$-q$	$-(l+q)$
Topography model									
(Intercept)	5.00E+00	2.00E-02	***	–	–		–	–	–
E.avg	6.42E-04	3.27E-05	***	−3.49E-07	1.05E-08	***	8.2	24.2	95.4
E.ran	8.58E-04	6.35E-05	***	−6.08E-07	6.85E-08	***	3.9	1.7	16.9
SLOPE	4.94E-03	6.17E-04	***	−3.79E-05	5.04E-06	***	1.4	1.2	12.5
N	−1.49E-03	1.61E-04	***	n.a.	n.a.	n.s.	1.8	n.a.	n.a.
Environmental model									
(Intercept)	4.33E+00	3.08E-02	***	–	–		–	–	–
TY.avg	1.27E-03	4.10E-05	***	−6.87E-07	4.10E-08	***	19.1	5.4	29.5
TR.ran	7.61E-03	3.65E-04	***	−3.34E-05	2.35E-06	***	8.2	3.9	12.6
GLAC	−3.47E-02	2.77E-03	***	2.82E-04	3.60E-05	***	3.1	1.1	6.6
CALC	3.85E-03	6.23E-04	***	−1.45E-05	5.40E-06	**	0.7	0.1	5.3
CRE.sd	4.42E-03	5.83E-04	***	−3.98E-05	9.33E-06	***	1.1	0.3	2.5
R3.avg	3.09E-05	3.45E-06	***	n.a.	n.a.	n.s.	1.5	n.a.	n.a.
RIV.max	n.a.	n.a.	n.s.	5.28E-06	6.69E-07	***	n.a.	1.1	n.a.
Land-cover model									
(Intercept)	6.29E+00	7.85E-02	***	–	–		–	–	–
L.bare	−3.60E-03	1.19E-03	**	−1.87E-04	1.09E-05	***	0.2	5.4	15.9
L.unprod	−8.01E-03	1.53E-03	***	−1.55E-04	2.33E-05	***	0.5	0.8	5.9
L.agrilow	−5.12E-03	9.86E-04	***	−7.45E-05	7.13E-06	***	0.5	2.0	4.8
L.lake	−9.41E-03	1.71E-03	***	−5.84E-05	1.91E-05	**	0.6	0.2	4.6
L.forest	−5.12E-03	1.10E-03	***	−4.60E-05	6.34E-06	***	0.4	1.0	4.4
L.tree	n.a.	n.a.	n.s.	−2.48E-04	1.71E-05	***	n.a.	4.1	n.a.
L.agrialp	−5.90E-03	1.09E-03	***	−6.69E-05	9.26E-06	***	0.5	1.0	4.3
L.urban	n.a.	n.a.	n.s.	−2.36E-04	2.21E-05	***	n.a.	2.1	n.a.
L.river	2.09E-02	5.69E-03	***	−2.69E-03	6.87E-04	***	0.2	0.3	0.3
Synthetic model									
(Intercept)	4.94E+00	2.50E-02	***	–	–		–	–	–
E.avg	2.21E-04	4.09E-05	***	−1.60E-07	1.47E-08	***	0.5	2.0	7.49
L.bare	6.52E-03	8.82E-04	***	−1.32E-04	8.98E-06	***	0.9	3.7	7.11
L.agrilow	5.80E-03	5.63E-04	***	−8.29E-05	6.54E-06	***	1.8	2.8	3.26
TR.ran	5.07E-03	4.12E-04	***	−2.36E-05	2.54E-06	***	2.6	1.5	3.17
CALC	4.02E-03	6.28E-04	***	−1.98E-05	5.38E-06	***	0.7	0.2	3.06
L.tree	1.13E-02	1.04E-03	***	−2.28E-04	2.03E-05	***	2.1	2.3	2.31
CRE.sd	5.39E-03	6.08E-04	***	−6.09E-05	9.68E-06	***	1.4	0.7	2.11

***$P < 0.001$; **$P < 0.01$.

For every variable, removal effects of linear and/or quadratic parameters [$-l$, $-q$, $-(l+q)$] are indicated by changes in explained deviance D^2. SE, standard error.

Patterns of modelled species richness

Two conspicuous patterns emerged from model predictions: (1) low species diversity on high mountains is visible in all maps, and (2) there is a high frequency of linear arrangements of increased species richness at the landscape level. The low species number in high mountain environments is widely reported in the literature (e.g. Grabherr *et al.*, 1995; Körner, 1999). About 24% of Switzerland's surface area lies in the alpine zone above the timberline. Here, the species pool of vascular plants is smaller (Wohlgemuth, 2002b) because plant life in high mountains is generally limited by physical components of the environment (Körner, 1999). As a result, species richness on landscape scales is also markedly reduced.

As a result of the peak of species richness at intermediate altitudes (Rahbek, 1995) in the Swiss sample, model-predicted richness maps show belt-like features of maximum species richness along steep hill slopes and around isolated mountains. In the synthetic model, the corresponding steep environmental gradients at the landscape scale are large or steep mountain slopes in the Alps, ridges with smaller ranges in the Jura Mountains, and the edges of large agricultural areas in the lowlands of the species-poorer Central Plateau. The moving window approach amplifies steep factor gradients and landscape structures because of the finer resolution involved (Araújo *et al.*, 2005). Equally, by expanding the real underlying richness features, the process can be considered a soft-focus effect.

Table 6 Model robustness tested by cross-validation: model fits D^2 and mean absolute errors (MAE) in number of species for the four proposed models.

Model	Number of Variables	Number of Parameters	D^2	D^2 10-fold CV*	MAE	MAE 10-fold CV*
Topography	4	7	0.609	0.589	32.5	33.3
Environmental	7	12	0.686	0.653	29.7	31.1
Land cover	9	16	0.696	0.652	29.0	30.9
Synthetic	7	14	0.742	0.706	27.0	28.5

CV*, mean of 100 internal cross-validations (10-fold).

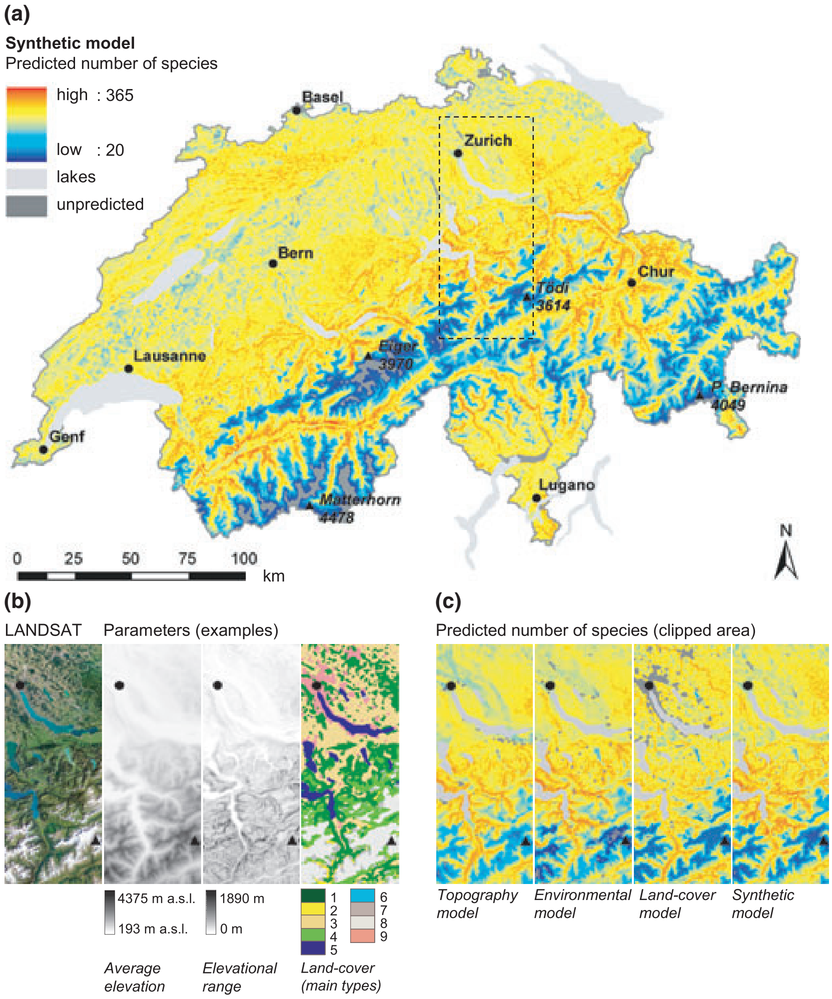


Figure 2 Extrapolation of vascular plant species richness in Switzerland using parameters of different generalized linear models: (a) synthetic model; (b) clipped area: composed satellite image ESA/Eurimage/swisstopo, NPOC 2006 swisstopo (DV033492), mean and range of elevation, dominant land-cover types; (c) topography model, environmental model, land-cover model, synthetic model. Variables are defined in Table 1.

Richness belts as spatial extensions of mid-elevational peaks

In the richness map derived from the synthetic model shown in Fig. 2, hotspots in the form of more-or-less isolated areas or localities are hardly visible. Rather, linearly shaped features or belts are frequent. Currently, it seems there is no review available of the occurrence of such belt-like, linear or curvilinear richness patterns within landscapes. However, many studies have highlighted the importance of linear structures such as riverine landscapes (Ward, 1998; Stohlgren *et al.*, 2005), green lanes (Croxton *et al.*, 2005), roads (Saarinen *et al.*, 2005) and field edges (Croxton *et al.*, 2002; Meek *et al.*, 2002). Many of the belt-like richness features found in the present study correspond to the edges of different land-covers (Nagy, 1997; Cullen *et al.*, 2001). In contrast, the belt-like features related to steep topographic gradients, for example along the valleys in the Alps, need a different explanation. In the literature, mid-elevational peaks of species richness or, more generally, mid-domain effects have been the subject of lively discussion (Rahbek, 1997; Zapata *et al.*, 2003; Colwell *et al.*, 2004; McCain, 2005). Many single factors have

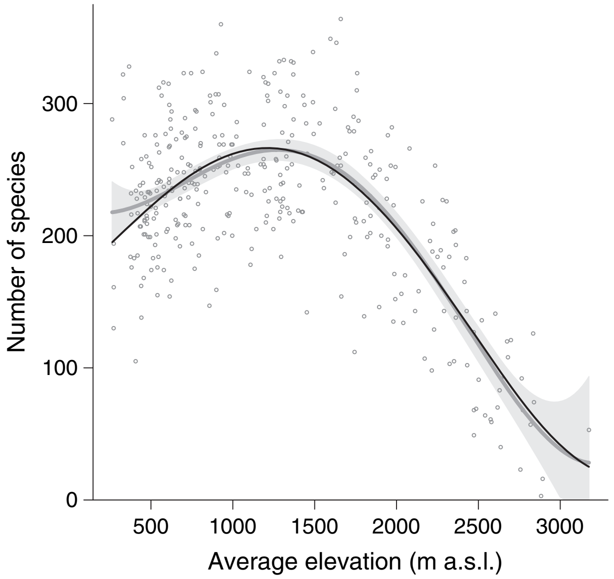


Figure 3 Mid-elevation peaks of vascular plant species richness on landscape scales (1 km^2) in Switzerland: grey line, fourth-order polynomial regression curve for the Swiss sample (dots: $n = 353$; $SR_t = 224.3–590.2 \times E.avg - 666.9 \times E.avg^2 + 20.5 \times E.avg^3 + 118.9 \times E.avg^4$; $R^2 = 0.54$; $P < 0.0001$); hatching, corresponding 95% confidence interval of the prediction; black line, fourth-order polynomial regression curve for samples of the simulated map (synthetic model: 1-km step for sampling; $SR_t = 215.9–7225.4 \times E.avg - 7420.0 \times E.avg^2 + 1081.2 \times E.avg^3 + 715.8 \times E.avg^4$; $R^2 = 0.77$; $P < 0.0001$).

been cited to explain these mid-elevational peaks, and complex interrelationships among climatic factors are presumed to influence these diversity trends (Brown, 2001; Lomolino, 2001). In the present study, peaks of increased species richness were found at average elevations of 1200–1300 m a.s.l. both in the real data and in maps produced by the spatially applied model predictors (Fig. 3). In the richness maps, the unimodal peak appeared as linear or curvilinear features along the valley slopes in the Alps.

Implications for monitoring strategies

The rapid progress made recently in modelling both species distribution and species richness (Guisan *et al.*, 2002; Deutschewitz *et al.*, 2003; Engler *et al.*, 2004) has led to pressure to implement model results in the development of nature-conservation strategies (Ferrier, 2002; Noss, 2004). Systematic field samples, such as those presented here, help to improve the comprehensiveness of spatial biodiversity data across a planning region and may reduce sampling and expert bias (Noss, 2004). Model predictions of species richness based on fine-grained information in the environment have proved to be a cost-efficient approach for conservation. As a surrogate for factor maps over larger regions, fine-grained, remotely sensed information has great potential for use at landscape scales (Gould, 2000; Ortega *et al.*, 2004; Rocchini *et al.*, 2005).

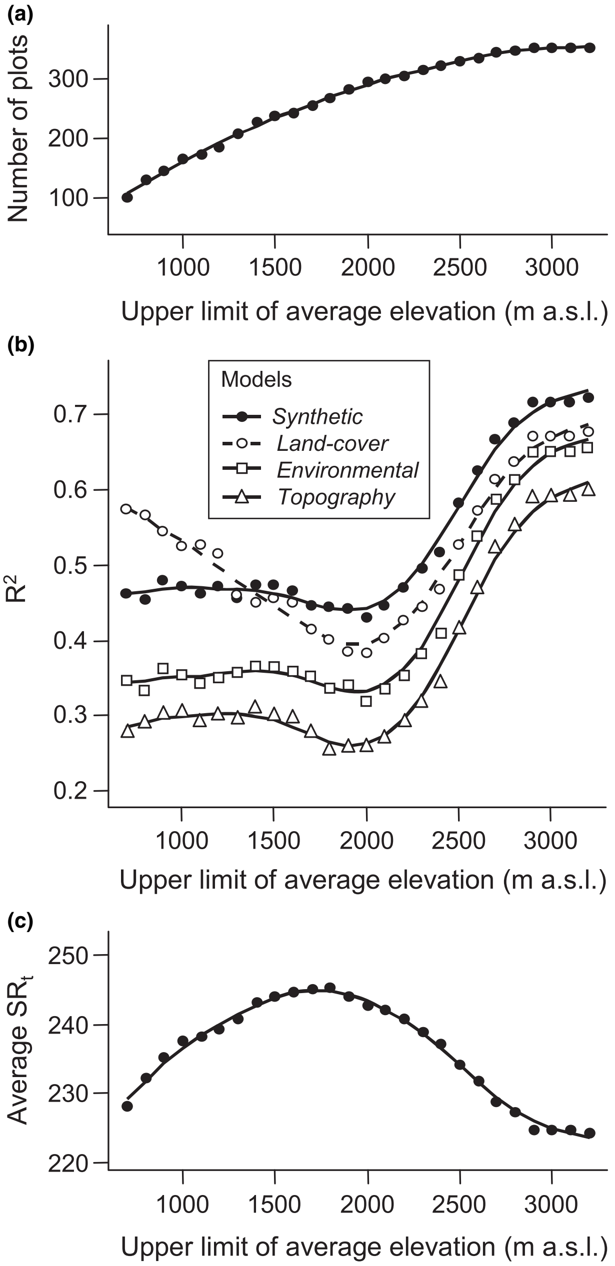


Figure 4 Effects of reducing sample size on model performance. (a) Cumulative number of sample plots sorted by mean elevation of each quadrat. (b) Change of model fits as a result of reduced sample size according to (a). Each model fit is expressed as the correlation (R^2) between model prediction and sampled transect species richness SR_t. (c) Average SR_t of plots with the same sample restrictions as applied in (a) and (b). All data series have been smoothed with cubic smoothing spline functions.

In the Swiss sample, there is inadequate information on urban environments, which cover up to 7% of Switzerland. The impact of urban areas on biodiversity is important, and recent studies have reported high species richness in the city areas of Basel, Zurich and Geneva (Brodtbeck *et al.*, 1998; Landolt, 2001; Wyler, 2004). Either such areas were excluded from the model predictions (land-cover model), or the species richness at these locations was underestimated (synthetic model). A careful analysis of the features in the Central Plateau revealed that a locally high species richness often coincided with the presence of smaller villages and forests in the vicinity where the land-cover diversity increases. Corresponding quadrats for cities and urban centres are lacking in the Swiss sample (Table 2). The largest portion of urban land encountered in a sample quadrat was 50%. The only sample quadrat assessed in a city with 96% of urban area was eliminated as an outlier. For denser urban landscapes, no data on transect species richness were available. However, not only are cities species-rich because of the occurrence of many non-native species (Landolt, 2001; Tait *et al.*, 2005), but when present in comparable landscapes, they have also been found to be naturally rich in vascular plant species (Kühn *et al.*, 2004). To conduct better surveys of biodiversity in regions experiencing rapid change (Antrop, 2004; Wania *et al.*, 2006), the survey grid should be extended or stratified to include urban land.

The model-predicted richness maps presented here can be used to detect zones of low and high species richness, and to derive strategies for either upgrading or protecting landscape biodiversity as part of national conservation plans. This analysis is a first step that should be extended, for dependent variables, by including analyses of additional taxa (Bonn & Gaston, 2005) and specific species lists such as rare and common species (Vázquez & Gaston, 2004), Red-Listed species and functional groups. For explanatory variables, the inclusion of more detailed and ecologically relevant land-cover categories will improve model performance.

CONCLUSIONS

The approach presented here has proved useful for the detection of species-rich and species-poor areas at a fine grain over large areas. It allows for a comparison of landscape species richness with respect to environmental variables, and provides a potentially valuable basis for deriving national nature conservation strategies. Our analyses lead us to propose that more emphasis should be placed on the implementation of 'hot belts' in conservation planning. The present study demonstrates the complexity of linear arrangements of increased species richness at the landscape scale, which in turn are the result of the different spatial effects of ecologically relevant variables such as steep environmental gradients in the mountains, or high land-use diversity along corridors. However, agricultural and urban land that can undergo rapid temporal and spatial environmental change still needs further study.

The approach of using a large extent/grain ratio for predicting richness may be applied to any landscape as long as the required basic data for species and environmental variables are available. It is axiomatic that, as the size of the region concerned expands, the diversity of landscape features is likely to increase, although in homogeneous landscapes, such as the prairies in the USA, the extension will have to be very large. It follows that the number of factors that influence species richness at landscape scale are also likely to increase. In order to deal with this increasing factor complexity, it is proposed that species richness should be modelled using sets of appropriate variables that reflect the underlying spatial characteristics of the region concerned.

ACKNOWLEDGEMENTS

We are grateful to the following for their help with field work: Alain Jotterand, Andrea Persico, Barbara Berner, Christian Hadorn, Christoph Bühler, Christoph Käsermann, Daniel Knecht, David Galeuchet, Dunja Al-Jabaji, Elisabeth Danner, Gabriele Carraro, Jean-François Burri, Jens Paulsen, Karin Marti, Markus Bichsel, Martin Camenisch, Martin Frei, Martin Valencak, Matthias Vust, Michael Ryf, Nils Tonascia, Philippe Druart, Regula Langenauer, Sabine Joss, Stefan Birrer, Thomas Breunig, Urs Weber, Ursula Bollens and Ursula Kradolfer. The Swiss Federal Office for the Environment provided the new data set. We thank Helene Wagner for constructive comments on the manuscript, Tom Edwards, Bill Kunin, Michael W. Palmer, Ole R. Vetaas, Darius Weber, Nick Zimmermann and two referees for their valuable advice, and Silvia Dingwall, Tom Edwards, Bob and Freda Bunce for revising the English.

REFERENCES

Antrop, M. (2004) Landscape change and the urbanization process in Europe. *Landscape and Urban Planning*, **67,** 9–26.

Araújo, M.B., Thuiller, W., Williams, P.H. & Reginster, I. (2005) Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography*, **14,** 17–30.

BFS (1992/1997) *Arealstatistik*. Bundesamt für Statistik, Servicestelle GEOSTAT, Neuchâtel, Switzerland.

Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, **31,** 389–400.

Bonn, A. & Gaston, K.J. (2005) Capturing biodiversity: selecting priority areas for conservation using different criteria. *Biodiversity and Conservation*, **14,** 1083–1100.

Brodtbeck, T., Zemp, M., Frei, M., Kienzle, U. & Knecht, D. (1998) Flora von Basel und Umgebung. Teil 1. *Mitteilungen der Naturforschenden Gesellschaften beider Basel*, **2,** 1–543.

Brown, J.H. (2001) Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography*, **10,** 101–109.

Bruun, H.H., Moen, J. & Angerbjorn, A. (2003) Environmental correlates of meso-scale plant species richness in the province of Harjedalen, Sweden. *Biodiversity and Conservation*, **12,** 2025–2041.

Bundesamt für Statistik (2001) *GEOSTAT Benutzerhandbuch*. Bundesamt für Statistik, Neuchâtel.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, **163,** E1–E23.

Crawley, M.J. (1993) *GLIM for ecologists*. Blackwell Scientific, Oxford, UK.

Croxton, P.J., Carvell, C., Mountford, J.O. & Sparks, T.H. (2002) A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. *Biological Conservation*, **107,** 365–374.

Croxton, P.J., Hann, J.P., Greatorex-Davies, J.N. & Sparks, T.H. (2005) Linear hotspots? The floral and butterfly diversity of green lanes. *Biological Conservation*, **121,** 579–584.

Cullen, L., Schmink, M., Padua, C.V. & Morato, M.I.R. (2001) Agroforestry benefit zones: a tool for the conservation and management of Atlantic forest fragments, São Paulo, Brazil. *Natural Areas Journal*, **21,** 346–356.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, **137,** 27–49.

Currie, D.J. & Francis, A.P. (2004) Taxon richness and climate in angiosperms: is there a globally consistent relationship that precludes region effects? Reply. *The American Naturalist*, **163,** 780–785.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7,** 1121–1134.

De Quervain, F., Hofmänner, F., Jenny, V., Köppel, V. & Frey, D. (1963–1967) *Geotechnische Karte der Schweiz, 1:200 000, 2. Aufl.* Kümmerly & Frei, Bern.

Deutschewitz, K., Lausch, A., Kühn, I. & Klotz, S. (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, **12,** 299–311.

Dullinger, S., Dirnbock, T. & Grabherr, G. (2003) Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria. *Arctic, Antarctic and Alpine Research*, **35,** 434–441.

Engler, R., Guisan, A. & Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, **41,** 263–274.

Ewald, J. (2003) The calcareous riddle: why are there so many calciphilous species in the central European flora? *Folia Geobotanica*, **38,** 357–366.

Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology*, **51,** 331–363.

Ferrier, S., Powell, G.V.N., Richardson, K.S., Manion, G., Overton, J.M., Allnutt, T.F., Cameron, S.E., Mantle, K., Burgess, N.D., Faith, D.P., Lamoreux, J.F., Kier, G., Hijmans, R.J., Funk, V.A., Cassis, G.A., Fisher, B.L., Flemons, P., Lees, D., Lovett, J.C. & Van Rompaey, R. (2004) Mapping more of terrestrial biodiversity for global conservation assessment. *BioScience*, **54,** 1101–1109.

Fleishman, E. & Mac Nally, R. (2002) Topographic determinants of faunal nestedness in Great Basin butterfly assemblages: applications to conservation planning. *Conservation Biology*, **16,** 422–429.

Forman, R.T.T. (1995) Some general principles of landscape and regional ecology. *Landscape Ecology*, **10,** 133–142.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness–climate relationship for angiosperms. *The American Naturalist*, **161,** 523–536.

Gottfried, M., Pauli, H. & Grabherr, G. (1998) Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research*, **30,** 207–221.

Gould, W. (2000) Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. *Ecological Applications*, **10,** 1861–1870.

Grabherr, G., Gottfried, M., Gruber, A. & Pauli, H. (1995) Patterns and current changes in alpine plant diversity. *Arctic and alpine biodiversity* (ed. by F.S. Chapin and C. Körner), pp. 167–181. Ecological Studies, Springer, Berlin.

Grytnes, J.A., Birks, H.J.B. & Peglar, S.M. (1999) Plant species richness in Fennoscandia: evaluating the relative importance of climate and history. *Nordic Journal of Botany*, **19,** 489–503.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135,** 147–186.

Guisan, A., Edwards, T.C. & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157,** 89–100.

Harner, R.F. & Harper, K.T. (1976) Role of area, heterogeneity, and favorability in plant species-diversity of pinyon-juniper ecosystems. *Ecology*, **57,** 1254–1263.

Hawkins, B.A. & Pausas, J.G. (2004) Does plant richness influence animal richness? The mammals of Catalonia (NE Spain). *Diversity and Distributions*, **10,** 247–252.

Heikkinen, R.K. (1996) Predicting patterns of vascular plant species richness with composite variables: a meso-scale study in Finnish Lapland. *Vegetatio*, **126,** 151–165.

Heikkinen, R.K. & Birks, H.J.B. (1996) Spatial and environmental components of variation in the distribution patterns of subarctic plant species at Kevo, N. Finland – a case study at the meso-scale level. *Ecography*, **19,** 341–351.

Heikkinen, R.K., Luoto, M., Virkkala, R. & Rainio, K. (2004) Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural–forest mosaic. *Journal of Applied Ecology*, **41,** 824–835.

Hintermann, U., Weber, D. & Zangger, A. (2000) Biodiversity monitoring in Switzerland. *Schriftenreihe für Landschaftspflege und Naturschutz*, **62,** 47–58.

Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6,** 65–70.

Kerr, J.T. & Cihlar, J. (2004) Patterns and causes of species endangerment in Canada. *Ecological Applications*, **14,** 743–753.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Kuper, W., Kreft, H. & Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography*, **32,** 1107–1116.

Körner, C. (1999) *Alpine plant life*. Springer, Berlin.

Kühn, I., Brandl, R. & Klotz, S. (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6,** 749–764.

Landolt, E. (1983) Probleme der Höhenstufen in den Alpen. *Botanica Helvetica*, **93,** 255–268.

Landolt, E. (2001) *Flora der Stadt Zürich (1984–1998)*. Birkhäuser, Biel-Benken.

Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, **10,** 3–13.

Luoto, M., Toivonen, T. & Heikkinen, R.K. (2002) Prediction of total and rare plant species richness in agricultural landscapes from satellite images and topographic data. *Landscape Ecology*, **17,** 195–217.

Lütolf, M., Kienast, F. & Guisan, A. (2006) The ghost of past species presences: improving species distribution models for presence-only data. *Journal of Applied Ecology*, **43,** 892–815.

McCain, C.M. (2005) Elevational gradients in diversity of small mammals. *Ecology*, **86,** 366–372.

McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd edn. Chapman & Hall, London.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, **106,** 259–271.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82,** 2381–2396.

Moor, M. (1952) Die Fagion-Gesellschaften im Schweizer Jura. *Beiträge zur geobotanischen Landesaufnahme der Schweiz*, **31,** 1–201.

Moser, D., Dullinger, S., Englisch, T., Niklfeld, H., Plutzar, C., Sauberer, R., Zechmeister, H.G. & Grabherr, G. (2005) Environmental determinants of vascular plant species richness in the Austrian Alps. *Journal of Biogeography*, **32,** 1117–1127.

Nagy, B. (1997) Orthoptera species and assemblages in the main habitat types of some urban areas in the Carpathian Basin. *Biologia*, **52,** 233–240.

Nicholls, R.J. (1989) How to make biological surveys go further with generalised linear models. *Biological Conservation*, **50,** 51–75.

Nichols, W.F., Killingbeck, K.T. & August, P.V. (1998) The influence of geomorphological heterogeneity on biodiversity. II. A landscape perspective. *Conservation Biology*, **12,** 371–379.

Noss, R.F. (2004) Conservation targets and information needs for regional conservation planning. *Natural Areas Journal*, **24,** 223–231.

Ortega, M., Elena-Rosello, R. & Del Barrio, J.M.G. (2004) Estimation of plant diversity at landscape level: a methodological approach applied to three Spanish rural areas. *Environmental Monitoring and Assessment*, **95,** 97–116.

Pärtel, M. (2002) Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, **83,** 2361–2366.

Pimm, S.L. & Brown, J.H. (2004) Domains of diversity. *Science*, **304,** 831–833.

Plattner, M., Birrer, S. & Weber, D. (2004) Data quality in monitoring plant species richness in Switzerland. *Community Ecology*, **5,** 135–143.

Poiani, K.A., Richter, B.D., Anderson, M.G. & Richter, H.E. (2000) Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *BioScience*, **50,** 133–146.

Pyšek, P., Kucera, T. & Jarosik, V. (2002) Plant species richness of nature reserves: the interplay of area, climate and habitat in a central European landscape. *Global Ecology and Biogeography*, **11,** 279–289.

R Development Core Team (2005) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18,** 200–205.

Rahbek, C. (1997) The relationship among area, elevation, and regional species richness in Neotropical birds. *The American Naturalist*, **149,** 875–902.

Rocchini, D., Andreini Butini, S. & Chiarucci, A. (2005) Maximizing plant species inventory efficiency by means of remotely sensed spectral distances. *Global Ecology and Biogeography*, **14,** 431–437.

Saarinen, K., Valtonen, A., Jantunen, J. & Saarnio, S. (2005) Butterflies and diurnal moths along road verges: does road type affect diversity and abundance? *Biological Conservation*, **123,** 403–412.

Sarr, D.A., Hibbs, D.E. & Huston, M.A. (2005) A hierarchical perspective of plant diversity. *Quarterly Review of Biology*, **80,** 187–212.

Schmidtlein, S. & Ewald, J. (2003) Landscape patterns of indicator plants for soil acidity in the Bavarian Alps. *Journal of Biogeography*, **30,** 1493–1503.

Schwarz, M. & Zimmermann, N.E. (2005) A new GLM-based method for mapping tree cover continuous fields using regional MODIS reflectance data. *Remote Sensing of Environment*, **95,** 428–443.

Searcy, K.B., Wilson, B.F. & Fownes, J.H. (2003) Influence of bedrock and aspect on soils and plant distribution in the Holyoke Range, Massachusetts. *Journal of the Torrey Botanical Society*, **130,** 158–169.

Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12,** 1–20.

Stohlgren, T.J., Guenther, D.A., Evangelista, P.H. & Alley, N. (2005) Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. *Ecological Applications*, **15,** 715–725.

Tait, C.J., Daniels, C.B. & Hill, R.S. (2005) Changes in species assemblages within the Adelaide Metropolitan Area, Australia, 1836–2002. *Ecological Applications*, **15,** 346–359.

Turc, L. (1961) Evaluation des besoins en eau d'irrigation, évapotranspiration potentielle, formule simplifié et mise à jour. *Annales Agronomiques*, **12,** 13–49.

Vázquez, L.B. & Gaston, K.J. (2004) Rarity, commonness, and patterns of species richness: the mammals of Mexico. *Global Ecology and Biogeography*, **13,** 535–542.

Venables, W.N. & Ripley, B.D. (1999) *Modern applied statistics with S-PLUS*, 3rd edn. Springer, New York.

Vetaas, O.R. & Grytnes, J.A. (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, **11,** 291–301.

Vormisto, J., Tuomisto, H. & Oksanen, J. (2004) Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation? *Journal of Vegetation Science*, **15,** 485–494.

Waldhardt, R., Simmering, D. & Otte, A. (2004) Estimation and prediction of plant species richness in a mosaic landscape. *Landscape Ecology*, **19,** 211–226.

Wania, A., Kuhn, I. & Klotz, S. (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning*, **75,** 97–110.

Ward, J.V. (1998) Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, **83,** 269–278.

Weber, D., Hintermann, U. & Zangger, A. (2004) Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Global Ecology and Biogeography*, **13,** 97–104.

Wohlgemuth, T. (1993) The distribution atlas of pteridophytes and phanerograms of Switzerland (Welten and Sutter 1982) in a relational database – species number per mapping unit and its dependence on various factors. *Botanica Helvetica*, **103,** 55–71.

Wohlgemuth, T. (1998) Modelling floristic species richness on a regional scale: a case study in Switzerland. *Biodiversity and Conservation*, **7,** 159–177.

Wohlgemuth, T. (2002a) Alpine plant species richness in the Swiss Alps: diversity hot spots reconsidered. *Mémoires de la Societé botanique de Genève*, **3,** 63–74.

Wohlgemuth, T. (2002b) Environmental determinants of vascular plant species richness in the Swiss Alpine zone. *Mountain biodiversity: a global assessment* (ed. by C. Körner and E.M. Spehn), pp. 103–116. Parthenon Publishing Group, Boca Raton.

Wohlgemuth, T. & Gigon, A. (2003) Calcicole plant diversity in Switzerland may reflect a variety of habitat templets. *Folia Geobotanica*, **38,** 443–452.

Wyler, N. (2004) *Analyse du paysage et richesse spécifique: Le cas de la flore du canton de Genève (Suisse)*. Thèse No. 3493, Université de Genève, Genève.

Zapata, F.A., Gaston, K.J. & Chown, S.L. (2003) Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology*, **72,** 677–690.

Zimmermann, N.E. & Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science*, **10,** 469–482.

BIOSKETCHES

Thomas Wohlgemuth heads the Disturbance Ecology research group at the Swiss Federal Research Institute WSL in Birmensdorf. His research focuses on biodiversity of plant species at various scales and on forest dynamics.

Michael P. Nobis heads the Spatial Ecology research group at the Swiss Federal Research Institute WSL in Birmensdorf. His research concentrates on spatial analysis of species distribution and biodiversity patterns.

Felix Kienast is Professor of Landscape Ecology at the Swiss Federal Institute of Technology ETH in Zürich, and heads the Landscape Modelling research group at the Swiss Federal Research Institute WSL in Birmensdorf. He works on land-use change and its drivers.

Matthias Plattner is a project manager at Hintermann & Weber AG, Reinach. He is responsible for field assessments and data quality control in the frame of Switzerland's Biodiversity Monitoring programme.

Editor: Ole Vetaas

6 Chapter IV: Plants, Birds and Butterflies: Short-Term Responses of Species Communities to Climate Warming Vary by Taxon and with Altitude

Plants, Birds and Butterflies: Short-Term Responses of Species Communities to Climate Warming Vary by Taxon and with Altitude

Tobias Roth[1,2,3]*, **Matthias Plattner**[1], **Valentin Amrhein**[2,3]

1 Hintermann & Weber AG, Reinach, Switzerland, **2** University of Basel, Zoological Institute, Basel, Switzerland, **3** Research Station Petite Camargue Alsacienne, Saint-Louis, France

Abstract

As a consequence of climate warming, species usually shift their distribution towards higher latitudes or altitudes. Yet, it is unclear how different taxonomic groups may respond to climate warming over larger altitudinal ranges. Here, we used data from the national biodiversity monitoring program of Switzerland, collected over an altitudinal range of 2500 m. Within the short period of eight years (2003–2010), we found significant shifts in communities of vascular plants, butterflies and birds. At low altitudes, communities of all species groups changed towards warm-dwelling species, corresponding to an average uphill shift of 8 m, 38 m and 42 m in plant, butterfly and bird communities, respectively. However, rates of community changes decreased with altitude in plants and butterflies, while bird communities changed towards warm-dwelling species at all altitudes. We found no decrease in community variation with respect to temperature niches of species, suggesting that climate warming has not led to more homogenous communities. The different community changes depending on altitude could not be explained by different changes of air temperatures, since during the 16 years between 1995 and 2010, summer temperatures in Switzerland rose by about 0.07°C per year at all altitudes. We discuss that land-use changes or increased disturbances may have prevented alpine plant and butterfly communities from changing towards warm-dwelling species. However, the findings are also consistent with the hypothesis that unlike birds, many alpine plant species in a warming climate could find suitable habitats within just a few metres, due to the highly varied surface of alpine landscapes. Our results may thus support the idea that for plants and butterflies and on a short temporal scale, alpine landscapes are safer places than lowlands in a warming world.

Citation: Roth T, Plattner M, Amrhein V (2014) Plants, Birds and Butterflies: Short-Term Responses of Species Communities to Climate Warming Vary by Taxon and with Altitude. PLoS ONE 9(1): e82490. doi:10.1371/journal.pone.0082490

Editor: Francesco de Bello, Institute of Botany, Czech Academy of Sciences, Czech Republic

Received May 31, 2013; **Accepted** October 25, 2013; **Published** January 8, 2014

Funding: Financial support was provided by the Swiss Federal Office for the Environment and the Swiss Association Pro Petite Camargue Alsacienne. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: roth@hintermannweber.ch

Introduction

Among the currently occurring changes in environmental conditions, climate warming presumably has the greatest potential to change species communities [1,2]. An apparent response to climate warming is that species shift their distribution towards higher latitudes or altitudes [3–6]. However, species seem to vary greatly in their range shifts, probably depending on the particular traits of the species [7]. For instance, the differential mobility of taxa such as plants or birds likely predicts the rate at which they can track climate change [8,9].

Yet, whether the response to climate change of different taxonomic groups is constant over larger environmental ranges is currently unclear [8]. Our lack of knowledge is particularly evident with regard to responses to climate warming across altitudinal ranges [10]. It has been suggested that lowland forests are one of the least reactive terrestrial ecosystems and are particularly threatened by climate warming, because adaptation of communities lags behind environmental change [11]. Other studies proposed that mountain ecosystems are particularly threatened [10,12], e.g. because climate warming causes a significant upward shift in optimum habitat of species, leading to decreasing species ranges, because land area is usually decreasing with altitude [13,14]. Recently, however, it was suggested that the velocity of temperature change is lowest in alpine landscapes [15]. Further, alpine landscapes could be relatively safe places in a warming world, because in the highly varied surface of alpine landscapes, thermal mosaics usually create fine-scale habitats inhabited by species with different thermal preferences; thus, in a warming climate, many alpine plant species could find suitable habitats fitting their thermal preferences within just a few metres [16].

Here, we used data from the Swiss biodiversity monitoring program [17,18] that were collected over the diverse altitudinal gradients but small latitudinal ranges of Switzerland. We studied temporal changes in communities of vascular plants, butterflies and breeding birds over an altitudinal range of about 2500 metres. Data were collected in 214 1-km^2 sample squares that were regularly distributed over the entire country. Sample squares were surveyed twice between 2003 and 2010, with five years between two surveys of a sample square. For all three species groups, data were collected on the same study sites during the same years, and thus, communities of the three species groups largely experienced the same changes in environmental conditions.

To measure whether communities changed towards warm-dwelling species, we used the recently developed community temperature index CTI [9]. For this index, each species is given an indicator value reflecting its temperature niche on a national or continental scale; the CTI then describes a community as the average of the individual indicator values of the recorded species [9,19]. A low CTI would thus reflect a large proportion of low-temperature dwelling species, and a temporal increase of CTI would indicate that the proportion of high-temperature species has increased. Unlike traditional measures such as species richness, the CTI accounts for species-specific sensitivity to temperature: if in a community a warm-dwelling species were replacing a cold-dwelling species, the CTI would increase, while a traditional measure such as species richness would remain constant. Furthermore, we extended the current CTI framework by additionally inferring the variation of temperature indicator values of the individual species present in a community, which we call the community temperature variation CTV. Using the CTV, we aimed to test whether as a response to climate warming, communities tended to become more homogeneous with respect to temperature niches of species [20].

Following the argument by Scherrer & Körner [16] that in the varied alpine terrain, many plant species could find habitats with suitable micro-climatic conditions within just a few metres, we predicted that CTIs of plants would change at a slower rate in alpine environments than in lowlands. However, different species groups are likely to respond to environmental factors at different spatial scales, with important consequences on how they may react to climate change [2,21]. For example, birds and butterflies are among the most dispersive species, so they should be able to track climate change more easily than plants [8]. Further, given that birds are to a large extent airborne organisms and thus are probably influenced more by air temperatures than by micro-climatic conditions, we predicted that community changes in alpine environments are larger in birds than in plants. Predictions for butterflies are less straightforward, because while being generally mobile, butterflies strongly depend on their relatively sedentary host plants both for feeding and reproduction [22]. We therefore expected butterflies to show a response to climate change that is intermediate between plants and birds.

Materials and Methods

The study took place between 2003 and 2010 in Switzerland. About 70% of Switzerland is mountainous, with the Alps covering about 60% and the Jura Mountains covering about 10% of the country. Overall, Switzerland covers altitudes from 193 to 4634 m. In Switzerland, temperatures increased from 1959 to 2008 at all altitudes, with an average warming rate of 0.35°C per decade, which is about 1.6 times the northern hemispheric warming rate [23].

Ethics statement

No specific permits were required for the described field studies, as plants, birds and butterflies were surveyed along existing trails that are not privately owned. The field studies did not involve collecting of endangered or protected species, except for rare cases in butterflies where a few specimens of faunistic interest were collected with the permission of the Swiss Federal Office for the Environment (FOEN).

Swiss biodiversity monitoring scheme. We used data from the Swiss Biodiversity Monitoring scheme (BDM, *www.biodiversitymonitoring.ch*) that was launched in 2001 to monitor Switzerland's biodiversity and to meet the Convention on Biological Diversity of Rio de Janeiro [18]. Fieldwork was done using standardised protocols (Text S1). For the BDM scheme, 428 sample squares of 1 km^2 were selected that were regularly distributed and aligned within the approximately 41'295 km^2 units of the Swiss national coordinate system. Excluding sample squares of 100% water surface, as well as sample squares that were too dangerous to do field work because of their exposed alpine terrain, 396 squares were surveyed for the presence of vascular plants, butterflies and breeding birds. Each year, one fifth of sample squares were surveyed, chosen to constitute a regularly spaced subsample of all sites, and each site was surveyed every five years. Between 2003 and 2010, three fifths of sample squares were thus surveyed twice. From the 237 sample squares on which two surveys were done, we excluded *a priori* 23 squares because surveys did not meet our standards of data collection or of weather conditions according to the protocol (Text S1). We analysed data from 214 sample squares (Fig. 1). Average altitudes within the 214 sample squares ranged from 263 m to 2840 m, and mean ± SD altitude of sample squares was 1190±693 m. In Switzerland, the tree line varies in altitude from 1750 m above sea level in the northern front ranges to 2350 m in some parts of the central Alps [24]. Of the 214 sample squares, 22 (10%) were mostly above 2350 m. Average (± SD) numbers of species counted at a sample square during the first survey were 220.4±59.5 for vascular plants, 28.6±15.1 for butterflies, and 33.2±12.6 for birds, and during the second survey 228.1±59.9 for vascular plants, 28.5±14.1 for butterflies, and 32.6±12.5 for birds.

Temperature data. To examine possible altitudinal effects on the changes of air temperatures over the years, we used data on air temperatures from the 14 meteorological stations that were freely available from the Federal Office of Meteorology and Climatology [25]. These 14 meteorological stations were selected by the Federal Office of Meteorology and Climatology to represent the different climatic regions of Switzerland [26], and stations were distributed over an altitudinal range from 273 to 2501 m, with an average (± SD) of 1042±767 m. We present results on air temperatures to aid the interpretation of the results on temporal change of species communities, but note that air temperature data were not directly used in the analyses on species communities (see below).

Because survey methods for temperature differed among meteorological stations (e.g., regarding the number of measurements taken per day), the time-series of temperatures were homogenized using the method for homogenization of monthly data series as described in Begert et al. [25]. As community changes usually lag behind climate change [8,9], we decided haphazardly to examine temperature data for a period from 1995 to 2010 that was twice as long as our study period on community change that lasted from 2003 to 2010. Further, since different species may react to different aspects of temperature, we examined for a given year both the mean of the monthly temperature averages from April to September, which is the period when data on species communities were collected, and the mean temperature of the coldest month. We chose these two measures of temperature because we believe that they are likely to be relevant for many species under study, but we acknowledge that they may not be appropriate for all species. To analyse the two measures of temperature, we used separate linear mixed models (LMMs) with either the average temperature from April to September or the average temperature of the coldest month as dependent variable and altitude and linear trend as well as their interaction as predictor variables. Because temperature measures taken from the same meteorological stations and measures taken in the same years are statistically dependent, we used meteorological station and

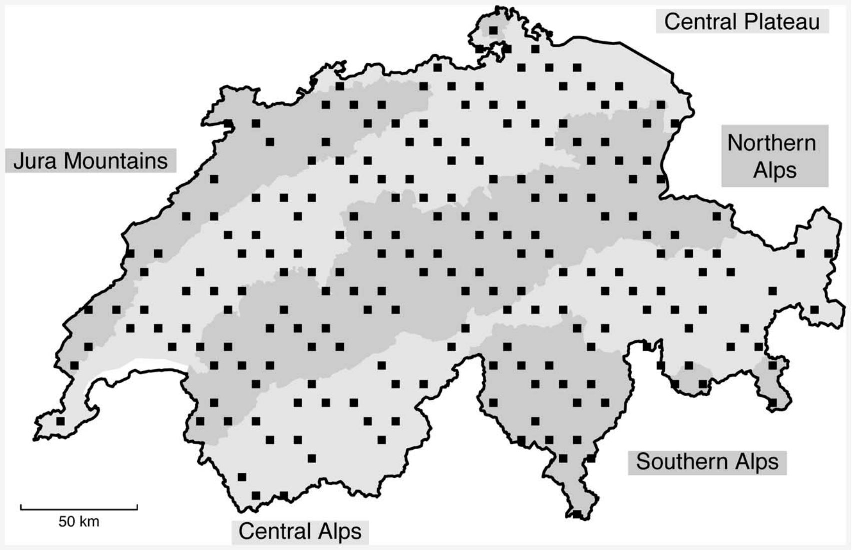


Figure 1. Distribution of sample sites over Switzerland. Locations of the 214 analysed 1-km^2 sample squares from the Swiss national biodiversity monitoring program for which data for all three species groups were available (vascular plants, butterflies and breeding birds).
doi:10.1371/journal.pone.0082490.g001

year as random factors in the LMMs. We then tested whether the temporal trends of temperature measures differed among altitudes (interaction temporal trend×altitude) and whether mean air temperatures were increasing over years (main effect temporal trend).

Species temperature index STI. Analyses on species communities were based on a recently developed framework to measure change in community composition in response to climate warming [9]. The framework is centred on species-specific long-term average temperatures that are experienced by individuals of a species over its larger (e.g., national or continental) range, which is the species temperature index (STI). The STI is a species-specific measure of the temperature niche of a species [9]. For the species investigated in this study, we used STI values that were successfully applied in other studies [8,9,16]. For plant STIs, we used Ellenberg species indicator values for temperature that were developed for Switzerland [27]. Ellenberg temperature values are based on expert knowledge (values 1–5 in 0.5 steps), and recent studies showed that they give reasonable results on conditions at patches of habitat even at a very fine spatial scale [16]. For butterflies and birds, we used STIs obtained as the mean temperature at which a butterfly or breeding bird species occurred in Europe (for our sources of butterfly and bird STI values, see [28] and Acknowledgements). We used Settele et al. [29] as reference for the distribution of butterflies, and Hagenmeijer & Blair [30] for birds. Three butterfly species were excluded *a priori* from the analyses because they are largely wandering species in Switzerland (*Colias crocea*, *Vanessa atalanta* and *Vanessa cardui*).

Community temperature index CTI and community temperature variation CTV. Any local species assemblage can be characterized by a community temperature index (CTI) calculated as the average of the species temperature indices (STI) of the species recorded in the assemblage [9]. A low CTI would thus reflect a large proportion of low-temperature dwelling species (i.e. species with low temperature indices STI), and an increase of CTI over time would indicate that the proportion of species with higher temperature niches has increased. In site-based approaches such as the CTI, mean values of all species per site are often calculated taking into account the abundances of the species [9,31]; however, this leads to abundant species having larger influence on the results than rare species [31]. Because we aimed at measuring a community response to climate change that is similarly influenced by common and by rare species, we based our calculations of CTIs on occurrence (presence/absence) data and did not weight them with the abundance of a species. Note, however, that when accounting for the abundance of a species, presence-absence based CTIs are usually very similar to the results obtained from CTIs based on occurrence data [8,9].

We extended the current CTI framework to test whether as a response to climate warming, communities tended to become more homogeneous with respect to temperature niches of species. We used the standard deviation of species temperature indices (STI) of the species recorded in a community at a sample square as our measure of community temperature variation (CTV). CTV values are large if the range of temperature niches of species occurring in a community is broad. Community averages as given by the CTI and community variation as given by the CTV are complementary measures and may reveal different patterns: For instance, if in a community, there were warm-dwelling species invading, the CTV would increase, and if there were cold-dwelling species disappearing, the CTV would decrease; in both cases, the CTI would increase. Note, however, that particularly in plants where species temperature values were restricted to discrete values between one and five (see above), CTI and CTV may be inherently correlated to some extend because communities with CTIs close to one or five can vary less than communities with intermediate CTI values.

Statistical analysis. For each sample square i and each species group, we calculated

$$\Delta \mathrm{CTI}_i = \frac{\mathrm{CTI}_i[\text{second survey}]\text{-}\mathrm{CTI}_i[\text{first survey}]}{-b}$$

$\Delta\mathrm{CTI}_i$ is thus a measure of the temporal change of local species composition from the first to the second survey. If $\Delta\mathrm{CTI}_i > 0$, then the species community at a sample square i changed towards warm-dwelling species from the first to the second survey, and if $\Delta\mathrm{CTI}_i < 0$, then the species community at a sample square i

changed towards cold-dwelling species. Because we aimed at comparing changes in species composition between species groups, and because the methods for obtaining species temperature indices (STI) differed among species groups (see above), we standardized the change in species composition using the group-specific constant b. b is the slope of the group-specific linear regression of CTI values from the first survey on altitude and was -9.2×10^{-4}, -1.2×10^{-3} and -5.4×10^{-4} for plants, butterflies and birds, respectively.

Using standardized $\Delta\mathbf{CTI}_i$ values, local changes in CTI can be interpreted as the difference in altitude in metres needed to go uphill or downhill to find the same difference in CTI as we measured for the temporal change in CTI at a sample square. For example, a constant b of -0.001 for butterflies means that the CTI of butterflies on average decreases by 0.001 per metre increase in altitude. If at a sample square, we would find a temporal change in CTI of 0.05, then, on a national or continental scale, we would on average need to go $0.05/-0.001=-50$ m downhill to find the same CTI with more warm-dwelling species as we found at our sample square at the second survey as compared to the first survey. This would mean that at our sample square, the butterfly community showed an uphill shift of 50 m between 2003 and 2010 (or more exactly, in the five years from the first to the second survey at the particular sample square).

For the community temperature variation CTV, we calculated for each sample square i and each species group

$$\Delta\mathrm{CTV}_i=\frac{\mathrm{CTV}_i[\text{second survey}]\text{-}\mathrm{CTV}_i[\text{first survey}]}{-b}$$

Here, the constant b is the slope of the group-specific linear regression of CTV values from the first survey on altitude and was -8.6×10^{-5}, -5.4×10^{-4} and -3.9×10^{-4} for plants, butterflies and birds, respectively. If $\Delta\mathrm{CTV}_i>0$, then the temperature niches of the species present in the community at a sample square i became more variable from the first to the second survey, and if $\Delta\mathrm{CTV}_i<0$, then the temperature niches of the species present in the community at a sample square i became more homogenous.

To test whether standardized local changes in community average ($\Delta\mathbf{CTI}_i$) or in community variation ($\Delta\mathbf{CTV}_i$) depended on altitude, we used linear models with $\Delta\mathbf{CTI}_i$ or $\Delta\mathbf{CTV}_i$ as dependent variables and with linear, quadratic and cubic polynomials of altitude as independent variables. To control for a possible confounding effect of altitudinal range within a sample square, we added altitudinal range (m) within a sample square as a covariate. For the LMMs, we subtracted 500 m from the true altitude of each sample square, which shifts the intercept of the model from 0 m to 500 m. Consequently, the estimated value for the intercept obtained from the LMMs reflected CTI and CTV predictions for a community at an altitude of 500 m, which is about the average altitude of the central plateau in Switzerland (Fig. 1). To predict CTIs and CTVs for communities at the upper limit of the tree line in Switzerland (about 2350 m in the central Alps [24]), we made model predictions for an altitude of 2350 m.

It seems likely that the CTI or CTV in an assemblage of many species is more precise than the measure of CTI in an assemblage of fewer species. We therefore expected that the residual variation in our linear models would decrease with increasing species richness. As this would violate the assumption of homogeneity of variances [32], we used the gls-function of the R-package nlme [33] and followed the protocol as proposed by Zuur et al. [32] to account for heterogeneity of residuals: first, we used full models that included linear, quadratic and cubic polynomials of altitude as well as the altitudinal range within squares and tested three different variance-covariance structures, i.e. fixed variance (like in traditional linear models), power of species richness, and constant plus power of species richness [32]. We then selected the variance structure of the model with the lowest AIC value and visually checked the residuals for heterogeneity and other model violations. Second, to select the model on which we based inference, we started with the full model that included linear, quadratic and cubic polynomials of altitude as well as the altitudinal range and the respective variance-covariance structure found during the first step. We backward selected based on AIC values to obtain the minimal adequate model. Third, likelihood ratio tests using restricted maximum likelihood were performed to test for significance of the independent variables; restricted maximum likelihood is used in mixed models to correct the estimator for the variance [32]. Finally, to obtain p-values and confidence intervals for model predictions, we used bootstrap methods with 1000 iterations [32].

To analyse the temporal trends of air temperatures, we used the lmer-function of the R-package nlme [33]. All analyses were performed using the software R [34].

Results

Our results are based on the assumption that community temperature index (CTI) and community temperature variation (CTV) are accurate descriptions of the average and variation of temperature niches of species in the local communities. If this assumption is correct, then CTI and CTV values of different species groups in local communities that experienced the same climatic conditions should be positively correlated. In our case, the three species groups were surveyed on the same study sites during the same years, and indeed, community averages (CTIs) of species groups at the 214 sample squares were strongly positively correlated (Pearson's correlation of CTIs of first surveys of each sample square; plants-butterflies: $r=0.97$, $t=54.8$, d.f. = 212, $p=<0.001$; plants-birds: $r=0.83$, $t=21.7$, d.f. = 212, $p=<0.001$; butterflies-birds: $r=0.81$, $t=20.4$, d.f. = 212, $p=<0.001$). Likewise, the community variations (CTVs) of the species groups were positively correlated (plants-butterflies: $r=0.69$, $t=13.7$, d.f. = 212, $p=<0.001$; plants-birds: $r=0.38$, $t=5.6$, d.f. = 212, $p=<0.001$; butterflies-birds: $r=0.67$, $t=13.0$, d.f. = 212, $p=<0.001$).

The temporal changes of community average ($\Delta\mathbf{CTI}_i$), however, differed between species groups and were thus not significantly correlated (plants-butterflies: $r=-0.06$, $t=0.9$, d.f. = 212, $p=0.37$; plants-birds: $r=-0.05$, $t=0.7$, d.f. = 212, $p=0.50$) or were even negatively correlated (butterflies-birds: $r=-0.22$, $t=3.3$, d.f. = 212, $p=0.001$). Similarly, the temporal changes of community variation ($\Delta\mathrm{CTV}_i$) were not significantly correlated between species groups (plants-butterflies: $r=0.02$, $t=0.4$, d.f. = 212, $p=0.72$; plants-birds: $r=0.02$, $t=0.2$, d.f. = 212, $p=0.81$; butterflies-birds: $r=-0.01$, $t=0.1$, d.f. = 212, $p=0.94$).

We found that at low altitudes, CTIs of vascular plants, butterflies and birds increased during the eight years of the study, and thus species communities changed towards warm-dwelling species (Table 1, Fig. 2). Model predictions for 500 m above sea level indicated a shift of communities towards average CTI values that are usually found at an altitude that is on average 8 m downhill from our study sites for plants ($p=0.010$), 38 m downhill for butterflies ($p=0.006$), and 42 m downhill for birds ($p=0.004$; see Table 1). In other words, plant, butterfly and bird communities at 500 m apparently showed an average uphill shift of 8 m, 38 m and 42 m, respectively, within eight years. The change of plant communities at 500 m towards warm-dwelling species was thus

4.8 times slower compared to the change in butterflies ($p = 0.021$) and 5.3 times slower compared to the change in birds ($p = 0.033$). CTI changes of butterflies and birds were not significantly different ($p = 0.415$), with birds estimated to change 1.1 times faster than butterflies. The shifts in community averages of the three species groups at low altitudes were not accompanied by a decrease of community temperature variation CTV: while community variation in plants and birds apparently was largely stable over the study period, temperature niches of butterfly species in lowland communities even became more variable (Table 1, Fig. 2).

However, the rates of temporal changes towards warm-dwelling species decreased with altitude in plants and butterflies. At the highest altitudes, vascular plant and butterfly species communities even tended to change towards cold-dwelling species, although this trend was not statistically significant (Fig. 2): at 2350 m above sea level, which is the upper limit of the tree line in Switzerland [24], the models predicted a trend of plant and butterfly communities that was towards cold-dwelling species and towards CTI values that are usually found at an altitude that is on average 12 m uphill from our study sites for plants ($p = 0.073$), and 40 m uphill for butterflies ($p = 0.055$). In other words, plant and butterfly communities at the upper limit of the tree line showed a trend for an average downhill shift of 12 m and 40 m, respectively, within the eight years of the study.

In Fig. S1 we give the same results as in Fig. 2 but included all data points. Note that most apparent outliers in Fig. S1 were from sample squares with low species richness; because in the linear models, we accounted for the effect of species richness on heterogeneity of residuals, these data points had little influence on the results of the models. Accordingly, the effects of altitude on temporal change of plant and butterfly communities remained stable if outliers ($\Delta \mathrm{CTI}_i < -150$ and $\Delta \mathrm{CTI}_i > 150$ for plants; $\Delta \mathrm{CTI}_i < -500$ and $\Delta \mathrm{CTI}_i > 500$ for butterflies) were excluded. In birds, the temporal change in CTI was not found to significantly depend on altitude, and the change of bird communities was towards warm-dwelling species at all altitudes (Fig. 2).

The increase in community variation that we found for butterflies in lowland communities decreased with altitude (Table 1, Fig. 2), and at higher altitudes, community variation for all three species groups did not significantly change over the study period (Fig. 2). Further, butterfly community variation showed a stronger temporal increase in sample squares with larger altitudinal ranges (Table 1). In all other analyses, altitudinal range within sample squares seemed not to affect the results, as in none

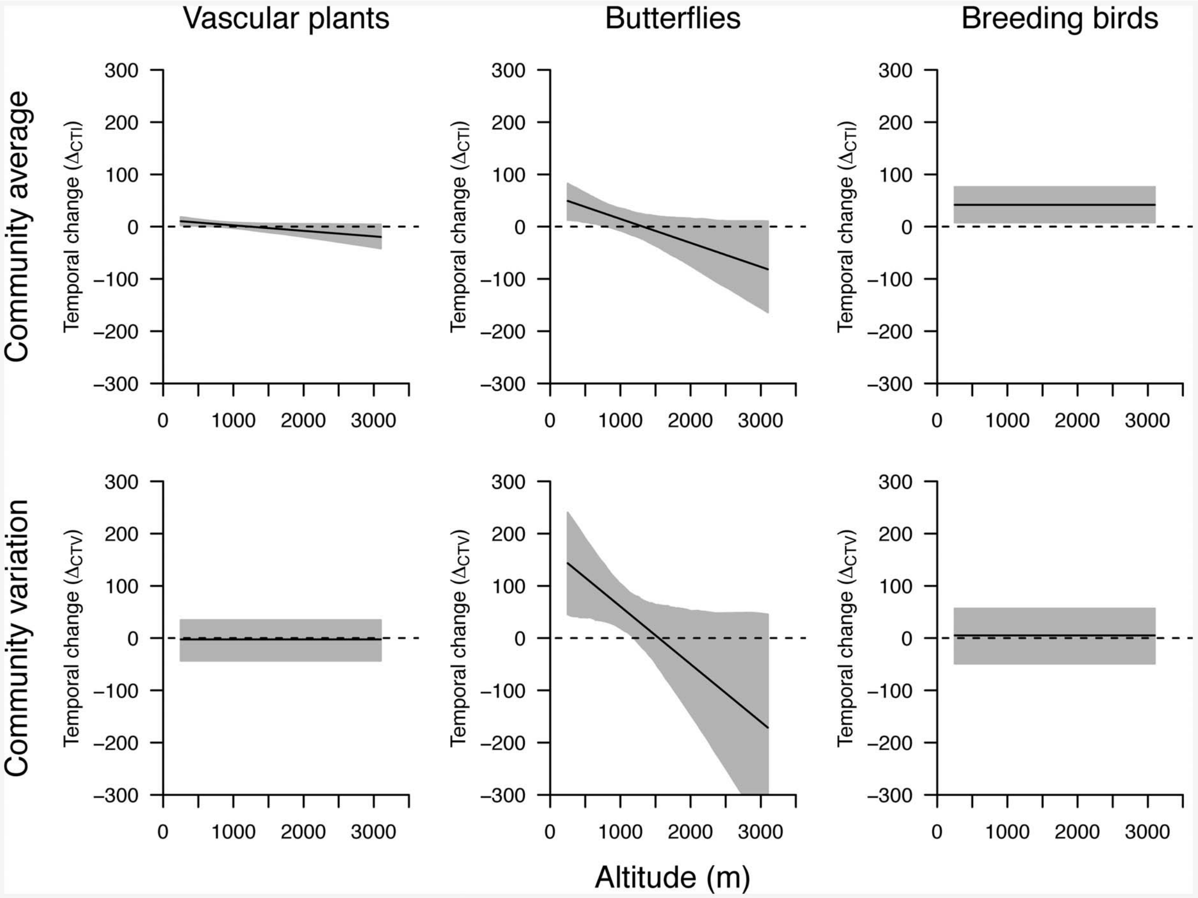


Figure 2. Temporal change of temperature indices of plant, butterfly and bird communities. Given are model predictions for temporal changes of community average of temperature indices ($\Delta \mathrm{CTI}_i$, upper panels) and of community variation in temperature indices ($\Delta \mathrm{CTV}_i$, lower panels) between two surveys at a sample square *i* separated by five years within the period 2003–2010, across the altitudinal range covered in the Swiss national biodiversity monitoring program. Black lines are regression lines from minimal adequate linear models, and grey areas represent bootstrapped 95% confidence intervals. Predicted values with confidence intervals that do not include zero are judged as being significantly different from zero.
doi:10.1371/journal.pone.0082490.g002

Table 1. Estimated parameter values from minimal adequate linear models on temporal changes in a) community average (ΔCTI_i) and b) community variation (ΔCTV_i) between 2003 and 2010 as a function of altitude, with linear (L), quadratic (Q) and cubic (C) polynomials of altitude as predictors and altitudinal ranges within 214 1-km^2 sample squares as covariates.

	plants		butterflies		birds	
a) community average ΔCTI$_i$						
Intercept	7.78	*	37.75	*	41.65	*
altitude (L)	-1.10×10^{-2}	*	-4.59×10^{-2}	*	4.09×10^{-2}	
altitude (Q)	-3.00×10^{-6}		-1.00×10^{-6}		2.00×10^{-6}	
altitude (C)	$<1.00\times10^{-6}$		$<1.00\times10^{-6}$		$<1.00\times10^{-6}$	
altitudinal range	-3.10×10^{-2}		4.35×10^{-2}		-2.00×10^{-1}	
b) community variation ΔCTV$_i$						
Intercept	−2.39		27.89	*	5.21	
altitude (L)	6.01×10^{-2}		-1.10×10^{-1}	*	3.91×10^{-1}	
altitude (Q)	7.00×10^{-5}		-1.50×10^{-5}		2.80×10^{-5}	
altitude (C)	$<-1.00\times10^{-6}$		$<1.00\times10^{-6}$		$<1.00\times10^{-6}$	
altitudinal range	-1.46×10^{-1}		2.93×10^{-1}	*	-3.39×10^{-1}	

Intercepts indicate ΔCTI_i and ΔCTV_i at 500 m above sea level. Asterisks (*) indicate significant values ($p<0.05$).
doi:10.1371/journal.pone.0082490.t001

of the statistical models altitudinal range had a significant effect on the temporal change of CTIs and CTVs (all $p>0.108$).

The finding that temporal changes of plant and butterfly communities varied with altitude could not be explained by different temporal trends of air temperature at different altitudes: temporal trends in mean summer temperature and in mean temperature of the coldest month as measured at 14 meteorological stations were not found to vary with altitude (upper panels in Fig. 3; mean summer temperature: interaction temporal trend×altitude $= -4.62\times10^{-6}$, $t = 1.51$, $p = 0.11$; average temperature of coldest month: interaction temporal trend×altitude $= -3.69\times10^{-6}$, $t = 0.23$, $p = 0.80$). While summer temperatures increased over the years 1995–2010 by on average 0.07°C per year (Fig. 3; linear temporal trend $= 0.07$, $t = 2.02$, $p = 0.048$), mean temperatures of the coldest month did not significantly change over the years 1995–2010 (Fig. 3; linear temporal trend $= -0.07$, $t = 1.24$, $p = 0.80$).

Discussion

In this study, we compared the temporal changes in average temperature indices of communities (CTIs) of vascular plants, butterflies and birds over an altitudinal range of about 2500 m. We found that in a rather short period of eight years (2003–2010), lowland communities of all three species groups changed towards warm-dwelling species. Such a change in communities was expected as resulting from current climatic warming.

In contrast, community temperature variation (CTV) was not found to decrease in any of the species groups, suggesting that climate warming has not led to more homogenous communities in terms of temperature niches of species. A trend towards more homogenous communities would be expected if due to climate warming, cold-dwelling species were decreasing without being replaced by warm-dwelling species, or if climate warming would promote a few ‘winning’ species at the expense of many other species [20,35]. Rather, the change of lowland butterfly communities towards warm-dwelling species was accompanied by an increase in community variation. Variation in temperature niche breadths among species has been found to increase with increasing local variation of temperatures [36]; our study suggests that at least on the short term, variation in temperature niche breadths may also increase with warming air temperatures.

Although our data were collected on the same study sites during the same years for all three species groups, and thus species groups experienced largely the same overall environmental conditions, the community changes in CTI of butterflies and birds were about four to five times as fast as in plants. Still, the observed short-term shifts in plant communities seemed surprising, as short-term shifts of plant communities are mainly known from experimental studies that exposed plant communities to climatic conditions expected to occur at about the end of the century [37,38]. Observational studies investigating entire communities in natural settings and suggesting shifts of plant communities over a period of just a few years seem to be scarce; so far, studies were mainly conducted at high elevations such as mountain summits [3,4] or considered only selected plant species [13].

One main aim of our study was to investigate whether changes towards warm-dwelling species that are found in lowland communities (this study; [8,9]) remain stable across the altitudinal gradient. We found that bird communities changed towards warm-dwelling species at similar rates at all altitudes. It seems likely that the uniform change of bird communities was due to warming air temperatures that were found over the entire altitudinal range (this study; [23]), rather than being mainly caused, e.g., by land-use changes that usually vary across the altitudinal range in Switzerland [39]. Strikingly, however, we found that temporal changes in CTI of plants and butterflies tended to decrease with altitude. Thus, while temporal changes of air temperatures were not found to depend on altitude, plant and butterfly communities changed towards warm-dwelling species at low altitudes but remained stable or even tended to change towards cold-dwelling species at high altitudes.

A decrease of changes in CTI with increasing altitude would be expected if the number of species with downhill range shifts were increasing with altitude. However, recent studies investigating species range shifts in relation to climate change mainly reported range shifts towards higher altitudes [3–6,40]. Few studies also reported species moving towards lower altitudes [41,42]. So far, most studies investigating altitudinal range shifts in alpine species focused on mountain summits. However, at mountain summits, it is by definition not possible to observe species from higher altitudes that have moved downhill, which could have led to a relative overestimation of species with uphill range shifts and underestimation of species with downhill range shifts. In contrast, our results are based on study sites that were randomly selected within the alpine environment, and based on those data, stable distributional ranges or even downhill range shifts at high altitudes seem to be more common than previously thought.

We can only speculate about potential mechanism that could have caused plant and butterfly communities to change towards warm-dwelling species at low altitudes but to remain relatively stable at higher altitudes. One reason could be that conditions in micro-habitats of alpine environments are often decoupled from conditions in the larger environment; this is due to the topographically induced variability of micro-climatic conditions that is usually much larger in alpine areas compared to lowland areas [16,43,44], and to the small size of alpine plants leading to

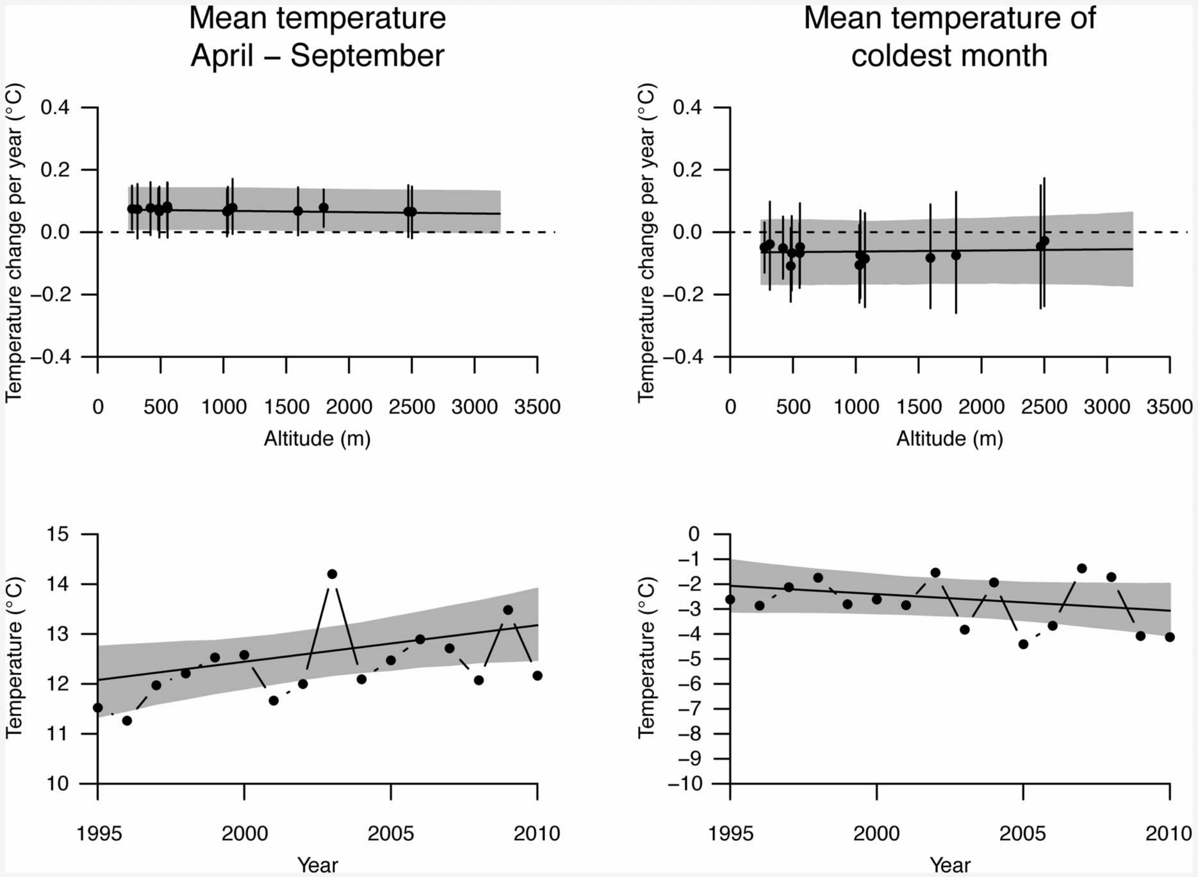


Figure 3. Temporal trends of air temperatures. Upper panels present temporal changes in mean temperatures for summer half-years (April to September, left panel) and for the coldest month (right panel) for the years 1995–2010 as depending on altitude. Points represent linear changes of temperatures over years, given in °C per year, for 14 meteorological stations distributed over Switzerland. Error bars are 95% confidence intervals, and grey areas represent 95% confidence intervals of the linear mixed model predictions for the average trend of temperature over years (solid line). Lower panels present mean temperatures for summer half-years (April to September, left panel) and for the coldest month (right panel). Solid lines indicate temporal trends as estimated from linear mixed models, and grey areas represent 95% confidence intervals of the model predictions.
doi:10.1371/journal.pone.0082490.g003

communities that are aerodynamically decoupled from temperatures in the free atmosphere [43,45]. Therefore, at higher altitudes, plant species do not necessarily need to shift their altitudinal ranges to escape climate warming [43,46]. We thus predicted that temporal changes in CTIs of plants should be highest in the lowlands and should be decreasing with altitude, which was supported by our data. Butterfly communities showed a temporal change in CTIs that was similar to plants, probably because butterflies depend on their host plants for reproduction [47]. In contrast, birds with their larger body sizes and mobile behaviour are likely to be more strongly influenced by air temperatures than by micro-climatic conditions, and as a particularly mobile species group, birds have been shown to respond particularly fast to climate change [40]. This may explain why in contrast to plants and butterflies, bird communities changed towards warm-dwelling species across the entire altitudinal range of the study.

However, other mechanisms may equally likely explain our results. For example, possible downhill range shifts of alpine plant species may be explained by transient competitive release at the lower altitudinal margins of species distributions [41]. In alpine species, lower distributional margins are often characterised by intense competition among species [48], because species richness increases from alpine to subalpine areas [49]. Due to climate warming, degradation of permafrost at high altitudes increasingly leads to debris flow and landslides [41,50]. Such habitat disturbances at lower distributional margins of alpine species might relax the role of competition as a selective filter for community assembly and could thus lead to downhill range shifts of alpine species [41] and therefore counteract the community effects of climate warming.

A further alternative cause for a temporal trend of plant and butterfly communities towards decreasing CTIs at higher altitudes could be land-use related habitat modification [51,52]. For example, many pastures are now abandoned in the Swiss Alps, and trees are currently recolonizing subalpine grasslands [53]. It has been shown that abandonment of pastures could outweigh the effect of climate warming on species communities [53,54]. If species temperature indices (STIs) of species that are promoted by land-use change are below the CTIs of communities that are present before a land-use change, this could lead to a decrease of CTIs over time that is not caused by climate change. Therefore, both climate warming and land-use change could generally be expected to affect CTIs, and they may do so in opposing directions [9,55].

Manipulative experiments testing *a priori* hypotheses would be needed to make strong inference about mechanistic effects of global change and to disentangle effects of climate warming and land-use change on communities (for strong inference see [56]). Manipulative small-scale experiments, however, are hardly sufficient to draw conclusions on how multiple human pressures are affecting biodiversity in the real world; thus, understanding human impacts on natural biological systems requires surveys on biological change that is the integrated result of all human pressures over larger spatial scales [57], which is the focus of many long-term monitoring programs [58,59]. Although biodiversity monitoring schemes usually have been implemented to assess spatial and temporal trends in biological systems without necessarily addressing underlying mechanisms [58], we here show that analysing data from such monitoring programs may at least help to develop hypotheses on mechanisms leading to biodiversity change [60].

Currently, most of the evidence for effects of climate warming on biodiversity comes from models forecasting future responses under different long-term scenarios for climate change [61,62]. However, the temporal scales of such studies usually ranged from 20 to 100 years, considering biological consequences of climate change for periods of time that are far beyond the time frames in which policy makers are usually operating [63]. Here, we presented evidence that on the surprisingly short temporal scale of eight years, there were significant altitudinal shifts in communities of plants, birds and butterflies. We hope that our study contributes to fostering further research on short-term responses of local ecosystems to climate change that is urgently needed to set conservation practices [64]. Further, our results may support the idea that at least for plants and butterflies, alpine landscapes are buffering the effects of climate warming on species communities [43]. Whether such a buffering effect of alpine environments could be maintained over longer periods of time remains to be seen.

Supporting Information

Text S1 Field protocols for vascular plants, butterflies and breeding birds.
(DOCX)

Figure S1 Temporal change of temperature indices of plant, butterfly and bird communities. The figure presents the same results as in Fig. 2, but additionally shows data points.
(DOCX)

Acknowledgments

We thank the dedicated and qualified volunteers who conducted the fieldwork for the Swiss breeding bird survey, and the about 85 persons who conducted fieldwork on plants and butterflies. Further, we thank Vincent Devictor for providing species temperature indices (STIs) for birds, Oliver Schweiger and Chris van Swaay for providing STIs for butterflies, and the Swiss Federal Office for the Environment (FOEN) for providing data from the Swiss biodiversity monitoring scheme. We also thank Christian Körner for discussions and three anonymous referees for comments on the manuscript.

Author Contributions

Conceived and designed the experiments: TR MP VA. Performed the experiments: TR MP VA. Analyzed the data: TR. Wrote the paper: TR MP VA.

References

1. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37: 637–669.
2. Walther GR, Post E, Convey P, Menzel A, Parmesan C, et al. (2002) Ecological responses to recent climate change. Nature 416: 389–395.
3. Walther GR, Beissner S, Burga CA (2005) Trends in the upward shift of alpine plants. Journal of Vegetation Science 16: 541–548.
4. Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, et al. (2012) Recent plant diversity changes on Europe's mountain summits. Science 336: 353–355.
5. Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barancok P, et al. (2012) Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2: 111–115.
6. Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, et al. (2011) Upslope migration of Andean trees. Journal of Biogeography 38: 783–791.
7. Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024–1026.
8. Devictor V, Van Swaay C, Brereton T, Brotons L, Chamberlain D, et al. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change 2: 121–124.
9. Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B-Biological Sciences 275: 2743–2748.
10. Chamberlain D, Arlettaz R, Caprio E, Maggini R, Pedrini P, et al. (2012) The altitudinal frontier in avian climate impact research. Ibis 154: 205–209.
11. Bertrand R, Lenoir J, Piedallu C, Riofrio-Dillon G, de Ruffray P, et al. (2011) Changes in plant community composition lag behind climate warming in lowland forests. Nature 479: 517–520.
12. Franzen M, Molander M (2012) How threatened are alpine environments? A cross taxonomic study. Biodiversity and Conservation 21: 517–526.
13. Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768–1771.
14. Körner C (2007) The use of 'altitude' in ecological research. Trends in Ecology & Evolution 22: 569–574.
15. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, et al. (2009) The velocity of climate change. Nature 462: 1052–1055.
16. Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography 38: 406–416.
17. Roth T, Weber D (2008) Top predators as indicators for species richness? Prey species are just as useful. Journal of Applied Ecology 45: 987–991.
18. Hintermann U, Weber D, Zangger A (2000) Biodiversity monitoring in Switzerland. Schriftenreihe Landschaftspflege Naturschutz 62: 47–58.
19. Kampichler C, van Turnhout CAM, Devictor V, van der Jeugd HP (2012) Large-scale changes in community composition: determining land use and climate change signals. PLOS ONE 7: e35272.
20. Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A (2012) Rise of the generalists: evidence for climate driven homogenization in avian communities. Global Ecology and Biogeography 21: 568–578.
21. Schweiger O, Settele J, Kudrna O, Klotz S, Kuhn I (2008) Climate change can cause spatial mismatch of trophically interacting species. Ecology 89: 3472–3479.
22. Hanspach J, Schweiger O, Kühn I, Plattner M, Pearman PB, et al. (*in press*) Host plant availability potentially limits butterfly distributions under cold environmental conditions. Ecography.
23. Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2010) Revisiting Swiss temperature trends 1959–2008. International Journal of Climatology 32: 203–213.
24. Paulsen J, Körner C (2001) GIS-analysis of tree-line elevation in the Swiss Alps suggests no exposure effect. Journal of Vegetation Science 12: 817–824.
25. Begert M, Schlegel T, Kirchhofer W (2005) Homogeneous temperature and precipitation series of Switzerland from 1864 to 2000. International Journal of Climatology 25: 65–80.
26. Schüepp M, Gensler G (1980) Klimaregionen der Schweiz. In Die Beobachtungsnetze der Schweizerischen Meteorologischen Anstalt. Zürich: Schweizerische Meteorologische Anstalt.
27. Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, et al. (2010) Flora Indicativa, Ecological Indicator Values and Biological Attributes of the Flora of Switzerland and the Alps. Bern: Haupt-Verlag.
28. Schweiger O, Harpke A, Wiemers M, Settele J (*in press*) CLIMBER: Climatic niche characteristics of the butterflies in Europe. ZooKeys.
29. Settele J, Kudrna O, Harpke A, Kühn I, Van Swaay C, et al. (2008) Climatic Risk Atlas of European Butterflies. Moscow: Pensoft.
30. Hagemeijer WJM, Blair MJ (1997) The EBCC Atlas of European Breeding Birds: their Distribution and Abundance. London: Poyser.
31. Van Strien AJ, Soldaat LL, Gregory RD (2012) Desirable mathematical properties of indicators for biodiversity change. Ecological Indicators 14: 202–208.
32. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. New York: Springer.
33. Pinheiro J, Bates D, DebRoy S, Sarkar D (2011) NLME: linear and nonlinear mixed effects models. R package, version 3.1-102. http://cran.r-project.org.

34. R Development Core Team (2013) R: A language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
35. McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14: 450–453.
36. Quintero I, Wiens JJ (2013) What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. Global Ecology and Biogeography 22: 422–432.
37. Cantarel AAM, Bloor JMG, Soussana JF (2013) Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. Journal of Vegetation Science 24: 113–126.
38. Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, et al. (2000) The response of two contrasting limestone grasslands to simulated climate change. Science 289: 762–765.
39. Gusewell S, Peter M, Birrer S (2012) Altitude modifies species richness-nutrient indicator value relationships in a country-wide survey of grassland vegetation. Ecological Indicators 20: 134–142.
40. Maggini R, Lehmann A, Kéry M, Schmid H, Beniston M, et al. (2011) Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes. Ecological Modelling 222: 21–32.
41. Lenoir J, Gegout JC, Guisan A, Vittoz P, Wohlgemuth T, et al. (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography 33: 295–303.
42. Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science 331: 324–327.
43. Scherrer D, Körner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. Global Change Biology 16: 2602–2613.
44. Lenoir J, Graae BJ, Aarrestad PA, Alsos IG, Armbruster WS, et al. (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. Global Change Biology 19: 1470–1481.
45. Körner C (2003) Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Berlin: Springer.
46. Graham EA, Rundel PW, Kaiser W, Lam Y, Stealey M, et al. (2012) Fine-scale patterns of soil and plant surface temperatures in an alpine fellfield habitat, White Mountains, California. Arctic, Antarctic, and Alpine Research 44: 288–295.
47. Pellissier L, Alvarez N, Espíndola A, Pottier J, Dubuis A, et al. (2012) Phylogenetic alpha and beta diversities of butterfly communities correlate with climate in the western Swiss Alps. Ecography 36: 541–550.
48. Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, et al. (2002) Positive interactions among alpine plants increase with stress. Nature 417: 844–848.
49. Vetaas OR (2002) Realized and potential climate niches: a comparison of four Rhododendron tree species. Journal of Biogeography 29: 545–554.
50. Cannone N, Sgorbati S, Guglielmin M (2007) Unexpected impacts of climate change on alpine vegetation. Frontiers in Ecology and the Environment 5: 360–364.
51. Hättenschwiler S, Körner C (1995) Responses to recent climatewarming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. Journal of Vegetation Science 6: 357–368.
52. Archaux F (2004) Breeding upwards when climate is becoming warmer: no bird response in the French Alps. Ibis 146: 138–144.
53. Vittoz P, Rulence B, Largey T, Frelechoux F (2008) Effects of climate and land-use change on the establishment and growth of cembran pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the central Swiss Alps. Arctic, Antarctic, and Alpine Research 40: 225–232.
54. Körner C (2005) The Green Cover of Mountains in a Changing Environment. In: Huber UM, Bugmann HKM, Reasoner MA, editors. Global change and mountain regions. Springer. pp. 367–375.
55. Clavero M, Villero D, Brotons L (2011) Climate change or land use dynamics: do we know what climate change indicators indicate? PLOS ONE 6: e18581.
56. Platt JR (1964) Strong inference. Science 146: 347–353.
57. Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, et al. (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology & Evolution 25: 574–582.
58. Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16: 446–453.
59. Lindenmayer DB, Likens GE (2009) Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution 24: 482–486.
60. Couvet D, Devictor V, Jiguet F, Julliard R (2011) Scientific contributions of extensive biodiversity monitoring. Comptes Rendus Biologies 334: 370–377.
61. Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, et al. (2011) 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology 17: 2330–2341.
62. Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE (2012) Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change 3: 203–207.
63. Sinclair SJ, White MD, Newell GR (2010) How useful are species distribution models for managing biodiversity under future climates? Ecology and Society 15: 8.
64. Ibáñez I, Gornish ES, Buckley L, Debinski DM, Hellmann J, et al. (2012) Moving forward in global-change ecology: capitalizing on natural variability. Ecology and Evolution 3: 170–181.

S1. Field protocols for vascular plants, butterflies and breeding birds.

Vascular plants

Plant surveys were performed by qualified botanists who received special training to reduce among-observer variation. For each sample square of 1 km^2, occurrences (presence / absence) of vascular plant species were surveyed along a 2.5 km transect that followed existing trails wherever possible. If no trails existed, surveyors marked the transect route in the field and plotted it on a map. At a sample square in a given year, transects were inspected once in spring and again in late summer, assuring that data collection spanned a large variation in flowering phenologies that likely influenced species detection [1]. Exceptions were sample squares at high altitudes with short vegetation period, where only one inspection per field season was conducted. During each inspection of a sample square, surveyors walked the transects in both directions and recorded all plant species within 2.5 m to each side of the transects on the way forth and back, respectively. Sampling characteristics of plant surveys were assessed in a previous study [2]: two botanists independently assessed 23 transects; the mean of the relative differences between two assessments was 7.9%, corresponding to a difference of 19.7 ± 4.9 species (mean ± SE), with a total of 250 species recorded. For more information and quality measures on the field methods, see [2] and [3].

Butterflies

The field protocol for butterflies was based on the British butterfly monitoring scheme [4]. Surveys of butterfly species occurrences (presence / absence) were performed by qualified entomologists who received special training to reduce among-observer variation. At a sample square in a given year, transects were inspected seven times between 21 April and 21 September in the lowlands, and four times between July and August above approximately 2000 m. The difference in numbers of inspections corresponds to the shorter flying season at higher altitudes; sites at high and low altitudes received approximately equal sampling effort per week of flight season, and differences in the number of visits should thus not bias the results [1]. Surveys were conducted within separate time windows of 14 or 21 days, depending on a seasonal schedule, following a standardized protocol. Butterfly surveys were performed on the same transects as the surveys of vascular plants. Inspections of transects were conducted during favourable weather conditions, i.e. sunshine during more that 80% of the duration of the inspection, temperature of more than 13°C, and wind of less than 19 km/h (Beauford level 1-2). During each inspection of transects, surveyors walked the transects in both directions and recorded all day-flying butterfly species (including Hesperiidae and Zygaenidae) within 5 m to each side of the transects on the way forth and back, respectively. Detectability varied by species and averaged 88% per inspection [5]. For more information and quality measures on the field methods, see [5-8].

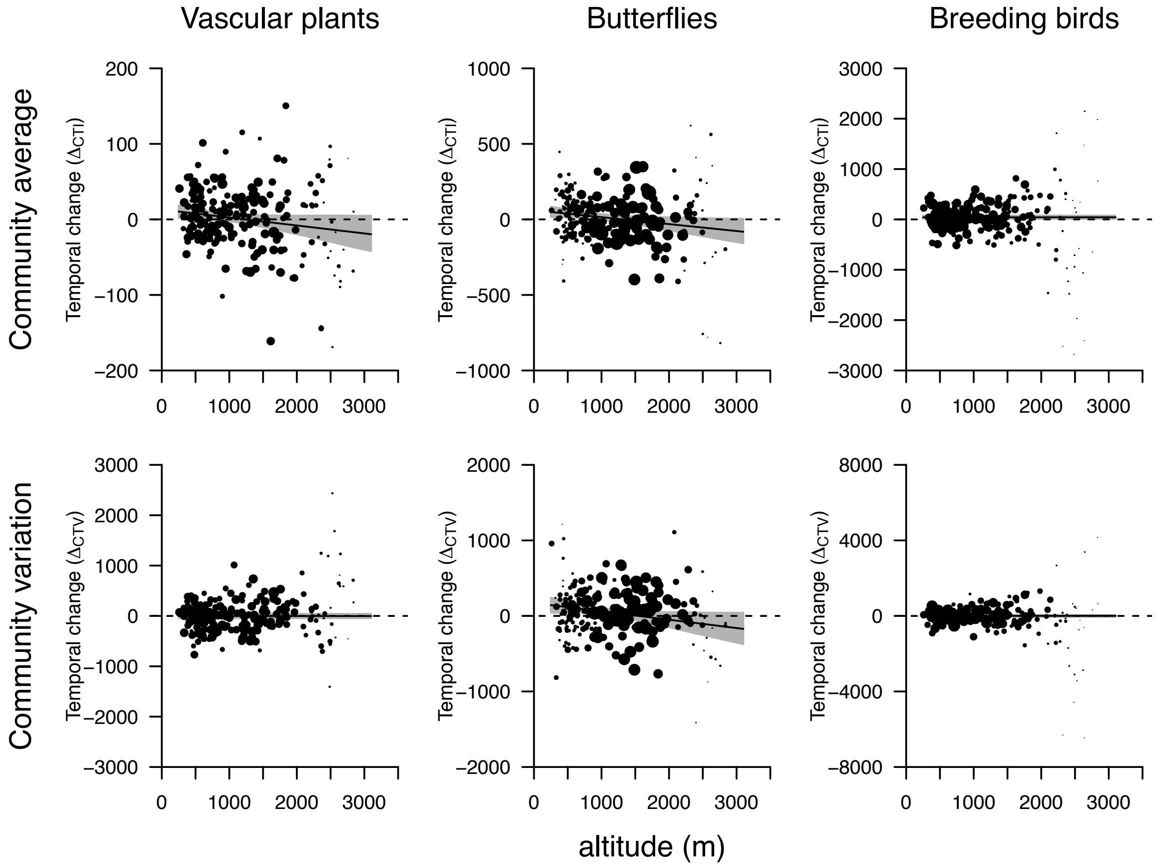
Breeding birds

Surveys and surveying methods were largely identical to the Swiss Ornithological Institute's common breeding bird survey [9,10]. Bird surveys were performed by qualified volunteer ornithologists who used a territory mapping method [11]. Breeding birds were surveyed using different transects than in vascular plants and butterflies, aiming at fully covering each sample square and at detecting all breeding bird species. This resulted in forested areas having greater transect lengths than did open sites. Transect lengths averaged 5.1 km (range 1.2 - 9.4 km). In inaccessible regions with very steep slopes, sample squares could sometimes not be fully covered. In such cases, any part of an area that was impossible to sample was marked on a map. Depending on altitude, each square was sampled two or three times between 15 April and 15 July. High altitude squares with less than 10% forest cover were only visited twice, corresponding to the shorter breeding season compared to low altitude squares. Mean detectability of birds across sites was estimated 89%, with a somewhat higher detectability at high altitude sites, in spite of receiving fewer visits [10]. For more information and quality measures on the field methods, see [9,10,12].

References

1. Pearman P, Weber D (2007) Common species detemine richness patterns in biodiversity indicator taxa. Biological Conservation 138: 109-119.
2. Plattner M, Weber D, Birrer S (2004) Data quality in monitoring plant species richness in Switzerland. Community Ecology 5: 135-143.
3. Wohlgemuth T, Nobis MP, Kienast F, Plattner M (2008) Modelling vascular plant diversity at the landscape scale using systematic samples. Journal of Biogeography 35: 1226-1240.
4. Pollard E, Moss D, Yates TJ (1995) Population trends of common british butterflies at monitored sites. Journal of Applied Ecology 32: 9-16.
5. Kéry M, Royle JA, Plattner M, Dorazio RM (2009) Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90: 1279-1290.
6. Kéry M, Plattner M (2007) Species richness estimation and determinants of species detectability in butterfly monitoring programmes. Ecological Entomology 32: 53-61.
7. Altermatt F, Birrer S, Plattner M, Ramseier P, Stalling T (2008) Erste Resultate zu den Tagfaltern im Biodiversitätsmonitoring Schweiz. Entomo Helvetica 1: 75-83.
8. Dorazio RM, Kéry M, Royle JA, Plattner M (2010) Models for inference in dynamic metacommunity systems. Ecology 91: 2466-2475.
9. Schmid H, Zbinden N, Keller V (2004) Überwachung der Bestandsentwicklung häufiger Brutvögel in der Schweiz. Sempach: Schweizerische Vogelwarte.
10. Kéry M, Schmid H (2006) Estimating species richness: calibrating a large avian monitoring programme. Journal of Applied Ecology 43: 101-110.
11. Bibby C-J, Burgess ND, Hill DA, Mustoe SH (2000) Bird census techniques. London: Academic Press.
12. Kéry M, Schmid H (2004) Monitoring programs need to take into account imperfect species detectability. Basic and Applied Ecology 5: 65-73.

Figure S2. Temporal change of temperature indices of plant, butterfly and bird communities. Given are model predictions for temporal changes of community averages of temperature indices ($\Delta\mathrm{CTIi}$, upper panels) and of community variation in temperature indices ($\Delta\mathrm{CTV}_i$, lower panels) for vascular plants (left panels), butterflies (middle panels) and birds (right panels) between two surveys separated by five years within the period 2003 - 2010, across the altitudinal range covered in the Swiss national biodiversity monitoring program. Points represent 214 1-km^2 sample squares, and sizes of points are proportional to the number of species recorded during the first survey. Black lines are regression lines from minimal adequate linear models, and grey areas represent bootstrapped 95%-confidence intervals. Predicted values with confidence intervals that do not include zero are judged as being significantly different from zero.



7 Chapter V: Host plant availability potentially limits butterfly distributions under cold environmental conditions

Ecography 37: 301–308, 2014
doi: 10.1111/j.1600-0587.2013.00195.x

Subject Editor: J. R. Spence. Accepted 23 July 2013

Host plant availability potentially limits butterfly distributions under cold environmental conditions

Jan Hanspach, Oliver Schweiger, Ingolf Kühn, Matthias Plattner, Peter B. Pearman, Niklaus E. Zimmermann and Josef Settele

J. Hanspach (hanspach@leuphana.de), O. Schweiger, I. Kühn and J. Settele, UFZ, Helmholtz Centre for Environmental Research – UFZ, Dept of Community Ecology, Theodor-Lieser-Str. 4, DE-06120 Halle (Saale), Germany. JH also at: Leuphana Univ. Lüneburg, Inst. of Ecology, Scharnhorststr. 1, DE-21335 Lüneburg, Germany. IK and JS also at: iDiv, German Centre for Integrative Biodiversity Research, Halle-Jena-Leipzig, Deutscher Platz 5e, DE-04103 Leipzig, Germany. – M. Plattner, Hintermann & Weber AG, Ecological Consultancy, Planning and Research, Austrasse 2a, CH-4153 Reinach BL, Switzerland. – P. B. Pearman and N. E. Zimmermann, Landscape Dynamics Unit, Swiss Federal Research Inst. WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

Species ranges are shaped by both climatic factors and interactions with other species. The stress gradient hypothesis predicts that under physiologically stressful environmental conditions abiotic factors shape range edges while in less stressful environments negative biotic interactions are more important. Butterflies provide a suitable system to test this hypothesis since larvae of most species depend on biotic interactions with a specific set of host plants, which in turn can shape patterns of occurrence and distribution. Here we modelled the distribution of 92 butterfly and 136 host plant species with three different modelling algorithms, using distribution data from the Swiss biodiversity monitoring scheme at a 1 × 1 km spatial resolution. By comparing the ensemble prediction for each butterfly species and the corresponding host plant(s), we assessed potential constraints imposed by host plant availability on distribution of butterflies at their distributional limits along the main environmental gradient, which closely parallels an elevational gradient. Our results indicate that host limitation does not play a role at the lower limit. At the upper limit 50% of butterfly species have a higher elevational limit than their primary host plant, and 33% have upper elevational limits that exceed the limits of both primary and secondary hosts. We conclude that host plant limitation was not relevant to butterfly distributional limits in less stressful environments and that distributions are more likely limited by climate, land use or antagonistic biotic interactions. Obligatory dependency of butterflies on their host plants, however, seems to represent an important limiting factor for the distribution of some species towards the cold, upper end of the environmental gradient, suggesting that biotic factors can shape ranges in stressful environments. Thus, predictions by the stress gradient hypothesis were not always applicable.

Understanding causal mechanisms determining species distributions is an important topic in biogeography and macroecology (Brown et al. 1996). Species distributions are limited by the range of abiotic conditions under which individuals of a species can survive and reproduce. Biotic factors further constrain this fundamental niche to the realized niche, which encompasses all the conditions under which a species actually occurs (Hutchinson 1957). Biotic factors are interspecific interactions that affect the performance of species positively or negatively and, therefore, likely strongly influence range limits (Brown et al. 1996). Such influences are probably context dependent and likely show geographical and environmental patterns. For example, the stress gradient hypothesis predicts that abiotic conditions limit ranges when resource availability is low and under unfavourable biophysical conditions (high altitude/latitude, dry environments). Negative biotic interactions (mainly competition) limit ranges under less physiologically stressful conditions, i.e. lower altitude/latitude, more humid environments (Bertness and Callaway 1994). While observational studies support this hypothesis (Callaway 1992, Merrill et al. 2008), it has not received much attention so far (but see Normand et al. 2009, Meier et al. 2011 for large scale examples in plants).

Species distribution models (SDMs) correlate species occurrence patterns with independent sets of variables to identify parameters relevant to the distribution of species. Frequently, SDMs incorporate climatic factors (Huntley et al. 1995) and variables describing land-cover patterns (Pearson et al. 2004, Pompe et al. 2008). The incorporation of biotic interactions into SDMs presents a challenge to present research (Kissling et al. 2012, Wisz et al. 2013). So far, few studies incorporate biotic interactions into species distribution models. Most such studies focus on tree species, while for animals only a few single-species studies exist (Araújo and Luoto 2007, Heikkinen et al. 2007, Schweiger et al. 2008, Meier et al. 2010). Heikkinen et al. (2007) show that species distribution models of tree-hole breeding owls in Finland could be improved by incorporating variables expressing presence of woodpeckers. For common tree species in the Swiss Alps, performance of species distribution models is superior to a simple climatic model when the abundances of other tree species are included as predictor variables (Meier et al. 2010). According to Meier et al. (2011), biotic interaction with competing species generally increases towards the southern latitudinal distribution limit of the European beech *Fagus sylvatica*. In another example, the distribution of the butterfly *Parnassius mnemosyne* in Europe is tightly linked to the distribution of its four host plants (Araújo and Luoto 2007). Additionally, Schweiger et al. (2008) show that the distribution of the butterfly *Boloria titania* is limited by both its larval host plant *Polygonum bistorta* and other factors, most likely climate. These studies suggest a frequent role for biotic interactions in limiting the geographic distributions of species.

Most butterflies depend on a limited set of plant species as food resources during larval development. Such dependencies generally determine local occurrence patterns of butterfly species. How this translates into effects on large-scale species distributions is particularly important, especially when considering projections under scenarios of climate change, to which butterflies and their host plants may respond differently (Schweiger et al. 2008). Although Schweiger et al. (2012) conclude from a study of a subset of European butterflies that only few butterfly species are significantly limited by their host plants at large spatial scales, their study does not consider that biotic interactions might only be relevant at particular range limits, as is predicted by the stress gradient hypothesis. However, the findings of Meier et al. (2011) challenge the generality of the stress gradient hypothesis by showing that the potential for competition among tree species in Switzerland is especially high under cold, dry and harsh climate, and not under warm, wet and more favourable conditions as predicted by the hypothesis.

In order to improve our understanding of the effects of different drivers on range limits we have tested the hypothesis that abiotic factors are more important under less favourable environments while the biotic relationships between butterflies and their host plants are more important in benign environments. We used the distribution of a large set of butterflies in Switzerland together with topo-climatic variables and the availability of host plants to represent one important biotic factor. Further, we evaluate whether host plant limitation is biased towards certain environmental conditions.

Methods

Study area

Our study area is Switzerland, a country covering over 41 293 km^2 between 45°N and 48°N and 5°E to 11°E. The country has an altitudinal gradient ranging from 193 to 4634 m a.s.l and includes climatic conditions analogous to large parts of Europe. Mean annual temperatures range from -11°C to 12°C and mean annual rainfall varies from 438 to 2950 mm (Kirchhofer 1982–2000). In the lowlands the main land use is intensified agriculture while in montane areas forests are dominant. Extensively used pastures dominate above the tree line.

Environmental variables

Topo-climatic data were available on a 1×1 km grid across Switzerland (Zimmermann and Kienast 1999, Pearman et al. 2011). We extracted variables that are ecologically relevant and non-redundant (Pearson correlation coefficient < 0.7). These variables included growing degree days above 0°C [°C], mean annual precipitation sum [mm], mean annual solar radiation [MJ m^{-2}], slope [°] and topographic exposure [unitless]. Topographic exposure describes the relative elevation of the centre of a grid cell compared to its surrounding elevation. It ranged between –2.39 and 3.92 with low values indicating concavity and high values convexity. We excluded all grid cells that were covered by more than 50% water according to the Swiss 'Arealstatistik 1992/1997' land cover summary (Bundesamt für Statistik, <www.bfs.admin.ch>). Environmental variables were standardized to zero mean and unit variance prior to analysis.

We performed principal components analysis (PCA) on the environmental variables across all grid cells in order to describe the main environmental gradients (Fig. 1). The first principal component explained 47.6% of the variance and described a gradient from grid cells with a predominantly flat topography and warm and dry climates (negative values on the principal component) to grid cells

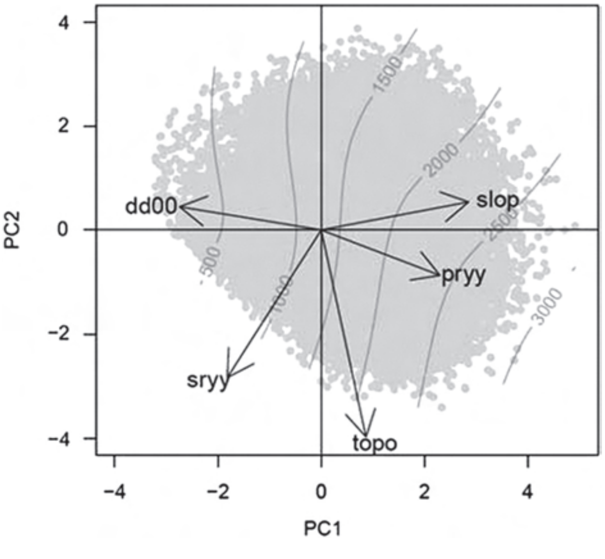


Figure 1. Result of the principal component analysis on the environmental variables used for model calibration. The environmental variables are growing degree days (dd00), solar radiation (sryy), topographic position (topo), annual precipitation (pryy) and slope (slop). The first axis is further used to compare the agreement between the butterfly and host distribution. Contour lines represent the altitudinal gradient and were fitted to the plot a posteriori.

with steep slopes and cold and wet climates (positive values), thus resembling the altitudinal gradient. The second principal component explained 22.2% and described a gradient from grid cells with a convex topography receiving large amounts of solar radiation (negative values) to grid cells with a concave topography and little exposure to sun (positive values). We used the first principal component scores as the main environmental gradient along which we assessed the potential limitation of butterfly species distributions by their host plants.

Survey data

We extracted butterfly and vascular plant survey data from the Swiss biodiversity monitoring programme (< www.biodiversitymonitoring.ch >) from the period 2005–2009. Swiss biodiversity monitoring is realized within the same grid system as used for the environmental data (1 × 1 km) but relies on a subset of 473 sites that are regularly placed all over Switzerland. Each year 20% of the sites that are evenly distributed over the whole country are sampled. Per year and site butterfly occurrence was surveyed four to seven times along a 2.5 km transect within a site covering the whole flight period at different elevations. Presence of vascular plants was recorded once in the high Alps and twice at all lower elevations in the given year along the same transects for 462 sites. We assume that the species distributions were stable during the sampling period, but acknowledge that some species might have have experienced small range shifts due to recent warming in Switzerland. However, due to the rotational sampling scheme and the joint surveys of plants and butterflies in the same year, this should not bias the data.

Host plant data

Host plant selectivity was extracted from scientific literature (Ebert and Rennwald 1991a, b, Ebert 1994, Schweizer Bund für Naturschutz 1994, Sonderegger 2005) and complemented by expert knowledge, including information on different levels of fidelity and data quality. We used those plant species that were classified as exclusive host, main host or secondary host, respectively. Host information describing exceptional use, very broad preference (e.g. feeding on most species of an entire family), or uncertain data was excluded from the analysis. For the ease of presentation we grouped the results for exclusive host type (e.g. feeding only on one species) together with those for main host and refer to them as main host. In total, host plant information was available for 169 butterfly species. 184 plant species and 3 genera without any detailed information about the species level were listed as hosts.

Modelling

We separately modelled species distribution for those butterfly and plant species with more than 20 presences and absences, respectively (92 butterflies and 136 plant species). Species distribution models were calibrated using presence/absence data on each species as response variables and the topo-climatic variables as explanatory variables. We applied three different modelling algorithms, namely generalized linear models (GLMs) using linear and quadratic terms and stepwise selection based on AIC, generalized additive models (GAMs) using a spline smoother with three degrees of freedom, and boosted regression trees (BRTs) allowing for a maximum of 5000 trees, a learning rate of 0.001 and a maximum depth of seven interactions.

Models were validated internally using the True Skill Statistic ($TSS_{GLM} = 0.58 \pm 0.14$ mean ± SD; $TSS_{GAM} = 0.58 \pm 0.14$; $TSS_{BRT} = 0.77 \pm 0.11$). TSS is a measure of predictive accuracy ranging from -1 (perfect disagreement) to 1 (perfect agreement) and is not influenced by prevalence (Allouche et al. 2006).

We combined the results of the different modelling algorithms and applied an ensemble prediction weighted by individual model performance (TSS) to describe the modelled species distribution for the 39 470 grid cells (each 1 × 1 km) across Switzerland. Grid cells with environmental conditions exceeding those of the calibration data by more than 5% were not included in the prediction. Predicted probabilities of occurrence were transformed into presence/absence maximizing the model accuracy using TSS. Species distribution modelling was conducted with BIOMOD (Thuiller et al. 2009).

Comparing distribution of host and butterfly

We evaluated the agreement between the modelled distribution of a given butterfly species and the modelled distribution of its host plant(s) in order to evaluate potential host plant limitation. If more than one host species was given, we considered the host to be present if at least one of the host species was modelled as present. We assessed the agreement between host and butterfly distribution separately for both the main hosts alone and the main plus secondary hosts. If host information was not species specific (e.g. species feeds on species from a whole genus), we considered all modelled species of that genus.

Agreement was estimated via the relative proportion of modelled presences and absences of hosts and butterfly along the main environmental gradient as described by GAMs. The main environmental gradient was determined using the first axis of the principal component analysis on the climatic data used for model calibration (Fig. 1), and was used as the independent variable in the GAMs. Agreement per grid cell is given by the four possible outcomes: neither host nor butterfly are modelled as present (Fig. 2A, B), both host and butterfly are modelled as present (Fig. 2C, D), only the host is modelled as present (Fig. 2E, F), or only the butterfly is modelled as present (Fig. 2G, H). We separately modelled the agreement levels 'only host present', 'host and butterfly present' and 'only butterfly present' as the binomial response variables and as a function of the main environmental gradient in GAMs. The results were plotted and the type of agreement was estimated visually for the upper and the lower limits of joint occurrence (Fig. 2, Fig. 3.). All statistical analyses were performed using the R environment (R Development Core Team).

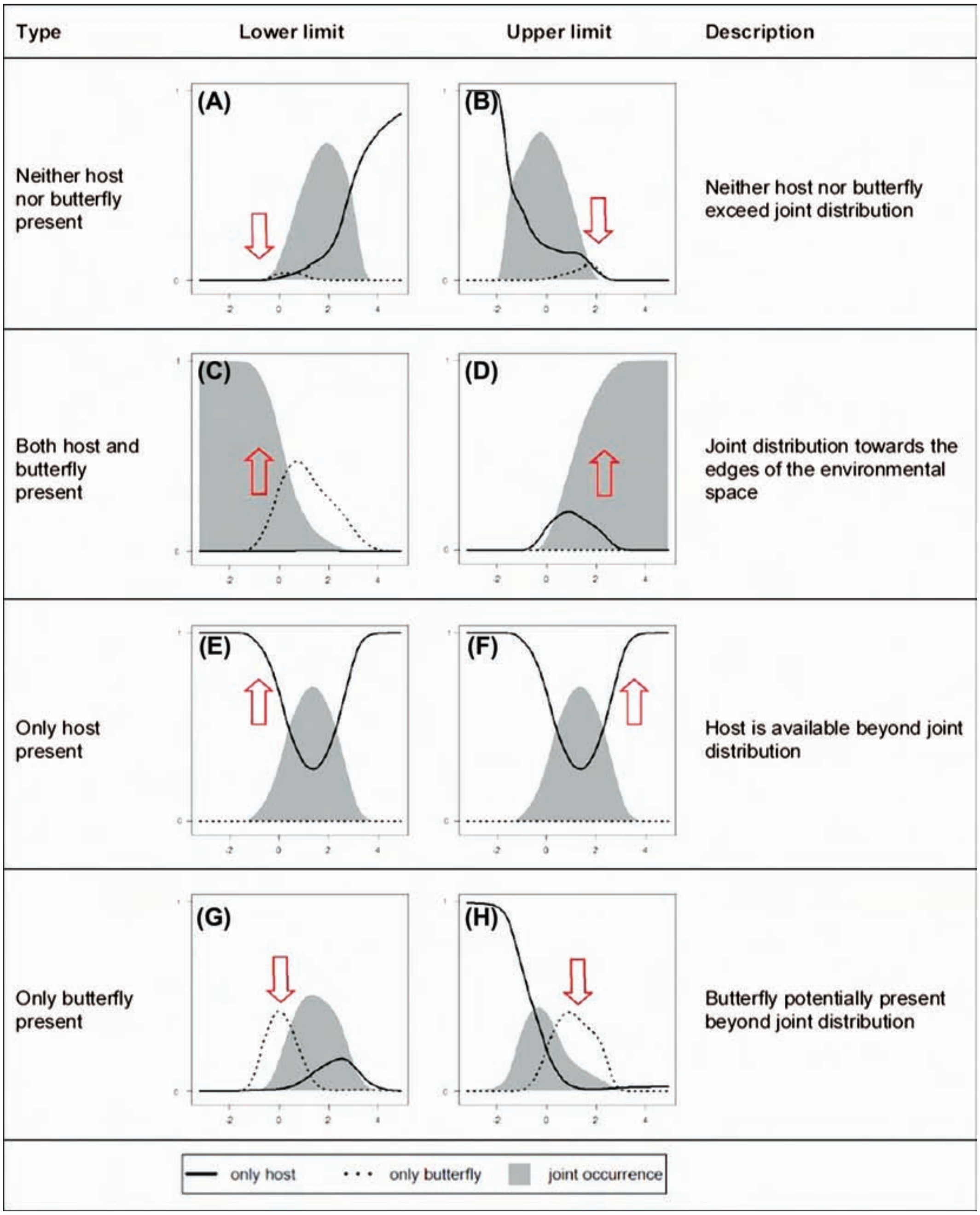


Figure 2. Different types of agreement between the modelled distribution of host plants and butterflies. Graphs are showing the proportion of grid cells containing presences of host, butterfly or both along the main environmental gradient. Arrows indicate where a certain type of agreement occurs. Panel letters are used to enable a direct reference in the text. The x-axis is the first axis of a principal component analysis of a PCA of the environmental data (Fig. 1). See methods section for further description.

Results

Most frequently, the modelled host distribution exceeded the butterfly distribution along the main environmental gradient (Table 1). Most of the butterfly species showed a unimodal response to the main environmental gradient, meaning that the modelled altitudinal limits occurred within the study area (e.g. Fig. 3B). However, patterns of agreement between butterfly and host plant distribution differed quite strongly between lower and upper environmental limits.

At the lower environmental limit hosts were present beyond the modelled range limits of most butterfly species (69% when considering main hosts, 81% when considering main and secondary hosts; e.g. Fig. 3D). Much less frequently, neither the distribution of the butterfly nor the distribution of the host exceeded the joint distribution (19% main host; 5% main and secondary host). The modelled butterfly distribution exceeded modelled host plant distribution only once for main host and three times for main host and secondary host.

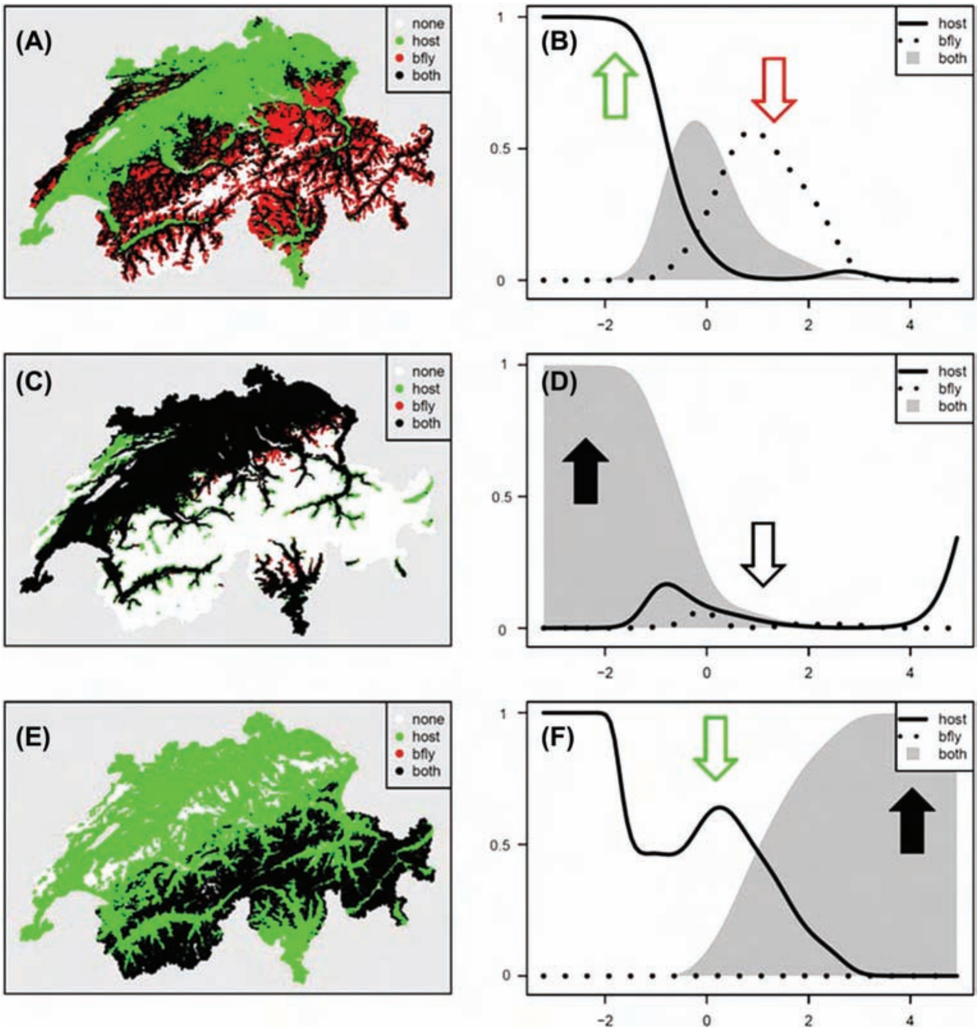


Figure 3. Modelling results for three different butterfly species and their host plants. Panels (A) and (B) show the agreement of the modelled distribution of *Polyommatus semiargus* and hist main host plant *Trifolium pratense*. In panel (A) either none of the two species is modelled as present ('none', white), only host is present ('host', green), only butterfly is present ('bfly', red) or host and butterfly are both present ('both', black). Panel (B) shows the modelled proportions of the distributional agreement along the main environmental gradient (i.e. the first principal component). At the lower limit (green arrow) of the joint distribution the host plant is available but the butterfly does not occur. At the upper limit (red arrow), the potential distribution of the butterfly exceeds the distribution of the host. Panels (C) and (D) show the agreement between *Celastrina argiolus* and its host plants *Frangula alnus* and *Cornus sanguinea*. At the lower environmental limit both butterfly and host plants are modelled present (filled black arrow) and none of the two exceed the upper joint distributional limit (empty black arrow). Panels (E) and (F) show the agreement between *Erebia pandrose* and its host plants *Festuca halleri*, *F. ovina*, *F. quadriflora*, *F. violacea* and *Sesleria caerulea*. Here, host plants are present beyond the lower limit of the butterfly (green arrow) and butterfly and host plants are modelled present towards the upper environmental limit (filled black arrow).

Towards the upper limit of the joint distribution the modelled butterfly distribution frequently exceeded the modelled distribution of host species, 54% in relation to main host and 33% in relation to main and secondary host respectively (e.g. Fig. 3B). For less than half of the butterfly species the modelled distribution of host species exceeded the modelled butterfly distribution (18 and 44% respectively). A joint upper limit of modelled host and butterfly occurred for 29 and 21% of the butterfly species (e.g. Fig. 3D).

Discussion

Species ranges are shaped by a multitude of factors, with climatic variables usually being considered among the most influential, at least at large spatial scales. Nonetheless, in recent years the importance of biotic interactions has been increasingly acknowledged (Araújo and Luoto 2007, Meier et al. 2010, Schweiger et al. 2010) and evidence is increasing that range limits are influenced by different factors, depending on location (Normand et al. 2009, Meier et al. 2011). Our results confirm this latter point, and we find indications that species interactions can have a strong effect in limiting species distributions.

The limitation patterns that we find do not support the stress gradient hypothesis for many butterfly species. We found potential host plant limitation for more than half of the species towards harsher environmental conditions, based on comparison between the modelled distribution of butterflies and their host plants (Table 1). This potential

Table 1. Number and proportion of butterfly species showing a certain pattern of agreement with the host distribution towards the lower or upper limit of the joint distribution. Joint distribution can be either exceeded by the host ('only host') or the butterfly distribution ('only butterfly'), or by neither of the two ('none') or the joint distribution is not limited ('host and butterfly').

	Lower environmental limit		Upper environmental limit	
	Main host	Main + secondary host	Main host	Main + secondary host
Total number of species	26	43	28	43
Neither host nor butterfly	5 (19%)	2 (5%)	8 (29%)	9 (21%)
Host and butterfly	3 (12%)	4 (9%)	0 (0%)	1 (2%)
Only host	18 (69%)	35 (81%)	5 (18%)	19 (44%)
Only butterfly	0 (0%)	2 (5%)	15 (54%)	14 (33%)

limitation is indicated by the fact that many butterflies are present at the upper range limit of their hosts (Fig. 2B, Fig. 3D), or the modelled distribution of the butterfly even exceeds the modelled distribution of the host plants (Fig. 2H, Fig. 3B).

A joint upper limit of host and butterfly distribution may either be caused by the coincidence that both are directly limited by the same abiotic factors or that only the host is limited by abiotic factors and the butterfly is indirectly limited by the absence of its host towards harsher conditions. While the former is unlikely given the quite distinct physiologies of plants and butterflies, the latter is supported by study of Gross and Price (2000) who found that the northern range margin of the bird *Phylloscopus humei* is limited by climate-induced disappearance of its arthropod food. Gutierrez and Thomas (2000) showed that the butterfly *Gonepteryx rhamni* extended its range in Great Britain after planting of host plants outside their natural ranges. Also in Great Britain, Pateman et al. (2012) report that the butterfly *Aricia agestis* extended its northern range limit only due to a shift in host plant utilization that was induced by a slight increase of temperature.

Under simulated climate change Pelini et al. (2009) found that the availability of a host plant and its interaction with climatic variables plays a key role for the survival of two butterfly species at their northern range edge in western North America. Boggs and Inouye (2012) found that one abiotic variable, namely snow melt date, can both directly and indirectly influence population dynamics of the butterfly *Speyeria mormonia* in North America, only that indirect effects were not found via larval host plants but nectar plants. Also, Cormont et al. (2013) found host plant mediated effects of climate change on the persistence of Alcon blue butterfly populations in the Netherlands using a complex modelling approach.

Since we find indications of host plant limitation at the harsher end of the environmental gradient for the majority of the butterfly species we analysed (i.e. the modelled butterfly distribution tightly matches or even exceeds the modelled distribution of the host(s)), our study extends previous findings to a more general level and to a larger spatial scale. By including context-dependency for the factors limiting species distributions, this work supports stronger host plant limitation than reported by Schweiger et al. (2012). That study addressed the agreement between the distributions of butterflies and host plants on a European scale and on a coarser grid (10 × 10 km) and highlights the importance of host plant limitation against a background of climate change. Past climate change is important in this discussion because post-glacial recolonisation might not be finished for some plant species that have not yet filled their climatic niches (Araújo and Pearson 2005, Svenning et al. 2008).

While butterflies overall have good dispersal abilities it seems possible that host plant availability still acts as a limiting factor at colder range edges. Future climate change will certainly affect chances of butterfly populations persisting especially when plants and butterflies react asynchronously, which could cause a spatial mismatches between butterfly and host distributions (Walther et al. 2002, Schweiger et al. 2012). Moreover, specialist species seem to be most susceptible to such changes (Warren et al. 2001).

Ecological and evolutionary adjustments, such as the shift to other host plants, can help to reduce the pressure of climate change on butterfly populations at least for some species (Pateman et al. 2012). In Switzerland it has been observed that for example *Cupido minimus* feeds on *Astragalus penduliflorus* at the upper elevational limit, while almost everywhere else it feeds on *Anthyllis*. Also, *Maculinea arion* showed a recent shift from *Thymus* to *Origanum* recently and it is not yet clear if it is in relation to climate change.

Host plant limitation is also indicated in our results when modelled butterfly distribution exceeded the distribution of the host plants (Fig. 3B). This would be the case when the model describes the potential non-host related niche of the butterfly that is broader than the aggregated niche of the hosts. However, other reasons might be responsible for this, too. For example, butterflies may locally feed on other species than those that are known to be main or secondary hosts, e.g. *Boloria titania* feeds mainly on *Polygonum bistorta* but may exceptionally use *Viola* species (Stettmer et al. 2007, Schweiger et al. 2008). Further, some butterfly species are rather mobile in their adult stage and can move far away from their larval habitat, extending the observed range beyond the range of the host plants. For very mobile species, this leads to low performance in model validation (e.g. *Vanessa cardui* TSS = 0.2; *Gonepteryx rhamni* TSS = 0.46; *Papilio machaon* TSS = 0.32; TSS from internal validation of GAMs).

Host plant limitation does not seem to play an important role at the lower limit of modelled butterfly distributions since most of the host plants occur far beyond the distribution of the corresponding butterfly (Fig. 2E). In general, such a pattern is supported by Quinn et al. (1998) who conclude from a study on 43 butterfly species in Great Britain that butterflies tend to feed on widespread species and occupy only small proportions of host plant range. Thus, factors other than host plant availability must be responsible for shaping range limits of most butterfly species at the less harsh range margins. Merrill et al. (2008) and Schweiger et al. (2012) suggest climatic variables as likely explanations but human land use might also play an important role here (see also Araújo and Rahbek 2006). McArthur (1972) observed that many species appear to have their range limited by habitat specialization rather than by any other factor (see also

Hardie and Hutchings 2010). Many butterfly species have retreated in the last decades from low altitude portions of their ranges in Switzerland, likely because of intensified agriculture (e.g. *Cupido minimus*, *Lasiommata maera*, *Maculinea arion*). However, land-use patterns in Switzerland are highly correlated with elevation and, therefore, it is difficult to disentangle effects of climate from effects of land use change.

Another important factor that limits species distributions at the warm range margins might be additional biotic interactions as predicted by the stress gradient hypothesis (Bertness and Callaway 1994, Callaway and Walker 1997). Further, we considered presence or absence of host plants but not host plant abundance or host plant species richness, which intuitively seem relevant. Quinn et al. (1998) showed that polyphagous butterflies tend to occur disproportionally in areas of high host plant richness. Evolutionary factors can also be considered influential via shared traits of closely related species. Many species from the genus *Erebia* or the family Satyridae generally feed on widely available grasses. Therefore, host plant limitation at the lower as well as the upper limit is likely not so relevant for these groups.

Our results support the stress gradient hypothesis to some extent in that under low abiotic stress, negative biotic interactions appear to be important in shaping the distribution of a species, while under harsh conditions abiotic factors are more important and only positive interactions influence distributional limits considerably. The influence of biotic factors on range margins seems to be caused by interplay between positive and negative interactions (Daleo and Iribarne 2009, Boggs and Inouye 2012) showing rather complex patterns along stress gradients (Maestre et al. 2006). Tight biotic interactions like the obligatory dependency of butterflies on its host plants might represent an important limiting factor for some, but not all, species distributions towards the cold end of environmental gradients in the Swiss Alps.

Acknowledgements – We are grateful to Markus Fluri for collating the database on host plants. JH and MP acknowledge funding by Swiss biodiversity monitoring, a programme of the Swiss Federal Office for the Environment (FOEN). JH, JS and OS acknowledge the support of the European Commission Framework Programme (FP) 7 via the Integrated Projects SCALES (grant 226,852; Henle et al. 2010) and STEP (grant 244090–STEP–CP–FP; Potts et al. 2011); JS also of the FP6 IP ALAR (GOCE-CT-2003-506675; Settele et al. 2012) NEZ and PBP acknowledge funding from FP6 project ECOCHANGE (GOCE-CT-2007-036866) and SNF project SPEED (CRS113-125240). This research was also supported by the Helmholtz Association, core subject area 'Land Use Options – Strategies and Adaptation to Global Change' (Seppelt et al. 2009).

References

Allouche, O. et al. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). – J. Appl. Ecol. 43: 1223–1232.

Araújo, M. B. and Pearson, R. G. 2005. Equilibrium of species' distributions with climate. – Ecography 28: 693–695.

Araújo, M. B. and Rahbek, C. 2006. How does climate change affect biodiversity? – Science 313: 1396–1397.

Araújo, M. B. and Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. – Global Ecol. Biogeogr. 16: 743–753.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.

Boggs, C. L. and Inouye, D. W. 2012. A single climate driver has direct and indirect effects on insect population dynamics. – Ecol. Lett. 15: 502–508.

Brown, J. H. et al. 1996. The geographic range: size, shape, boundaries, and internal structure. – Annu. Rev. Ecol. Syst. 27: 597–623.

Callaway, R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. – Ecology 73: 2118–2128.

Callaway, R. M. and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – Ecology 78: 1958–1965.

Cormont, A. et al. 2013. Host plant-mediated effects of climate change on the occurrence of the Alcon blue butterfly (*Phengaris alcon*). – Ecol. Model. 250: 329–337.

Daleo, P. and Iribarne, O. 2009. Beyond competition: the stress-gradient hypothesis tested in plant–herbivore interactions. – Ecology 90: 2368–2374.

Ebert, G. (ed.) 1994. Die Schmetterlinge Baden-Württembergs. Band 3 Nachtfalter 3. – Eugen Ulmer.

Ebert, G. and Rennwald, E. (eds) 1991a. Die Schmetterlinge Baden-Württembergs. Band 1 Tagfalter 1. – Eugen Ulmer.

Ebert, G. and Rennwald, E. (eds) 1991b. Die Schmetterlinge Baden-Württembergs. Band 2 Tagfalter 2. – Eugen Ulmer.

Gross, S. J. and Price, T. D. 2000. Determinants of the northern and southern range limits of a warbler. – J. Biogeogr. 27: 869–878.

Gutierrez, D. and Thomas, C. D. 2000. Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni*. – Ecol. Entomol. 25: 165–170.

Hardie, D. C. and Hutchings, J. A. 2010. Evolutionary ecology at the extremes of species ranges. – Environ. Rev. 18: 1–20.

Heikkinen, R. K. et al. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. – Global Ecol. Biogeogr. 16: 754–763.

Henle, K. et al. 2010. Securing the conservation of biodiversity across administrative levels and spatial, temporal, and ecological scales – research needs and approaches of the SCALES project. – Gaia 19: 187–193.

Huntley, B. et al. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces – J. Biogeogr. 22: 967–1001.

Hutchinson, G. E. 1957. Concluding remarks. – Cold Spring Harbor Symp. Quant. Biol. 22: 415–427.

Kirchhofer, W. 1982–2000. Klimaatlas der Schweiz. – Schweizerische Meteorologische Anstalt, Bundesamt für Landestopographie.

Kissling, W. D. et al. 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. – J. Biogeogr. 39: 2163–2178.

Maestre, F. T. et al. 2006. The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. – J. Ecol. 94: 17–22.

McArthur, R. H. 1972. Geographical ecology. – Harper and Row.

Meier, E. S. et al. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. – Ecography 33: 1038–1048.

Meier, E. S. et al. 2011. Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. – J. Biogeogr. 38: 371–382.

Merrill, R. M. et al. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. – J. Anim. Ecol. 77: 145–155.

Normand, S. et al. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. – Global Ecol. Biogeogr. 18: 437–449.

Pateman, R. M. et al. 2012. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. – Science 336: 1028–1030.

Pearman, P. et al. 2011. Impacts of climate change on Swiss biodiversity: an indicator taxa approach. – Biol. Conserv. 144: 866–875.

Pearson, R. G. et al. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. – Ecography 27: 285–298.

Pelini, S. L. et al. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. – Proc. Natl Acad. Sci. USA 106: 11160–11165.

Pompe, S. et al. 2008. Climate and land use change impacts on plant distributions in Germany. – Biol. Lett. 4: 564–567.

Potts, S. G. et al. 2011. Developing European conservation and mitigation tools for pollination services: approaches of the STEP (Status and Trends of European Pollinators) project. – J. Apic. Res. 50: 152–164.

Quinn, R. M. et al. 1998. Coincidence in the distributions of butterflies and their foodplants. – Ecography 21: 279–288.

Schweiger, O. et al. 2008. Climate change can cause spatial mismatch of trophically interacting species. – Ecology 89: 3472–3479.

Schweiger, O. et al. 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. – Biol. Rev. 85: 777–795.

Schweiger, O. et al. 2012. Increasing range mismatching of interacting species under global change is related to species traits. – Global Ecol. Biogeogr. 21: 88–99.

Schweizer Bund für Naturschutz (ed.) 1994. Tagfalter und ihre Lebensräume. Arten – Gefährdung – Schutz. Band 1. – Fotorotar AG (Egg.).

Seppelt, R. et al. 2009. Land use options – strategies and adaptation to global change terrestrial environmental research. – Gaia 18: 77–80.

Settele, J. et al. 2012. Scenarios as a tool for large-scale ecological research: experiences and legacy of the ALARM project. – Global Ecol. Biogeogr. 21: 1–4.

Sonderegger, P. 2005. Die Erebien der Schweiz. – Peter Sonderegger.

Stettmer, C. et al. 2007. Die Tagfalter Bayerns und Österreichs. – Bayerische Akademie für Naturschutz u. Landschaftspflege.

Svenning, J. C. et al. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. – Ecography 31: 316–326.

Thuiller, W. et al. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. – Ecography 32: 369–373.

Walther, G. R. et al. 2002. Ecological responses to recent climate change. – Nature 416: 389–395.

Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – Nature 414: 65–69.

Wisz, M. S. et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. – Biol. Rev. 88: 15–30.

Zimmermann, N. E. and Kienast, F. 1999. Predictive mapping of alpine grasslands in Switzerland: species versus community approach. – J. Veg. Sci. 10: 469–482.

Supplementary material (Appendix ECOG-00195 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

Ecography

ECOG-00195
Hanspach, J., Schweiger, O., Kühn, I., Plattner, M., Pearman, P. B., Zimmermann, N. E. and Settele, J. 2013. Host plant availability potentially limits butterfly distributions under cold environmental conditions. – Ecography 36: xxx–xxx.

Supplementary material

Appendix 1.

Table 1. Species-specific results for the agreement between butterfly distribution and host plant distribution (h – only host present; b – only butterfly present; n – neither host nor butterfly present; hb – host and butterfly present); Taxonomy according to http://www.biodiversitymonitoring.ch/fileadmin/user_upload/documents/daten/anleitungen/1010_Anleitung_Z7-Tagf_v15.pdf

	Lower limit		**Upper limit**	
Butterfly species	**Main host**	**Main and secondary host**	**Main host**	**Main and secondary host**
Aglais urticae	h		b	
Anthocharis cardamines		h	b	h
Apatura iris	h	h	n	h
Aporia crataegi	h	h	b	n
Araschnia levana	h		h	
Argynnis adippe		h		h
Argynnis aglaja		h		b
Argynnis niobe		h		h
Argynnis paphia		h		b
Aricia eumedon		h		n
Boloria dia		hb		h
Boloria euphrosyne		h		n
Boloria napaea complex		n		b
Boloria selene		b		n
Boloria thore		n		h
Boloria titania	h		b	
Brenthis daphne		h		h
Brenthis ino	h	h	b	b
Brintesia circe		h		n
Callophrys rubi		h		h
Carcharodus alceae		hb		h
Carterocephalus palaemon		b		n
Celastrina argiolus	hb		n	
Coenonympha pamphilus		hb		h
Colias croceus		hb		b
Colias hyale complex	b	hb	h	h
Colias palaeno	n		h	
Colias phicomone		h		b
Cupido argiades		hb		h
Cupido minimus	h	h	b	b
Erebia aethiops		h		h
Erebia alberganus		h		b
Erebia epiphron		h		h
Erebia euryale		h		h

Erebia gorge		n		hb
Erebia ligea		h		h
Erebia manto		h		h
Erebia medusa		h		b
Erebia melampus		h		h
Erebia meolans		h		h
Erebia mnestra		h		h
Erebia montana		h		h
Erebia oeme		h		h
Erebia pandrose		h		hb
Erebia pharte		h		h
Erebia pluto		h		hb
Erebia pronoe		h		h
Erebia tyndarus		h		h
Erynnis tages		h		n
Euphydryas aurinia	h	h	n	n
Euphydryas cynthia		h		b
Gonepteryx rhamni	h		b	
Hamearis lucina	h	h	b	b
Hesperia comma		b		h
Inachis io	hb		n	
Lasiommata maera		h		n
Lasiommata megera		hb		n
Lasiommata petropolitana		h		b
Limenitis camilla	h		n	
Lycaena hippothoe	h		b	
Lycaena tityrus	h		b	
Lycaena virgaureae	h		b	
Maculinea arion	h		b	
Melanargia galathea		h		n
Melitaea athalia		h		b
Melitaea diamina		h		b
Melitaea phoebe		h		n
Nymphalis antiopa	h		b	
Nymphalis polychloros	h		n	
Ochlodes venata		hb		n
Oeneis glacialis		h		b
Parnassius apollo	h		b	
Parnassius phoebus	n		b	
Plebeius argus		n		b
Plebeius idas		h		
Plebeius optilete	n		h	
Plebeius orbitulus		n		h
Polygonia c album		h		n
Polyommatus bellargus	n		h	
Polyommatus coridon	n		n	
Polyommatus damon	h		b	
Polyommatus dorylas			h	
Polyommatus icarus		hb		b

Polyommatus semiargus		h		b
Pyrgus malvae complex		h		n
Satyrium w album	h		n	
Satyrus ferula		h		n
Spialia sertorius	h		n	
Thymelicus lineola		h		b
Thymelicus sylvestris		h		h
Vanessa atalanta	hb		b	
Vanessa cardui		h		n

8 General Discussion

In my thesis I have presented five exemplary studies showing that design and data quality of a biodiversity monitoring scheme are important features regarding analysis and interpretation of biodiversity data. Measurements such as reproducibility and precision in detecting changes of species numbers (Chapter I) or detectability of species (Chapter II) have to be known and considered when collecting, analysing and interpreting biodiversity data. A well designed monitoring scheme positively affects the possibilities for its analysis, e.g. because nationwide data from a (preferably) unbiased sample grid can be used as a reference. This may be crucial for modelling distributions at a national level (Chapters III and V) or for analysing effects of climate change over different altitudes (Chapter IV). For the general discussion I will highlight points concerning the main conclusions of the single studies. Further I will rely on the experience obtained since the beginning of the Swiss Biodiversity Monitoring Programme (BDM) in 2001.

8.1 Data quality and detectability

Data quality

The value of the output from biodiversity surveys depends largely on the quality of the original data, as we have examined in **Chapter I,** looking at inter-observer variation of double-sampled vegetation plots. We showed that observers found almost the same number of species on the sampling plots *on an average*. This indicated that no observer-bias occurred and systematic (directed) methodological errors were minimal. But in regard to reproducibility of the counts and the accuracy of future conclusions also the undirected ("random") deviation must be addressed. Deviation can be seen as statistical noise which makes differences and changes more difficult to detect. The calculated MDDs differed considerably between the strata and some values turned out to be insufficiently precise, especially when comparing *the state* of species richness in highly heterogenous landscapes such as alpine regions. For the BDM has been optimised to control for *changes* in biodiversity over time (Weber et al. 2004) we recalculated MDDs using standard deviation values from subsequent surveys on the same plots. We could demonstrate that there is a relevant benefit from using *paired-measures* because temporal variance in species numbers is only about half of the variance in space. Reduction of the MDD by almost one species resulted and the deduced values averaged around 10% of mean species numbers. In other words, a 10% change in species numbers could be detected for most of the BDM strata of interest. By comparing estimated MDD values for biodiversity change with a simple change scenario we concluded that BDM methods are adequate for detecting possible future changes in plant species richness.

Actually BDM's experience is based on fifteen years of fieldwork and hundreds of double-samplings have been performed in the context of quality control. The measures regarding inter-observer variance that we have presented in the study in **Chapter I** have been widely confirmed (BDM, unpublished data). Reproducibility of measurements in space and especially over time is crucial to a long-lasting monitoring programme. Both small systematic errors caused by the observer, and the constancy of the values over time could be demonstrated for BDM species counts. Hence the training of the field crew is important for a successful programme. In the optimal case fieldworkers already can be integrated in method tests or trained during a pilot phase of a project. A slight improvement of data quality during the first years of a programme seems likely and must be faced by controlling and possibly correcting for observer effects. Field training is a permanent challenge and must be pursued by calibrating fieldworkers over time (quality of fieldworkers may change) and by integrating new persons into the team.

Detectability

Variability in species counts is caused by effects of the observer, by properties of the environment, and by the observed species itself. Species detectability is the link between counted and real species number. In **Chapter II** we asked to what extent capture-recapture methods are suitable to analyse differences in species detectability of butterflies and looked for underlying factors controlling it. We concluded that actual jack-knife methods could not be applied for analyzing BDM species surveys. On the one hand butterfly populations were not closed over the season because of the distinctive seasonal flight patterns of butterflies. On the other hand there was clear evidence for detectability to differ between species, which prevented us to use current open population models. Our analysis then focused on three mid-season counts where population closure was given and we could account for differences in species detectability. We found that mean species number was about 22 species *per count* and average detectability was estimated at 0.61. Looking at the underlying factors that influenced detectability on the level of species communities we found that observer, transect and biogeographic region were relevant but strongly confounded with each other. Individual species during one count were detected with a mean probability of 0.50 (range 0.17 - 0.81). The detectability of a species per se is likely to be a combined effect of abundance, size and behaviour (Dennis et al., 2006). We showed that abundant species were detected more easily, but the number of individuals explained only a surprisingly small amount of the total variation. The other characters were not tested in our study, but can be confirmed with recent data from BDM surveys. Conspicuous and abundant species such as *Pieris napi* and *Melanargia galathea* achieved the highest p-values, while more cryptic species, for example skippers, have low detectabilities (BDM, unpublished data). In the discussion of our study in **Chapter II** we recommended a slight adaptation of the BDM methodology by recording species detections separately on the way back and forth along the transects. This recommendation has been implemented in the BDM and allows a standard, robust-design approach for species-richness estimation in regular BDM surveys. In the meantime statistical methods for analysing species detectability have been developed further substantially and models that can cope with both open populations and heterogeneous species detectability are at hand today (Dorazio et al. 2010).

It is crucial to know the limitation and possible bias in monitoring data. Constraints should be both known and considered for interpretation. For examining biases that arise from incomplete sampling, several possibilities exist. As mentioned in **Chapter I and II** data from double samplings allow identifying the magnitude of observer variation and detectability of species. Further the excessive sampling in methodological tests, e.g. by multiplying the number of surveys in a certain location, and analysing the data with regression technics enabled us to estimate the proportion of species detected with a broader data basis. For the three species groups sampled with BDM methods in the indicator ‘species diversity in landscapes’ the different approaches lead to similar results, indicating that for birds 89% of all breeding species can be detected (Kéry and Schmid 2009), while the proportion for butterflies is estimated between 71% (Kéry et al. 2009) and 75% (BDM, unpublished data) and for plants at about 66% (BDM, unpublished data).

In the meantime many analyses, e.g. the study in Chapter IV, have proven that the data are suitable for detecting changes in species richness even over a short time period. An overview of publications and actual trends in BDM indicators is given on the BDM website (http://www.biodiversitymonitoring.ch/en/home).

8.2 Patterns of plant species richness in Switzerland

An important prerequisite for meaningful analyses of biodiversity data is the availability of environmental data, and the analytical methods used to combine them. Both the quality and the interpretability of models and the derived results strongly depend on variable selection. In the studies in Chapters III to V we have shown that geographically explicit data on abiotic factors, topography and human land-use play an important role. In the study in **Chapter III** we modelled plant species richness by using three sets of variables and built a synthetic model using the best variables out of these. The final models performed similarly with an explained deviance between 61% (topography set) and 69% (environmental and land-cover models). Average elevation was the best proxy variable for explaining plant species richness nationwide. Elevation range (topography set) and the corresponding temperature range (environmental set) were the second best variables. The land-cover model resulted in more interpretable patterns of species richness in cultural landscapes with flat topography such as the Central Plateau and in the higher Alps with bare (not vegetated) area as the best model predictor. The final synthetic model consisted of seven variables and explained 74% of the deviance. We then used the four models in a predictive way to generate diversity maps for Switzerland. The results showed only slight differences in diversity patterns. The most distinctive patterns were horizontal belts of highest species richness at intermediate altitudes along valley slopes at about 1200–1300 m. Belts of higher richness were also present along rivers and around large forest patches and larger villages. Areas of high species richness corresponded to the edges of different land cover units and steep environmental gradients. We argued that both could lead to an associated increase in local habitat diversity and local biodiversity.

Peaks of species richness at average elevations are known from many studies and often referred to as mid-elevational peaks, or mid-domain effect (Rahbek 1997, Colwell et al. 2004). Underlying reasons have been discussed and for example a combination of ecological and evolutionary processes may influence altitudinal diversity patterns (Lomolino, 2001). An actual study by Bertuzzo et al. (2016) combined a theoretic metacommunity model of species niches with real-live geomorphologic data from Switzerland. The resulting patterns of species richness strongly resembled the belt like patterns we found in our study. There is good evidence that local species richness is related to area and connectivity of landscape, and geomorphology plays an important role in determining richness patterns.

8.3 Effects of climate change on species distributions and interactions

In **Chapter IV** we analysed data from the first iteration of BDM surveys within a period of 5 years between the first and the second survey. We looked at changes in the Community Temperature Index (CTI) of plants, butterflies and birds, which described the average of single Species Temperature Indices in the survey squares (see introduction). As a response to climate warming, we expected species to shift their distribution ranges towards higher altitudes but to differ in the rates they were tracking climate change. Accordingly we found significant CTI increases for all three species groups in the lowlands. As expected, birds and butterflies tracked climate warming the fastest with an average uphill shift of 42 and 38 m respectively. We compared the amount of altitudinal shifts in Switzerland with latitudinal shifts from European studies (Devictor et al. 2012) and found that they were in the same magnitude. For plants we stated an uphill shift of 8 m, meeting our initial assumption of plants reacting slower to temperature warming. In contrast to the lowlands there was no significant CTI change in plants and butterflies at higher elevations, although we could demonstrate that temperature increased at a similar rate over all altitudes. More surprisingly, we found a trend for a down-hill shift in plant and butterfly communities. An explanation could be that debris flow and landslides caused by degradation of permafrost at high altitudes could lead to downhill range shifts of alpine species (Lenoir et al. 2016). We argued that such habitat disturbances at lower distributional margins of alpine species might relax the role of competition by creating initial habitats. Initial habitats with low competitive pressure from established species could allow the settlement of alpine species. Furthermore landslides could serve as a vector for dispersal. Lembrechts et al. (2016) have shown that cold-dwelling species reached significantly lower elevational ranges in roadsides than in adjacent vegetation. A further alternative cause for a temporal trend of plant and butterfly communities towards decreasing CTIs at higher altitudes could be land-use related habitat modification caused by abandonment of alpine meadows and pastures (Erhardt 1985, Strebel and Bühler 2015). It has been shown that abandonment of pastures could outweigh the effect of climate warming on species communities (Vittoz et al. 2008). Only birds were moving up at an equal rate over all altitudes. This could be due to the fact that birds were influenced more by air temperatures than by microclimatic conditions. In general our results supported the suggestions that the velocity of reactions to climate change in alpine landscapes were lowest. The idea that alpine landscapes are safer places because of their highly varied surfaces as proposed by Scherrer and Körner (2011) could well explain why no changes in CTI of plants and butterflies occurred. It also seemed plausible that butterflies reacted more like plants than like birds because of they depend on plants as larval hosts and nectar resources.

Various publications with BDM data have shown the importance of scale effects and highlighted the strength of compatible data from two scales (e.g. Hofer Hauck 2007, Bühler and Roth 2011, Roth et al. 2013, but see Concepcion, 2015). In **Chapter IV** we analysed sampling squares at the landscape scale. This is in contrast to most vegetation studies on climate change that refer to the situation of smaller sampling plots often situated on mountain tops (e.g. Walther et al. 2005, Pauli et al. 2012). I conclude that we must consider scale effects and complexity of landscapes when interpreting biodiversity patterns (Chapter III) and species reactions to climate change.

However, when interpreting our results we have to consider that observed changes occurred over a very short time period. Results therefore show likely the initial phase of species reactions to rising temperatures. The patterns may change over time because adaptation of communities lags behind environmental change (Bertrand, 2012). For example species will not disappear immediately if their habitats have become climatically unsuitable, and are creating an extinction debt (Dullinger, 2012). Another challenge is that species responses may not be constant over space and time but can be driven by extreme events. Extreme events can lead to population collapses (Oliver et al. 2015) but then also the range expansions. An example for the latter is the dispersion of warm-dwelling Short-tailed Blue *Cupido argiades* in Switzerland after the extreme hot summer 2003 (BDM, unpublished data).

Species interactions

In **Chapter V** we focused on the role of species interactions at the limits of species distributions. We examined, to what extent distributional patterns of butterfly species are shaped by interactions with their host plants or by environmental factors. How this translates into effects on large scale species distributions is particularly important. When considering projections under scenarios of climate change butterflies and their host plants may respond differently (Schweiger et al. 2008). Following the predictions of the stress gradient hypothesis we expected abiotic factors to shape species distributions under harsher environmental conditions. In contrast, species interactions should be more important under favourable conditions. Our findings contradicted the stress-gradient hypothesis for a major part of the species. At the lower environmental limits host plants were present beyond the modelled range limits of most butterfly species. This indicated that butterfly - host plant interactions were not the relevant factor in benign environments. We supposed that environmental factors, such as climate and the intensity of land-use, were more important. At the colder limits there was a strong coincidence between butterfly and plant ranges. In many cases butterfly distributions even exceeded those of their host plants. We argued that this could be evidence for butterfly species being limited by the distribution of their host plant at cold environmental range limits. We discussed alternative explanations and the implications of these findings under climate change conditions. Future climate change will certainly affect species interactions when plants and butterflies react asynchronously, which could cause a spatial mismatch between butterfly and host distributions (Schweiger et al. 2012). On the other hand, ecological and evolutionary adjustments, such as the shift to other host plants, can help to reduce the pressure of climate change on some species (Pateman et al. 2012).

However, the idea that species interactions could be described with a simple universal hypothesis has proven to oversimplify the situation. The influence of biotic factors on range margins seems to be caused by interplay of positive and negative interactions (Daleo and Iribarne 2009, Pellisier et al. 2012) showing rather complex patterns along stress gradients (Maestre et al. 2006). Manipulative experiments confirmed the importance of competitive interactions to predict species’ responses to climate change (Alexander et al. 2015). We conclude that tight biotic interactions like the dependency of butterflies on their host plants might represent an important limiting factor for some, but not all, species towards the cold end of environmental gradients in the Swiss Alps.

8.4 Implications and outlook

Biodiversity monitoring schemes usually have been implemented to assess spatial and temporal trends in biological systems without necessarily addressing underlying mechanisms. In Chapters III, IV and V we have shown that analysing data from monitoring programs can help to develop hypotheses on mechanisms leading to distributional patterns and biodiversity change. It is an important strength of base-line biodiversity monitoring schemes that they are capable to deal with newly upcoming questions. Compelling evidence is research on climate change, where existing data sets from long-term programmes are an important basis for deepening studies and experiments. Data from long-term monitoring schemes on their own are often not suitable for proving cause-and-effect relations. Hence they must not be seen as a replacement or a competition for experimentally orientated and otherwise directed research but as a complementary data source and reference.

There has been some controversial discussion about the justification of (base-line) biodiversity monitoring schemes. Base-line schemes have been questioned because they need a substantial long-term investment in time, money and institutional support. In contrast to ‘effectiveness monitorings’ focused on concrete questions, base-line monitoring schemes are surveying biodiversity without a priori hypotheses. In a strict sense this leads to conclusions that are not scientifically sound. This may be one of the reasons why data from monitoring schemes have been rarely used, and a huge set of data has not yet been properly evaluated (Roth, 2012). Lindenmayer and Likens (2010) have proposed *adaptive monitoring* as a new paradigm for long-term research and monitoring. An important step in the cycle of adaptive monitoring is a feedback mechanism that allows the adaption of a scheme to *a)* changing or new evolving questions, *b)* changing or evolving analytical approaches and *c)* to new technologies. In my opinion these points do not contradict the demands of a carefully designed and well-conducted base-line monitoring programme. All the requirements can be integrated in a running scheme but must be weighed always against other constraints. A crucial requirement is that all methodological adaptations do not compromise the continuation of the invaluable time-series of existing data.

8.5 References

Alexander, J. M., Diez, J. M., & Levine, J. M., 2015. Novel competitors shape species' responses to climate change. Nature 525, 515–518. doi:10.1038/nature14952

Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., et al., 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479: 517–520.

Bertuzzo, E., Carrara, F., Mari, L., Altermatt, F., Rodriguez-Iturbe, I., & Rinaldo, A., 2016. Geomorphic controls on elevational gradients of species richness. PNAS EI: 1-6.

Bühler, Ch., & Roth, T., 2011: Spread of common species results in local scale floristic homogenization in grassland of Switzerland. Diversity Distrib. 17(6): 1089-1098.

Colwell, R.K., Rahbek, C., & Gotelli, N.J., 2004. The mid-domain effect and species richness patterns: what have we learned so far? The American Naturalist, 163, E1–E23.

Concepcion, E.D., Obrist, M.K., Moretti, M., Altermatt, F., Baur, B., & Nobis, M.P., 2015a. Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. Urban Ecosyst: DOI 10.1007/s11252-015-0474-4.

Dennis, R. L. H., Shreeve, T. G., Isaac, N. J. B., Roy, D.B., Hardy, P. B., Fox, R., et al., 2006. The effects of visual apparency on bias in butterfly recording and monitoring. Biological Conservation, 128 486 – 492.

Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., et al., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change 2: 121–124.

Dorazio, R. M., Kéry, M., Royle, A. J., & Plattner, M., 2010. Models for inference in dynamic metacommunity systems. Ecology 91(8): 2466-2475.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Hülber, K., et al., 2012: Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change. 2, 619–622.

Erhardt , A ., 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. Journal of Applied Ecology, 22, 849–861.

Hofer Hauck, G.C., 2007. Multi-scale effects of topography on plant diversity in mountainous agricultural landscapes. DISS. ETH no. 16958. ETH.

Kéry, M., Royle, J.A., Plattner, M., & Dorazio, R.M., 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90: 1279-1290.

Kéry, M., & Schmid, H., 2006. Estimating species richness: calibrating a large avian monitoring programme. Journal of Applied Ecology 43: 101-110.

Lembrechts, J.J., Alexander, J.M., Cavieres, L.A., Haider, S., Milbau, A., et al., 2016: Mountain roads shift native and non-native plant species' ranges. Ecography 39: 001–012.

Lenoir, J., Gegout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., et al., 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography 33: 295–303.

Lindenmayer D.B., & Likens G.E., 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution, 24(9), 482-486.

Lomolino, M.V., 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography, 10, 3–13.

Maestre, F. T., Valladares, F., & Reynolds, J. F., 2006. The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. Journal of Ecology, 94(1), 17-22.

Oliver, T.H., Marshall, H.H., Morecroft, M.D., Brereton,T., Prudhomme,C., & Huntingford, C., 2015. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. Nature Climate Change.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., et al., 2012. Recent plant diversity changes on Europe's mountain summits. Science 336: 353–355.

Pellissier, L., Litsios, G., Fiedler, K., Pottier, J., Dubuis, A., Pradervand, J. N., Salamin, N., & Guisan, A., 2012. Loss of interactions with ants under cold climate in a regional myrmecophilous butterfly fauna. Journal of Biogeography, 39(10), 1782-1790.

Rahbek, C., 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. The American Naturalist, 149, 875–902.

Roth, T., 2012. Analyzing long-term data from biological surveys. Diss. University of Basel.

Roth, T., Kohli, L., Rihm, B., & Ackermann, B., 2013. Nitrogen deposition is negatively related to species richness and species composition of vascular plants and bryophytes in Swissmountain grassland. Agriculture, Ecosystems and Environment 178: 121-126.

Scherrer, D., & Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography 38: 406–416.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I., 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology, 89(12), 3472-3479.

Strebel, N., & Bühler, Ch., 2015: Recent shifts in plant species suggest opposing land-use changes in alpine pastures. Alp. Botany 125: 1-9.

Vittoz, P., Rulence, B., Largey, T., Frelechoux, F., 2008. Effects of climate and landuse change on the establishment and growth of cembran pine (Pinus cembra L.) over the altitudinal treeline ecotone in the central Swiss Alps. Arctic, Antarctic, and Alpine Research 40: 225–232.

Walther, G.R., Beissner, S., & Burga C.A., 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science 16: 541–548.

9 Acknowledgements

The studies presented in my thesis are based on the essential fieldwork of many experts, invaluable discussions with my colleagues and the long-standing cooperation with the Swiss Federal Office of the Environment and scientific institutions in Switzerland and all over the world. I am deeply indebted to all persons who supported me.

Foremost, my sincere thanks go to Res Erhardt and Bruno Baur for giving me the opportunity to perform my PhD in the Section of Conservation Biology at the University of Basel. Thank you for guiding and promoting me.

I am also very grateful for an ongoing and fruitful collaboration with my colleagues from Hintermann & Weber AG, their enthusiastic work and some long discussions.

Furthermore, I would like to thank all my co-authors and the people commenting on the manuscripts, all the people who collected data in the field and many colleagues at scientific institutions for collaboration.

The research would not have been possible without all the persons who developed and ideally supported the idea of a Biodiversity Monitoring Scheme in Switzerland from the beginning and the longstanding financing by the Swiss Federal Office for the Environment.

Last but not least I thank my wife, my daughters and my parents for their great and unconditional support (and for being quiet☺

10 Curriculum Vitae

Name	Matthias Plattner
Date of birth	25 July 1970
Nationality	Swiss
Marital status	married, two children
Private Address	Maienbühlweg, 3a, D-79540 Lörrach
Phone:	+49 7621 86 730
Email:	m.plattner@unibas.ch
Office Address:	Hintermann & Weber AG, Austrasse 2a, CH-4153 Reinach
Phone:	+41 61 717 88 84
Email:	plattner@hintermannweber.ch

Education

2016	PhD supervised by Prof. Dr. Andreas Erhardt, University of Basel, Switzerland
Since 1997	Hintermann & Weber AG, scientific assistant and project manager
1996	Diploma thesis, Institute of Botany, University of Basel: „Diversität und Artenzusammensetzung der Vegetation in Flachmooren in Abhängigkeit von Nutzung, Höhenlage, Flächengrösse und verschiedenen Bodenparametern".
1990 - 1996	Studies in biology, University of Basel, Switzerland
1985 - 1989:	Secondary School, Gymnasium Muttenz, Switzerland

Journal publications

Hanspach, J., Schweiger, O., Kühn, I., Plattner, M., Pearman, P.B., Zimmermann, N.E., & Settele, J., 2014. Host plant availability potentially limits butterfly distributions under cold environmental conditions. Ecography 37: 301-308

Roth, T., Plattner, M., & Amrhein, V., 2014. Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. PLoS ONE 9: e82490.

Chen, G., Kéry, M., Plattner, M., Ma, K., & Gardner, B., 2013. Imperfect detection is the rule rather than the exception in plant distribution studies. Journal of Ecology, 101: 183–191.

Schlup, B., Stalling, T., Plattner, P., & Weber, D., 2013. Die Artenvielfalt des durchschnittlichen Dauergrünlands der Schweiz. Ein Vergleich zu naturschutzfachlich wertvollen Wiesen und Weiden. Naturschutz und Landschaftsplanung 45(1): 13-20.

Dorazio, R. M., Kéry, M., Royle, A.J., & Plattner, M., 2010. Models for inference in dynamic metacommunity systems. Ecology 91(8): 2466-2475

Kobialka, H., Plattner, M., & Rüetschi, J., 2010. Das Biodiversitätsmonitoring der Schweiz. Methoden und Ergebnisse am Beispiel der Mollusken. Natur und Landschaft 85/4: 142-148.

Kéry, M, Royle, A.J., Plattner, M., & Dorazio, R. M., 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90 (5): 1279-1290.

Stalling, T., & Plattner, M., 2009. Wiederauftreten des Kronwickenbläulings (Plebeius argyrognomon Bergsträsser, 1779) in der Nordwestschweiz. Entomo Helvetica 2: 284-285.

Altermatt, F., Birrer, S., Plattner, M., Ramseier, P., & Stalling, T., 2008. Erste Resultate zu den Tagfaltern im Biodiversitätsmonitoring Schweiz. Entomo Helvetica 1: 75-83.

Wohlgemuth, T., Nobis, M.P., Kienast, F., & Plattner, M., 2008. Modelling vascular plant diversity at the landscape scale using systematic samples. J. Biogeogr. 35: 1226-1240.

Kéry, M., & Plattner, M., 2007. Species richness estimation and determinants of species detectability in butterfly monitoring programmes. Ecological Entomology 32: 53-61.

Plattner, M., Birrer, S., & Weber, D., 2004. Data quality in monitoring plant species richness in Switzerland. Community Ecology 5 (1): 135-143.

Posters

Plattner, M., Birrer, S., Fluri, M., Ramseier, P., Roth, T., & Stalling, T., 2014. Ten years of butterfly monitoring in Switzerland. Butterfly Conservation 7th International Symposium. Southampton University.

Altermatt, F., Nobis, M., & Plattner, M., 2008. Prognose der klimabedingten Veränderungen der Tagfalterdiversität in der Schweiz bis 2050. SWIFCOB, 31.10.2008. Bern.

Altermatt, F., Nobis, M., & Plattner, M., 2009. Projection of the butterfly diversity in Switzerland considering climatic changes until 2050. Biology09, 12.-13.05.2009. Bern.

Plattner, M., Ramseier, P., & Birrer, S., 2005. Evaluation of the Swiss transect method. Butterfly Conservation 5th International Symposium: Lepidoptera as Indicators of Biodiversity Conservation, 08. -10.04.2005. Southampton University.