Using change-point models to estimate empirical critical loads for nitrogen in mountain ecosystems

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Capsule

Applying change-point models to plant species richness data revealed that the critical load of Nitrogen for mountain hay meadows should be narrowed down to 10-15 kg N ha⁻¹ a⁻¹.

Abstract

To protect ecosystems and their services, the critical load concept has been implemented under the framework of the Convention on Long-range Transboundary Air Pollution (UNECE) to develop effects-oriented air pollution abatement strategies. Critical loads are thresholds below which damaging effects on sensitive habitats do not occur according to current knowledge. Here we use change-point models applied in a Bayesian context to overcome some of the difficulties when estimating empirical critical loads for nitrogen from empirical data. We tested the method using simulated data with varying sample sizes, varying effects of confounding variables, and with varying negative effects of N deposition on species richness. The method was applied to the national-scale plant species richness data from mountain hay meadows and (sub)alpine scrubs sites in Switzerland. Seven confounding factors (elevation, inclination, precipitation, calcareous content, aspect as well as indicator values for humidity and light) were selected based on earlier studies examining numerous environmental factors to explain Swiss vascular plant diversity. The estimated critical load confirmed the existing empirical critical load of 5-15 kg N ha⁻¹ a⁻¹ for (sub)alpine scrubs, while for mountain hay meadows the estimated critical load was at the lower end of the current empirical critical load range. Based on these results, we suggest to narrow down the critical load range for mountain hay meadows to 10-15 kg N ha⁻¹ a⁻¹.

Keywords: dose-response relationships; piecewise regression; plants; segmented regression; species diversity

Introduction

Globally, atmospheric nitrogen (N) deposition is the third most important driver of change in threatening terrestrial biodiversity and ecosystem functioning after land-use change and climate change (Sala et al. 2000, Bobbink et al. 2010). To protect ecosystems from elevated N deposition, critical loads of N deposition have been established and used in the framework of the Convention on Long-range Transboundary Air Pollution (Bobbink and Hettelingh 2011, De Vries et al. 2015). Critical loads are defined as 'quantitative estimates of deposition of one or more pollutants below which significant harmful effects on specified elements of the environment do not occur according to present knowledge' (Nilsson and Grennfelt 1988). Particularly in Europe international agreements designed to reduce or reverse unwanted effects of N and other pollutants extensively use critical loads (Hettelingh et al. 2013), which are periodically updated according to current scientific knowledge (i.e. empirical information from independent studies is reviewed and evaluated by experts). However, for some habitats, including mountain hay meadows, critical loads are still based exclusively on expert judgement because empirical information for these ecosystems is limited (Bobbink and Hettelingh 2011).

Empirical critical loads of N are usually based on field N addition experiments, mesocosm studies or observations of harmful effects along a gradient of N deposition (i.e. gradient studies). In this study, we advocate the use of change-point (or: segmented, piecewise, broken-stick) regression models to estimate empirical critical loads because in contrast to generalised linear or additive models they provide an estimate of the magnitude of the critical load (Ficetola and Denoel 2009) and they may overcome difficulties due to large spatial variation in system responses (Groffman et al. 2006, De Vries et al. 2015). Since change-point estimation problems can be addressed via regression methods they can be used to account for topographic, climatic or edaphic variation between sample sites by including confounding variables representing this variation. This allows for a more accurate estimation of the underlying change-points (Beckage et al. 2007).

It has to be noted, however, that the change-point approach has similar limitations as traditional regression models, especially if important confounding variables or ecological processes are not included in the model because they were not known or difficult to be quantified (e.g. the chapter on causal inference in Gelman and Hill 2007). In the ecological literature, these limitations are profoundly discussed in the context of

species distribution models (SDM) that relate species occurrence to environmental data (Guisan and Thuiller 2005, Elith and Leathwick 2009). While the focus on environmental data is justified because the environmental niche of species is usually the major driver of species' distributions (Soberon and Nakamura 2009), SDMs may still miss important drivers such as the time-lag until sites are recolonized after disturbance (i.e. dispersal limitation) or interactions between species (Dirnböck and Dullinger 2004, Thuiller et al. 2013). Nevertheless, well calibrated SDMs are still useful to capture diversity differences of species communities (Thuiller et al. 2015). Consequently, if variables are carefully selected, the change-point models that use similar statistical techniques as traditional SDMs should be able to accurately account for spatial variation in community diversity between sample sites.

Empirical critical loads may be interpreted as a change-point in exposure-response relationships where the relationship between N deposition and some measure of biodiversity changes from no effects below the change-point to negative effects above the change-point (Groffman et al. 2006). Note, that harmful effects above the change-point may occur gradually and the change-point model does not imply a sudden strong negative effect above the threshold (Beckage et al. 2007). While there is abundant evidence that such threshold behaviours occur in many ecosystems (Groffman et al. 2006), we are aware of only few studies that have successfully applied change-point models to estimate empirical critical loads for N deposition (Tipping et al. 2013, McDonough and Watmough 2015, Wilkins et al. in Press). While their results underpin the usefulness of change-point models to estimate critical loads, these studies did not investigate potential limitations of the approach. For example, sampling sites with low N deposition rates are often rather rare in gradient studies and, therefore, there might be only a limited number of data-points below the change-point. It is not evident, however, how strong this limits the application of change-point models to estimate critical loads from gradient studies.

We start with formalizing a model that has a single change-point where the relationship between the biodiversity measure and N deposition changes from flat to declining. With this formalization we aim to represent the idea of the critical load concept, which represent the amount of N deposition an ecosystem can safely absorb before there is a change in state or function (Groffman et al. 2006). Note, that traditionally change-point models are more general capturing different forms of abrupt changes in the relationships between two variables (Ficetola and Denoel 2009). We

conducted a simulation to investigate whether our change-point model provides unbiased results if the number of sample points in total or below the (unknown) critical load is small, and if there are confounding variables that cause large variation in the biodiversity measure that is unrelated to N deposition. Finally, we applied the method to plant species richness data from about 150 sites in Switzerland, with the aim of providing critical load estimates based on empirical information for mountain hay meadows (EUNIS E2.3; Davies et al. 2004) and (sub)alpine scrubs (EUNIS F2.2). We accounted for the same seven confounding variables that we used in an earlier study on the effects of N deposition on species richness and species composition of vascular plants and bryophytes in Swiss mountain grasslands (Roth et al. 2013). We applied the change-point model to the total number of species, the number of oligotrophic species and the number of target species for which Swiss agriculture has particular responsibility of conservation (BAFU and BLW 2008, Roth et al. 2013), to infer whether different measures of biodiversity result in different estimates of the critical load.

Material and methods

The change-point model

The backbone of our change-point model is a generalized linear model (GLM). We assume that we can describe the variation of the number of observed species S_i between the $i = 1, \dots, N$ sampling sites using a Poisson distribution with expected number of observed species λ_i :

$$S_i \sim \text{Poisson}(\lambda_i)$$

Similar as in many GLMs with Poisson distribution we use the log of the expected number of species λ_i as the link function. The link function is expressed as

$$\log(\lambda_i) = \beta_0 + \sum_{k=1}^K \beta_k X_{i,k} + \alpha_i$$

where β_0 is the intercept and β_k the linear slopes for the $k = 1, \dots, K$ confounding variables at sampling site i with covariate value $X_{i,k}$. While the first two terms in the above formula describe a traditional Poisson-GLM (Gelman and Hill 2007), we added a third term α_i to describe the effect of N deposition N_i on the log of the expected number of species λ_i as

$$\alpha_i = \begin{cases} 0 & \text{if } N_i < CL \\ \beta_N(N_i - CL) & \text{if } N_i \geq CL \end{cases}$$

The term α_i is how we try to formalize the critical load. It assumes no effect of N deposition on observed species if N deposition N_i is below the critical load CL . However, it assumes a linear change β_N of the expected number of species λ_i with increasing N deposition if N deposition N_i is equal or above the critical load CL . While usually a negative effect of N deposition on the number of species would be expected (i.e. $\beta_N < 0$), our model does not make an assumption about the direction and strength of this effect.

Simulation study

To examine the performance of the change-point model, we conducted four simulation studies. The aim was to simulate data that had the same structure as the data of the gradient study in mountain hay meadows (see below) and to vary a single parameter (i.e. the focus parameter) to infer its influence on the performance of our change-point model to estimate the critical load. In simulation study (A) we aimed to infer the effect of the total number of sampling sites. We assumed that additionally to N deposition two confounding variables were affecting species richness. The strength and direction of the relationships between confounding variables and species richness we assumed in the simulations were the ones estimated for the two confounding variables of the gradient study that had the strongest absolute effect on the species richness of conservation target species in mountain hay meadows. Also the simulation-setting for the intercept and the negative effect of N deposition on species richness above the critical load were chosen from the gradient study. Site-specific differences for the covariates were simulated using a uniform distribution from -2 to 2. To simulate site-specific differences in N deposition rates we assumed a negative binomial distribution with mean=16 and dispersion parameter = 30 to mimic the distribution of N deposition rates found for the 114 mountain hay meadow sampling sites of the gradient study. For simulation study (B) we aimed to infer whether the accuracy of the estimated critical loads was affected by the number of sampling sites that had a N deposition rate below the true critical load, while—in contrast to the first simulation study—the total number of sample sites with N deposition above the critical load was held constant at 100 sampling sites. Otherwise, the simulation setting was identical to the first simulation study. For simulation study (C), we varied the strength of the effect of one confounding variable to assess whether it affects the estimated critical loads of N. And finally, for simulation study (D) we increased the magnitude of the negative effect of N deposition above the critical load to assess its influence on the accuracy of the critical load estimation. In Supporting

Information A we provide commented R-code that can be used to reproduce our four simulation studies. For each of the four simulation studies we totally simulated 100 data sets. While for all simulations the critical load was held constant at 10 kg N ha⁻¹ yr⁻¹, for each data-set we systematically changed the value of the focus parameter. We then estimated the critical loads from the simulated data (see *Updating critical loads using the Bayesian approach*) and plotted these estimates against the value of the focus parameter to visually infer if there was a systematic change in the accuracy of the estimated critical loads along the gradient of the focus variable.

Gradient studies

We analysed the presence/absence of vascular plants sampled within the scope of Switzerland's Biodiversity Monitoring (BDM) programme that was launched in 2001 to monitor Switzerland's biodiversity and to comply with the Convention on Biological Diversity of Rio de Janeiro (Hintermann et al. 2000). The sampling sites were circles with a size of 10 m² that were arranged on a regular sampling grid covering the whole of Switzerland. Each sampling sites was surveyed once between 2010 and 2014. Data collection was carried out by qualified botanists who visited each sampling site twice per season. During each visit all the vascular plant species detected on the plot were recorded. After the sampling of the plant data the botanists also assigned a habitat type to each sampling site according to the classification system developed for Switzerland (Delarze and Gonseth 2008). We matched these habitat types with the categories from the EUNIS system (level-3 classification; Davies et al. 2004). In the present study, we analysed the 114 sampling sites in Mountain hay meadows (EUNIS E2.3) and the 40 sampling sites in (sub)alpine scrub habitats (EUNIS F2.2; Tab. 1). For more details on the field methods see Plattner et al. (2004) and Roth et al. (2013).

Table 1: Investigated habitat types with EUNIS code of level-3-classification (Davies et al. 2004), number of plots (n), empirical critical loads for nitrogen (CLempN in kg N ha⁻¹ yr⁻¹; Bobbink & Hettelingh 2011) with minimum (min), average (av) and maximum (max) critical load values, mean $\pm$ SD of nitrogen deposition in 2010 (N_{TOTAL}; in kg ha⁻¹ yr⁻¹) at the sampling sites and mean $\pm$ SD number of all species (total S), of oligotrophic species (oligo S), and of target species for which Swiss agriculture has particular responsibility of conservation (target S).

Habitat types	EUNIS code	n	CLempN min, av, max	N _{TOTAL} Mean $\pm$ SD	Total S Mean $\pm$ SD	Oligo S Mean $\pm$ SD	Target S Mean $\pm$ SD
Mountain hay meadows	E2.3	114	10, 15, 20	17.5 $\pm$ 6.4	46.1 $\pm$ 11.5	9.7 $\pm$ 8.9	13.8 $\pm$ 7.9
(sub)alpine scrub	F2.2	40	5, 10, 15	9.1 $\pm$ 3.0	28.0 $\pm$ 12.8	21.1 $\pm$ 9.6	7.8 $\pm$ 8.1

For each site we calculated three measures of species richness that we used in previous studies (Roth et al. 2013, Roth et al. 2015): 1) the total species richness (total S), 2) the number of species that are typically found on nutrient poor sites i.e., oligotrophic species with indicator values for nutrients of one or two (oligo S; Landolt et al. 2010) and the number of target species for which Swiss agriculture has particular responsibility of conservation (target S). The selection of the conservation target species were based on existing legal requirements as reflected in various acts, ordinances, international treaties and decisions of the Swiss Federal Council (BAFU and BLW 2008). Average numbers of species of the three groups of species are given in Tab. 1.

Atmospheric N deposition was estimated using a pragmatic approach described in Rihm and Kurz (2001) that combines monitoring data, spatial interpolation methods, emission inventories, statistical dispersion models and inferential deposition models. We modelled depositions of the reduced N compounds NH_x (gaseous NH₃ + wet and dry deposition of NH₄⁺) and oxidised N compounds NO_y (gaseous NO₂ + HNO₃ + wet and dry deposition of NO₃⁻) at a resolution of 0.1 x 0.1 km cells. A comparison with experimentally derived measures of N deposition showed that this approach is able to estimate site-specific N deposition (Seitler et al. 2016): for a single site, an uncertainty of 40-50% can be expected, and for regional/national applications 10-20%. Model predictions were made for the year 2010 (see Tab. 1 for the mean $\pm$ SD total N deposition on the study plots). For more details on the estimation of N deposition see Rihm and Kurz (2001) and Roth et al. (2013).

In the change-point models we used the same seven confounding variables that we used in an earlier study on the effects of N deposition on species richness and species

composition of vascular plants and bryophytes in Swiss mountain grasslands (Tab 2; Roth et al. 2013). We used elevation as a confounding variable because it summarizes the effects of a large number of environmental variables that are changing along elevation and that are more directly linked to plant species richness (Körner 2007, Chen et al. 2013). Earlier studies on plant species richness in Switzerland also acknowledged the importance of directly derived topographical variables such as inclination or aspect (Wohlgemuth et al. 2008b) and environmental variables such as precipitation (Wohlgemuth et al. 2008a). Further we included the calcareous content and the indicator value for soil humidity to account for edaphic features that are likely important for the maintenance of plant diversity (Letten et al. 2015). Finally, we included an indicator value for light as confounding variable because light limitation is an important driver of plant diversity (Borer et al. 2014). The sources of all confounding variables are given in Tab 2. To characterize the humidity and light conditions for each plot, the mean indicator values of recorded plant species using the recalibrated indicator values for the Swiss Flora (Landolt et al., 2010). For the analyses all confounding variables were standardized by subtracting the mean and dividing by the standard deviation.

Table 2: Summary of the confounding variables used in the change-point models to infer the relationship between nitrogen deposition and the different measures of plant diversity.

Description	Source
Elevation (meters above sea level)	Wohlgemuth et al. (2008b)
Inclination (degrees)	Wohlgemuth et al. (2008b)
Mean Annual precipitation (mm)	Wohlgemuth et al. (2008b)
Calcareous content (six classes; 1= absent; 6=massive)	BAFU and GRID-Europe (2010)
Average moisture value of recorded species (nine indicator values from one to five including .5 values ; 1=species grows on very dry soils; 5=water plant)	Landolt et al. (2010)
Average light value of recorded species (five indicator values; 1=species tolerates deep shade; 5=species grows only in full light)	Landolt et al. (2010)
Aspect (0-360°)	Wohlgemuth et al. (2008b)

To estimate the critical loads (i.e. the change-points) from simulated data or from data of the gradient studies, we used a Bayesian analysis based on Markov-chain Monte Carlo methods (MCMC; Link et al. 2002). The MCMC setting was similar to the ones we used in previous studies using Bayesian change-point regression techniques (Roth et al. 2012): the MCMC simulations were conducted using JAGS, version 3.4.0 (Plummer 2003), executed in R using the R add-on library rjags. We ran two parallel chains to assess convergence using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). We used vague priors for most parameters: for all slope parameters (i.e. the slope of the confounding variables and the slope of the N deposition effect above the critical load) we used a normal distribution with mean=0 and SD=2 ; for the critical load in the simulation study we used the positive values of the normal distribution with mean=0 and SD=100. The Bayesian analysis might be particularly useful because it allows to incorporate critical loads established at expert workshops as prior information, and to update this prior information based on the new empirical data. Thus, we used the approved critical loads according to Bobbink and Hettelingh (2011) to construct an informative prior for the critical loads in the gradient studies: we assumed a normal distribution with the approved critical load as its mean and half the range as its standard deviation [mountain hay meadows: Normal(mean=15, sd=5); (sub)alpine scrubs: Normal(mean=10, sd=5)]. In other words, prior to the analyses we assumed that the probability that the true critical load laid within the approved critical load range was about 68%, while there was a probability of about 16% that the true critical load is lower than the lower limit of the approved critical load. Posteriors were based on two parallel chains with 10,000 iterations each, discarding the first 5,000 values and thinning the remainder by using only every second value. For all estimates of the parameters, we give the median and the 95% credible interval (CrI; i.e. the Bayesian analogue to the 95% confidence interval; Korner-Nievergelt et al. 2015).

To show that our change-point model provides reasonable updated critical loads including situations where there was no clear breakpoint we simulated four data-sets using the simulation setting of simulation study (A) with 144 sampling sites: For the first data-set the negative effect of N already started at very low amount of N deposition (i.e. critical load = 0 kg N ha⁻¹ yr⁻¹), for the second data set the critical load was at 12.3 kg N ha⁻¹ yr⁻¹, which is the critical load estimated in the gradient study of conservation target species in mountain hay meadows (see below), for the third data set the critical load was assumed to be larger than the largest N deposition rate in the sample (critical

load = 60 kg N ha⁻¹ yr⁻¹), and for the fourth data set we assumed that there was no effect of N deposition on species richness (i.e. no critical load). We applied our change-point model to these four data set using the same prior for the critical load as in the gradient study in mountain hay meadows [i.e. Normal(mean=10, sd=5)].

Results

Simulation results

The change-point model succeeded well in reproducing the true critical loads from simulated data (Fig 1). Credible interval coverage, which is the number of times the true value for the critical load is contained in the 95% credible interval, was close to the nominal level of 95% (study A: 0.96; study B: 1.00; study C: 0.97; study D: 0.90), suggesting that model assumptions were met and that the change-point model provided accurate estimates of critical loads with reasonable precision. Simulation study (A), where we simulated data with varying sample sizes, revealed that for some of the simulated data sets with a sample size lower than about 40 sampling sites, the estimates of the critical loads were too high and accompanied by large 95% credible intervals. In all simulated data sets with more than 40 sampling sites, however, the estimated critical loads matched well with the critical load used to simulate the data (i.e. 10 kg N ha⁻¹ yr⁻¹; Fig 1A) suggesting that a sample size of at least 40 sampling sites was enough to obtain accurate estimates of critical loads. In simulation study (B) we varied the number of sampling sites with N deposition below the true critical load. The results revealed that the number of sampling sites with N deposition below the critical load did not strongly affect the estimated critical loads given that the total sample size (at least 100 in our simulations) was large (Fig 1B). The estimated critical loads were also accurate in the case when only few sampling sites with N deposition below the critical load were available. Simulation study (C), where we varied the strength of the effect of one confounding variable on species richness, revealed that our change-point model was successful in accounting for this confounding effect (i.e. comparatively small 95% credible intervals that mostly contained the true value of the critical load; Fig 1C). The estimates of the critical loads became even more accurate with increasing strength of the confounding variable as the length of the 95%-credible intervals tended to decrease with increasing strength of the confounding variable. A similar behaviour can be observed for traditional generalized linear models with Poisson distribution (Poisson-GLM): in Supporting Information B we simulated data under a Poisson-GLM with two

variables b1 and b2 but with no change-point. If the effect size of b1 increased the standard error for the estimated effect of b2 decreased. Simulation study (D), where we increased the negative effect of N deposition on species richness, revealed that estimated critical loads became more precise (i.e. smaller 95%-credible intervals) if the negative effect of N deposition increased (Fig 1D).

Figure 1. Results of the four simulation studies. Given are medians and 95% credible intervals of the estimated critical loads for each simulated data set and obtained from the posterior distributions. The true critical load was assumed to be 10 kg ha⁻¹ yr⁻¹ (dashed line) in all simulations. The variation between simulations are not only caused by differences in the simulation setting, but also due to the fact that the estimates are based on two data sets that were independently simulated (i.e. the Monte Carlo variation).

Updating critical loads using Bayesian analysis

Applying the change-point model in a Bayesian framework provides reasonable updated critical loads even when applied to simulated data with no clear breakpoint (Fig 2): If the negative effect of N started already at a very low deposition rate, which could be interpreted as a critical load of 0 kg N ha⁻¹ yr⁻¹, the updated critical load shifted down including 0 as a possible value for the critical load (Fig. 2A). If the critical load lied

within the range of the prior information, the new data could be used to narrow down the critical load range (Fig. 2B). If the critical load was high, the new data would be used to increase the critical load (Fig. 2C). Finally, if there was no negative effect of N deposition, new data would increase the uncertainty about the critical load as reflected by a broader posterior distribution (Fig. 2D).

Figure 2. The update of the critical load (i.e. posterior distribution; green) given the prior knowledge of the critical load (i.e. based on the critical load that was established at a previous expert workshop; orange). The figures show the outcome of applying the change-point to simulated data assuming (A) with a negative effect of N that started already at 0 kg N ha⁻¹ yr⁻¹, (B) with a realistic critical load, (C) with the critical load that was higher than the highest N deposition in the sample, and (D) with no negative effect of N deposition on plant diversity.

Critical loads estimated from gradient studies

The critical loads of N estimated for mountain hay meadows (E2.3) and (sub)alpine scrubs (F2.2) corresponded well with the current range of empirical critical loads set for these habitats (Fig. 3). The position of the change-points at 10.7-10.8 kg N ha⁻¹ yr⁻¹ estimated for the three species groups in (sub)alpine scrub were just in the middle of the range of the current critical load of 5-15 kg N ha⁻¹ yr⁻¹. The positions of the estimated change-points at 12-13 kg N ha⁻¹ yr⁻¹ for mountain hay meadows were between the lower end and the middle of the range of the current critical load of 10-20 kg N ha⁻¹ yr⁻¹ (Bobbink and Hettelingh 2011).

Figure 3. Total number of species (top panels), number of oligotrophic species (middle panels) and number of target species for which Swiss agriculture has particular responsibility of conservation (bottom panels) in mountain hay meadows (EUNIS E2.3; left panels) and in (sub)alpine scrubs (EUNIS F2.2; right panels) across a gradient of nitrogen (N) deposition in Swiss mountains. The dots represent the raw counts of species numbers in the sampling sites of 10m². The black line represents the change-point regression of species richness on N deposition that simultaneously accounted for the seven confounding variables. The vertical line represents the position of the change-point, the dashed lines the corresponding 95% credible intervals. The grey shaded area represents the expert-based current empirical critical load range (Bobbink and Hettelingh 2011).

Although there were marked differences in the average number of species between the three species groups (i.e. the total species richness, the number of oligotrophic species and the number of target species; Tab. 1) the estimated critical loads were surprisingly

consistent independent of the used measure of biodiversity (Tab. 3). The raw number of species were rather strongly (positively or negatively) correlated between species groups for both mountain hay meadows (Pearson product-moment correlation coefficient; $r[\text{total S, oligo S}] = -0.61$, $r[\text{total S, target S}] = -0.56$, $r[\text{oligo S, target S}] = 0.82$) and (sub)alpine scrubs ($r[\text{total S, oligo S}] = -0.48$, $r[\text{total S, target S}] = -0.25$, $r[\text{oligo S, target S}] = -0.83$) suggesting that the species groups were affected by similar drivers.

While for (sub)alpine scrubs the estimated critical load were precise (i.e. small 95% credible interval) for all three species groups, in mountain hay meadows the precision differed between species groups: the uncertainty in critical loads estimates was large for total species richness and oligotrophic species richness but comparatively small for the number of target species (Tab. 3, Fig. 3).

To test how strongly the estimate of critical load is driven by single data points, we estimated critical loads for (sub)alpine scrubs after the apparent outlier with highest N deposition has been removed: the results only marginally changed: the critical loads were estimated at 11.1 (95% credible interval 10.3–11.9), 11.0 (10.2–11.8) and 11.3 (10.5–11.9) for the number of all species, oligotrophic species and target species, respectively.

Table 3: Estimated critical loads (in $\text{kg N ha}^{-1} \text{ yr}^{-1}$) based on the change-point models for mountain hay meadows (E2.3) and (sub)alpine scrub habitats (F2.2) estimated for all species (total S), oligotrophic species (oligo S) and target species for which Swiss agriculture has particular responsibility of conservation (target S). Given are the 2.5%, the median (50%) and the 97.5% quantiles of the posterior distribution of the change-point in the regression of plant species richness and total nitrogen deposition. In the column 'Neg. ef' we give the probability based on the posterior distribution that the negative effect of N deposition occurs below the middle of the current critical load ranges ($15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for E2.3; $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for F2.2).

Species group	Mountain hay meadows (E2.3)				(sub)alpine scrubs (F2.2)			
	2.5%	50%	97.5%	Neg. ef.	2.5%	50%	97.5%	Neg. ef.
Total S	4.3	12.0	20.7	0.79	10.1	10.7	11.3	0.02
Oligo S	3.7	13.1	20.3	0.85	9.8	10.7	11.4	0.05
Target S	9.5	12.3	14.2	0.99	10.2	10.8	11.4	0.01

Discussion

In this study we developed and tested a change-point regression method to estimate critical loads from empirical studies along a gradient of N deposition. Our method was able to accurately estimate critical loads when applied to simulated data with known critical load. The method was robust if simulated data sets varied in sample size, in the strength of the effect of a confounding variable or in the magnitude of the negative effect of N deposition on species richness. Based on these results we are confident that the proposed method is able to accurately estimate critical loads from empirical data collected along a gradient of sites with varying N deposition levels.

Especially in Western Europe areas with low N deposition are rather rare, and consequently, sampling sites at or below the critical load might be difficult to find. We expected that this could limit the general applicability of our method. However, our simulation study revealed that it is mainly the total sampling size and the strength of the N deposition effect above the critical load that affects the precision of the critical load estimation and not the number of sampling sites with N deposition below the critical load. Overall, the simulation results suggest that empirical studies with at least 40 sampling locations covering a reasonable N deposition gradient should be appropriate to robustly estimate the critical load of a habitat.

Applying the method to the national-scale plant species richness data from Switzerland and the three measures of biodiversity (i.e. the total species richness, the number of oligotrophic species and the number of target species), the estimated critical loads were remarkably constant within a habitat type. This was rather surprising as we expect the species groups to reflect different aspects of plant diversity. Apparently, however, N deposition seems to have a similar effect on the different aspects of plant diversity. Indeed, in our earlier study on Swiss landscape-scale plant diversity, six measures of plant diversity (the three species groups we used in this study as well as community uniqueness, functional diversity and phylogenetic diversity) showed strong differences in elevational patterns, signifying that they reflected different aspects of plant diversity. In spite of the diverse nature of these six measures, however, low values of plant diversity were consistently associated with high atmospheric N deposition (Roth et al. 2015). The current study underpins that N deposition has similar effects on the different aspects of plant diversity.

From an ecological perspective it seems not evident why one should expect exactly one change-point in the exposure-response relationships between N deposition and some measure of biodiversity. Indeed, various studies show a simple gradual change without a

clear change-point (Stevens et al. 2004). However, from a theoretical point of view as well as from studies on experimental grassland one expects stabilizing effects of plant diversity through species asynchrony (Hautier et al. 2014). Consequently, the disturbance caused by N deposition needs to be strong enough (i.e. larger than the critical load) to overcome stabilizing effects and to shift an existing species community into another state. Since species asynchrony may vary between species communities of different habitats or regions, we can expect different change-points in different habitats or regions.

If the change-point model is used to update *a priori* knowledge of the critical load given empirical data, which is at the core of the Bayesian approach (McCarthy and Masters 2005), the up-dated critical load (*posterior* knowledge) is useful even if there is no clear change-point in the dose-response relationship (Fig. 2). For example, if negative effects of N occur already at very low deposition rates, the posterior distribution of the critical load would exclude large critical loads suggesting that the critical load should be lowered. In contrast, if there is no negative effect of N deposition empirical data could be used to broaden-up the range of the critical load reflecting our ambiguity about the critical load.

Semi-natural and natural habitats in montane regions across Europe still contain many rare species (Väre et al. 2003, Homburger and Hofer 2012). It is important to emphasise the negative effects of N deposition also in these montane habitats, because N deposition has also increased in mountainous regions (Williams and Tonnessen 2000, Weathers et al. 2006). However, the lack of information on effects of N deposition in montane ecosystems has been identified as a major gap in knowledge and as a consequence the critical load range of 10 to 20 kg N ha⁻¹yr⁻¹ for mountain hay meadows (EUNIS E2.3) are currently based on expert judgement only (Bobbink and Hettelingh 2011). While our results largely confirmed the critical load for (sub)alpine scrubs, the application of the change-point model to the number of conservation target species in mountain hay meadows revealed that the critical load lies with a probability of 0.95 within 9.5 and 14.2 kg N ha⁻¹yr⁻¹. Consequently, critical loads > 15 kg N ha⁻¹yr⁻¹ seem unlikely and, based on this results, we thus suggest to narrow down the critical load of N in mountain hay meadows.

Conclusions

We extensively tested change-point models to estimate critical loads using simulated data and are thus confident that change-point models could improve the statistical quantification of empirical critical loads of N deposition based on N-gradient studies subject to confounding variables. The application of our methods to the national-scale plant species richness data from Switzerland revealed that critical loads for (sub)alpine scrubs corresponded well with the current critical load, while for mountain hay meadows we found support that the upper end of the current critical load range is currently set too high. For the next expert workshop to revise and update empirical critical loads we therefore suggest to narrow down the critical load range for mountain hay meadow (EUNIS E2.3) to 10 – 15 kg N ha⁻¹ yr⁻¹.

Competing financial interests

The authors declare no competing financial interests.

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