How to assess species richness along single environmental gradients? Implications of potential versus realized species distributions.

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ABSTRACT

Quantifying relationships between species richness and single environmental factors is challenging as species richness typically depends on multiple environmental factors. Recently, various methods have been proposed to tackle this challenge. Using a dataset comprising field observations of grassland vegetation and measured pH values, we compared three methods for deriving species richness response curves. One of the methods estimates species richness close to the maximum species richness observed at the sites, whereas the other two provide estimates of the potential species richness along the environmental gradient. Our response curves suggest that potential species richness of grasslands is slightly more sensitive to acidification than realized plant species richness. However, differences in corresponding environmental quality standards (EQS) for acidification were small compared to intrinsic spatial differences in natural soil pH, indicating that natural background values are more important to consider in the derivation of EQS for pH than methodological differences between the three approaches.

Capsule: We compared three methods to derive field-based species sensitivity distributions (f-SSDs) from presence-absence data.

Key words: Survey data; pH; Stressor-Response Relationships; Species Sensitivity Distributions (SSDs); Environmental Quality Standards (EQS)

INTRODUCTION

Environmental factors that determine species distribution patterns and species richness are of primary interest to nature conservation (Pausas & Austin, 2001). Quantifying the influence of individual factors on species communities in a systematic way can help to improve our understanding and predictive ability of biodiversity patterns, derive environmental quality standards, and underpin abatement priorities (Latour and Reiling, 1993; Latour et al., 1994; Van Goethem et al., 2013; Wamelink et al., 2013). However, species distributions are typically dependent on multiple environmental factors, including both abiotic and biotic drivers (Pulliam, 2000; Schipper et al., 2014; Soberón, 2007). As confounding environmental factors generally result in considerable scatter among species richness observations, it is not straightforward to extract relationships between species richness and single factors from field data (Cade and Noon, 2003; Van den Brink et al., 2002).

Recently, various methods have been proposed to tackle this challenge (Leung et al., 2005; Struijs et al., 2011; Kefford et al., 2011; Iwasaki & Ormerod, 2012; Azevedo et al., 2013; Cormier & Suter II, 2013). Most of these methods are based on occurrence data (e.g. presence-absence data), which are generally more readily available than abundance data (Pearce & Boyce, 2006; Potts & Elith, 2006). One method is to relate site-specific observations of the number of species present to a particular environmental variable with quantile regression (Iwasaki & Ormerod, 2012). Most regression techniques relate changes in the mean of a response variable to one or more explanatory variables. With quantile regression, any part of the distribution of a variable can be used as response (Cade and Noon 2003). Quantile regression based on one of the upper boundaries of the response variable distribution (e.g. the 0.95 or 0.99 quantile) is expected to show the constraints imposed by the explanatory environmental variable of concern (Iwasaki & Ormerod, 2012; Lancaster and Belyea, 2006). A second method is to assess the number of species present within regular intervals along a particular environmental gradient by pooling multiple samples per interval (‘pooled samples

57 method'). The number of species per interval is then assessed either by simply counting the number
58 of unique species across all samples within the interval (Struijs et al., 2011) or by establishing a
59 species accumulation curve (SAC) per interval, thus correcting for potential differences in the
60 number of samples between the intervals (Kefford et al., 2011). With a third method, observations
61 of multiple species across multiple samples are used to first establish species-specific occurrence
62 ranges, represented by the minimum and maximum values of the environmental variable of concern
63 where the species has been observed. These occurrence ranges are then stacked across the species
64 to arrive at an estimate of species richness ('occurrence range method'; Verbrugge et al., 2012,
65 Azevedo et al., 2013, Cormier et al., 2013b).

66 Given the differences in approach, these three methods are expected to yield different species
67 richness estimates, reflecting differences in potential and realized species richness. Potential species
68 richness refers to the species that could occur at a specific site, while realized species richness refers
69 to the species that actually occur there (Jiménez-Valverde et al., 2008). By modelling an upper
70 quantile of the distribution of species richness actually observed at the sampling sites, the quantile
71 regression method yields an estimate of the maximum species richness that may be realized at a
72 particular location with a given pH. In contrast, the other two methods yield species richness
73 estimates representing the pool of plant species corresponding with a given pH, i.e., the potential
74 species richness. Species richness typically increases with an increasing number of samples (Kefford
75 et al., 2011). Hence, aggregating observations from multiple sampling sites at each given interval
76 along a particular environmental gradient, as is done in the pooled samples method, is expected to
77 yield considerably higher values of species richness than can be observed at specific sampling sites
78 (Kefford et al., 2011). The occurrence range method, finally, is expected to yield the highest
79 estimates of species richness, by aggregating the species occurrences over the full environmental
80 gradient rather than for each given interval separately.

The goal of this paper was to compare the three methods by applying them to the same species-environment dataset and quantifying the differences in the resulting species richness response curves. The dataset comprises presence-absence observations of terrestrial plant species along a gradient of soil pH measurements (pH 3-10) collected from 4412 sampling sites of grassland vegetation across the Netherlands (Wamelink et al., 2012). The methods were compared by quantifying the shapes of the response curves (magnitude, width) along the pH gradient. Furthermore, we compared the methods in terms of environmental quality standards, i.e. the pH levels corresponding with a predefined relative reduction in species richness (Van Straalen & Denneman, 1989; Posthuma et al., 2002). To achieve this we converted the species richness estimates to relative values with a maximum of 100%, thus obtaining field-based species sensitivity distributions (f-SSDs), i.e., empirical distributions describing interspecies variation in sensitivity to a particular environmental variable.

METHODS

Species richness response curves

Quantile regression

The quantile regression method to estimate species richness along the pH gradient was based on Cade & Noon (2003). In our study, three models were constructed at the 95% quantile (Visser & Sasser, 2009): a linear model ($y = \beta_0 + \beta_1 \cdot x$), a Gaussian model ($y = \beta_0 + \beta_1 \cdot x + \beta_2 \cdot x^2$) and a baseline model where species richness is estimated by a constant (i.e., an intercept-only model). The most parsimonious model was selected based on the Bayesian Information Criterion (Lee et al., 2013). The different models were also constructed for the 97.5% and 99% quantiles to assess the influence of the quantile selection on the species richness estimates. The quantile regression was performed with the quantreg package in R (Koenkers et al., 2013).

Pooled samples method

105 With the pooled samples method (Kefford et al., 2011), we derived species accumulation curves
106 (SACs) for each interval i along the pH gradient. The SACs were derived using a resampling
107 rarefaction method (100 times) that calculates the mean number of species observed (SR_{est}) in 1 to n
108 samples, where n is the total number of samples pooled. The SR_{est} in k samples, SR_{est} (k), is the mean
109 number of species estimated in k samples. The SR_{est} (inf) is the mean number of species where one
110 added sample leads to a maximum increase of less than one species (Verberk et al., 2006). For each
111 interval i we considered the SR_{est} (inf) as an estimate for $SR_{i,j}$ (Kefford et al., 2011). The intervals i
112 were set at 0.1 pH unit, so that there were enough observations in each interval to derive SR_{est} (inf)
113 (Table S2). The SACs were extrapolated up to a maximum of 5 times to ensure that SR_{est} (inf) could
114 be estimated for all intervals (Colwell, 2012). As a sensitivity check the response curves were also
115 derived based on 50, 20 and 1 samples. The SACs were determined using the computer software
116 EstimateS 7.5.1 (Colwell, 2004).

117 *Occurrence range method*

118 Following (Azevedo et al. 2013a), we defined the occurrence range for each species as the range
119 between minimum and maximum pH values corresponding to the occurrence of that species as
120 observed in the field. A species was considered to be absent at pH values outside this range, and
121 potentially present at values inside its occurrence range. Species richness (SR_i) was computed as the
122 number of species potentially present at each pH interval i as

123 $$SR_i = \sum_s O_{s,i} \qquad \text{(Eq. 1)}$$

124 where $O_{s,I}$ is the occurrence of each species s at pH interval i, with O = 0 when the pH value is outside
125 a species' occurrence range and O = 1 if the pH value is within its occurrence range. The intervals i
126 for pH were set at 0.1. To assess the sensitivity of SR to changes in occurrence ranges, the species

occurrences were also derived based on the 5th and 95th and 2.5th and 97.5th percentiles of the pH values corresponding to the field occurrence of that species.

Dataset

The ecological conditions (EC) database compiled by Wamelink et al. (2012) was used in this study. This database comprised vegetation relevés from the Netherlands, each accompanied by a measured value of at least one abiotic soil parameter. The database contained 5243 grassland relevés with a measured pH value, covering the period from 1936 to 2011 (Table 1). pH values were measured in H_2O extract and ranged from 3.0 to 10.1. Several relevés were part of a time series: the dataset included 141 sites where a relevé was made at least twice. To remove potential confounding influences of temporal autocorrelation, we included only the most recently recorded relevés from each time series in the dataset. This led to a decrease in the number of releves of 5243 to 4412. The vegetation relevés were made according to the Braun-Blanquet method and followed the syntaxonomical classification of Schaminée et al. (1995)(Braun-Blanquet, 1921). In total 1321 species were recorded in the relevés. More details regarding the EC database can be found in Wamelink et al. (2012).

Estimated vs. observed species richness

We compared the estimated species richness (SR_{est}) with the observed species richness (SR_{obs}) over the relevés by deriving the average relative difference over the pH gradient as

$$RD_{est-obs} = \frac{1}{N_i} \sum_i \frac{SR_{est,i} - \overline{SR_{obs,i}}}{\overline{SR_{obs,i}}} \quad \text{(Eq. 2)}$$

where $SR_{,est,j}$ represents the species richness estimated for interval i and N_j is the total number of intervals.

Field-based species sensitivity distributions (f-SSDs) and environmental quality standards (EQS)

We derived a field-based species sensitivity distribution (f-SSD), an approach developed in the field of ecotoxicology, from each of the three species response curves. To that end, the estimated species richness was transformed into a zero-to-one measure, the relative species richness (r-SR), as

$$rSR_i = \frac{SR_i}{SR_{\max}} \quad \text{(Eq. 3)}$$

where SR_{max} for a given method represents the highest species richness estimated in any interval i along the pH gradient. The maximum r-SR (i.e., r-SR = 1) is obtained if the species richness in a particular interval i equals SR_{max}, while r-SR = 0 represents the complete absence of species. The resulting f-SSDs thus represent changes in species richness in relation to the pH gradient, relative to the highest species richness estimated for a particular pH level in the study area. Subsequently, for the pooled samples and occurrence range methods, we applied least squares regression to the r-SR estimates to obtain an explicit function of r-SR in relation to pH. Next, we used the resulting functions to derive environmental quality standards (EQS). We defined the EQS as the pH value corresponding with a 5% reduction of the species richness due to acidification (Posthuma et al., 2002).

RESULTS

Species richness response curves

The response curves based on the quantile regression, pooled samples and occurrence range methods all showed a unimodal response along the pH gradient (pH 3-10) (Figure 1). Optimum pH values were found in the range of 6.1-6.5 (Table 2). The response curves differed in their width and relative amplitude, where width is defined as the pH range at half SR_{max} and relative amplitude as the relative difference between maximum and minimum species richness estimated along the pH

gradient (Table 2). The widths ranged from 4.7 units for the occurrence range method to 6.9 units for the quantile regression method. The relative amplitude ranged from 0.56 for the quantile regression method to 1.0 for the occurrence range method.

Comparison with observed species richness

The maximum estimated species richness was 50 for the quantile regression method, 590 for the pooled sample method and 702 for the occurrence range method (Table 2). The response curve based on the quantile regression method followed the highest observed species richness in the field, whereas the pooled samples and occurrence range methods estimated much higher SR (Figure 1). The average relative difference between SR_{est} and SR_{obs} ranged from 1.1 for the quantile regression method to 17.6 for the occurrence range method (Table 2). Per method, the average observed SR and estimated SR per interval are given in Table S2. Based on the average relative difference between the estimated and observed SR, the quantile regression method is placed on the left of the gradient from realized to potential species richness, whereas the occurrence range and pooled samples methods are placed towards the right (Figure 2).

Field-based species sensitivity distributions and environmental quality standards

Field-based species sensitivity distribution (f-SSDs) for the quantile regression, pooled sample and occurrence range methods are given in Figure 3. The environmental quality standards (EQS), i.e., the pH levels corresponding with a 5% reduction in species richness in case of accidification, were most stringent for the occurrence range method, followed by the pooled samples and quantile regression methods (Figure 4). However, the difference in EQS between the three methods was 0.3 pH unit at maximum.

Sensitivity analysis

Sensitivity of the quantile regression method to changes of the chosen quantile was tested by comparing response curves based on the 95th, 97.5th and 99th quantiles (Figure S1; Table S1). The response curves gave similar results, with a maximum pH of 6.5 irrespective of the quantile. The estimated SR in the pooled sample method depends on the number of samples used to derive the SACs and ranged from a maximum SR of 32 for one sample to a maximum SR of 601 for an infinite number of samples (Figure S2). At the extremes of the pH range, however, the differences in estimated SR are smaller, ranging from 13 to 122 at pH 3.5 and from 12 to 123 at pH 9. In the occurrence range method the width and maximum estimated SR is determined by the percentile that is used to derive the species occurrence ranges (Figure S3). The width ranged from 4.6 for the 100th to 3.6 for the 90th percentile. The maximum estimated SR ranged from 633 for the 90th to 721 for the 100th percentile.

DISCUSSION

Interpretation

Each of our response curves suggests a unimodal relationship between the species richness of grassland vegetation and pH (Figure 1). The unimodal response is in line with the results of other studies, with comparable optimum pH and shape of the curve (Azevedo et al., 2013; Chytrý et al., 2010; Olsson et al., 2009; Wamelink et al., 2005). This suggests that the relationship between species richness and pH was successfully extracted from the field data. We derived the response curves specifically for grassland vegetation, as different vegetation types respond differently to changes in pH (Wamelink et al., 2005). Response curves with multiple optima may result from a dataset including multiple vegetation types (Figure S4), suggesting that response curves are preferably derived per vegetation type. However, response curves based on species richness do not account for changes in species composition that may occur within a vegetation type, because the number of species may remain the same along a particular environmental gradient, whereas species

composition may change due to species replacements. Such species replacements may explain why the pooled samples method does not reveal major changes in species richness at intermediate pH levels (Figure 1). Species replacements along the pH gradient may also explain why the maximum number of species as obtained with the occurrence range method (702) is smaller than the total number of species in the dataset (1321). Apparently, there are no pH values that are within the occurrence range of all the species, and the gradient in pH values is large enough to encompass multiple non-overlapping tolerance ranges of individual species.

As expected, the quantile regression method estimated species richness close to the maximum species richness observed at the sampling sites, i.e. the maximum realized species richness (Figure 1; Table 2). The maximum realized species richness was around 50 at intermediate pH values. Because the quantile regression curve is directly derived from the species richness observed in the field sites, this method in particular may be sensitive to the size of the relevés, as bigger plot sizes may lead to higher species richness. Furthermore, the quantile regression method may be particularly sensitive to underestimated species richness due to false absence records, for example because some plant species may not have germinated yet at the moment the relevé was recorded. However, the surface area of the relevés is chosen to obtain a representative picture of the species composition and richness of the respective vegetation type, and sites are generally visited during the growing season, when most species are present and visible (Schaminee et al., 1995).

At intermediate pH values, the potential species richness as derived with the pooled samples and occurrence range methods was about 10 to 14 times larger than the maximum realized species richness (Figure 1). Potential species richness estimates were higher for the occurrence range method than for the pooled samples method. This difference is found because in the occurrence range method a species is assumed to occur anywhere between its minimum and maximum pH value, irrespective whether it was actually observed at the pH values in between, whereas in the

240 pooled samples method a species needs to be actually observed in a particular pH interval in order
241 to contribute to the potential species richness.

242 The shapes of our response curves suggest that acidification would result in greater reductions in
243 potential than in maximum realized plant species richness (Figure 1). This result is in line with two
244 recent studies that concluded that large-scale declines of species richness are not necessarily
245 accompanied by biodiversity loss at local scales (Dornelas et al., 2014; Vellend et al. 2013).

246 **Management implications**

247 For each response curve method we derived a field-based Species Sensitivity Distribution (f-SSD)
248 (Figure 3). SSDs are typically derived for toxicants, generally based on a limited number of species
249 tested in laboratory exposure experiments (Van Straalen & Denneman, 1989). To conduct laboratory
250 experiment for all possible combinations of stressors and species, however, is almost impossible
251 simply because there are so many (Azevedo et al., 2013; Cormier & Suter II, 2013a; Kefford et al.,
252 2012). SSDs based on field observation have therefore been proposed instead, as these include the
253 actual species pool and relevant environmental stressors of a particular area (Leung et al., 2005).
254 The resulting f-SSDs can be used (1) to derive environmental quality standards for a particular
255 environmental factor, and (2) to estimate relative changes in species richness along a specific
256 environmental gradient (Posthuma et al., 2002). However, in contrast to anthropogenic toxicants,
257 pH is a natural environmental factor, with varying natural background levels and ecological
258 communities adapted to these levels (Wamelink et al., 2005). In order to account for this natural
259 variation, we derived EQS based on a 5% reduction of the species richness corresponding with a
260 given natural background pH (Figure 4), rather than a 5% reduction of the overall maximum species
261 richness, as is common practice in EQS setting. EQS were slightly more stringent for potential than
262 for maximum realized species richness, thus reflecting that acidification would result in larger
263 declines of the former. However, differences in EQS between the three methods were only small and

EQS varied mainly in relation to the natural background pH. Hence, in the derivation of EQS for pH it is much more important to consider intrinsic spatial differences in soil pH than methodological differences between f-SSD approaches.

ASSOCIATED CONTENT

Additional supporting information may be found in the online version of this article.

Figure S1: Field-based stressor response curves based on the quantile regression method derived the 95^{th}, 97.5^{th} and 99^{th} quantiles.

Figure S2: Field-based stressor response curves based on the pooled sample method derived with infinite, 50, 20 and 1 samples.

Figure S3: Field-based stressor response curves based on the occurrence range method derived with different percentiles.

Figure S4: Field-based response curves for pH based on the pooled sample method derived for grasslands, forests and heathland.

Figure S5: Field-based stressor response curves based on the pooled sample method with the 5^{th} and 95^{th} confidence intervals.

Table S1: The regression coefficients for the regression models based on the 95^{th}, 97.5^{th} and 99^{th} quantile.

Table S2: The number of relevés, average observed SR and estimated SR per interval for each method.

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403 **Table 1. Characteristics (Mean, SD, Median, Min, Max and various percentiles) of the measured pH values**

404 **and species richness for 4412 relevés.**

	Mean	SD	Median	Min	0.025	0.25	0.75	0.975	Max
pH values	5.7	1.3	5.6	3.0	3.8	4.7	6.4	7.9	10.1
Species richness	25	12	24	1	5	14	31	48	73

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Table 2. Optimum pH (pH_{max}), the width at 0.5 SR (width $SR_{0.5}$) and relative amplitude of the species richness response curves, maximum SR (SR_{max}), average relative difference between the estimated SR and the observed SR ($RD_{est\text{-}obs}$) for each of the response curve methods.

	Quantile Regression	Pooled Samples	Occurrence Range
pH_{max}*	6.5	6.1	6.3
Width $SR_{0.5}$*	6.9	5.1	4.7
Relative amplitude*	0.56	0.76	1.00
SR_{max}	50	590	702
$RD_{est\text{-}obs}$	1.1	16.0	17.6

***pH_{max}, width $SR_{0.5}$ and relative amplitude based on the f-SSDs**

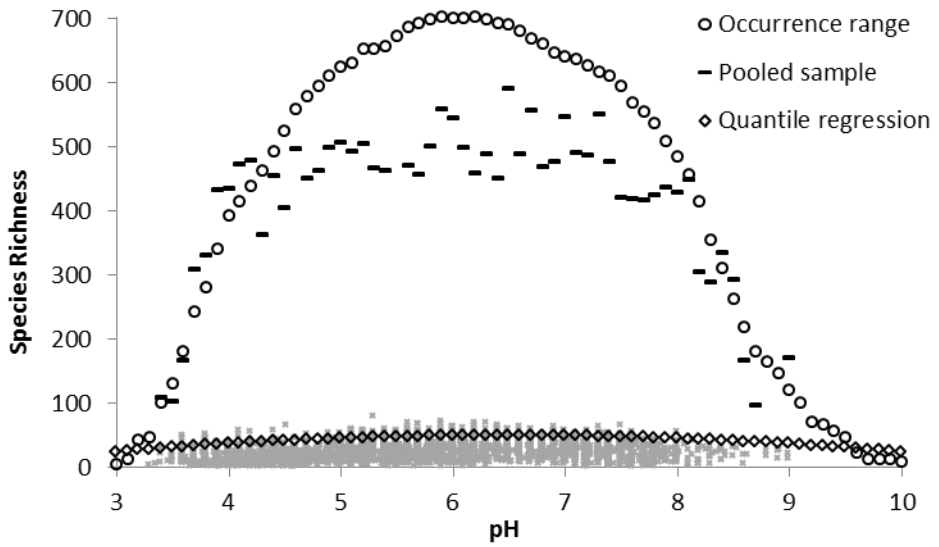
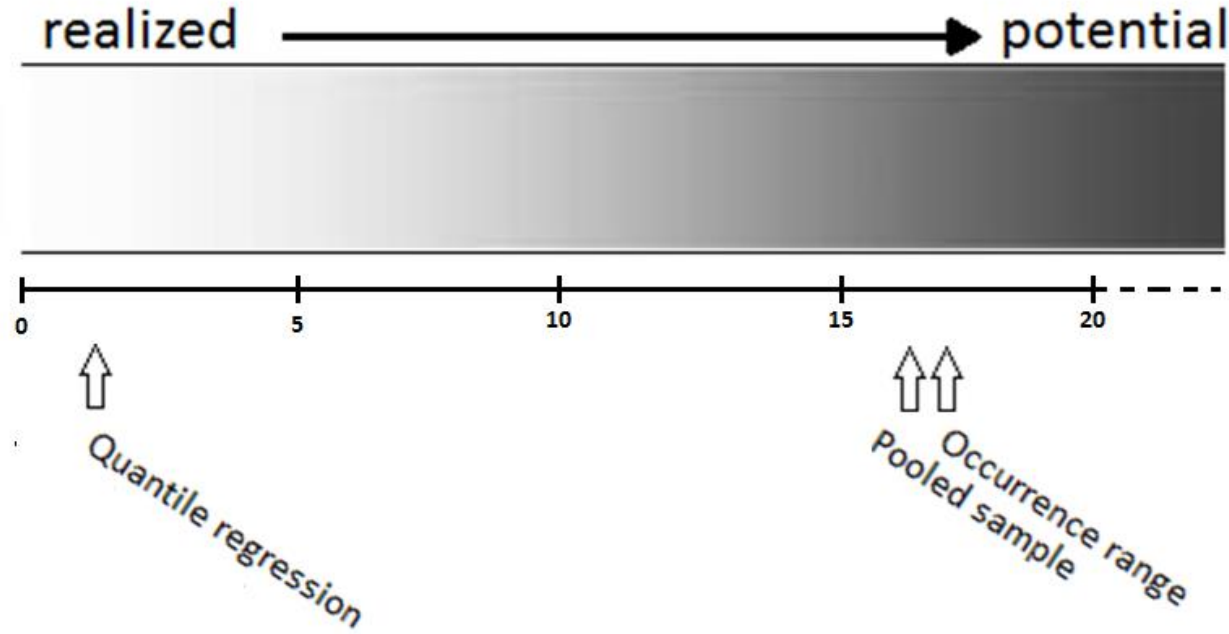


Figure 1. Field-based species richness response curves for pH derived with the quantile regression method, pooled samples method and the occurrence range method. Observed SR is plotted in gray. In the quantile regression method the Gaussian model was selected as the most parsimonious model based on the 0.95 quantile (Table S1; Figure S1). Confidence intervals for the SR estimates derived with the pooled sample method can be found in Figure S2.



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418 **Figure 2. Representation of the three response curve methods on a gradient from realized to potential**
419 **species richness (adapted from Jiménez-Valverde et al., 2008). Numbers on the axis indicate the average**
420 **relative difference between the estimated and average observed SR for each of the response curve**
421 **methods.**

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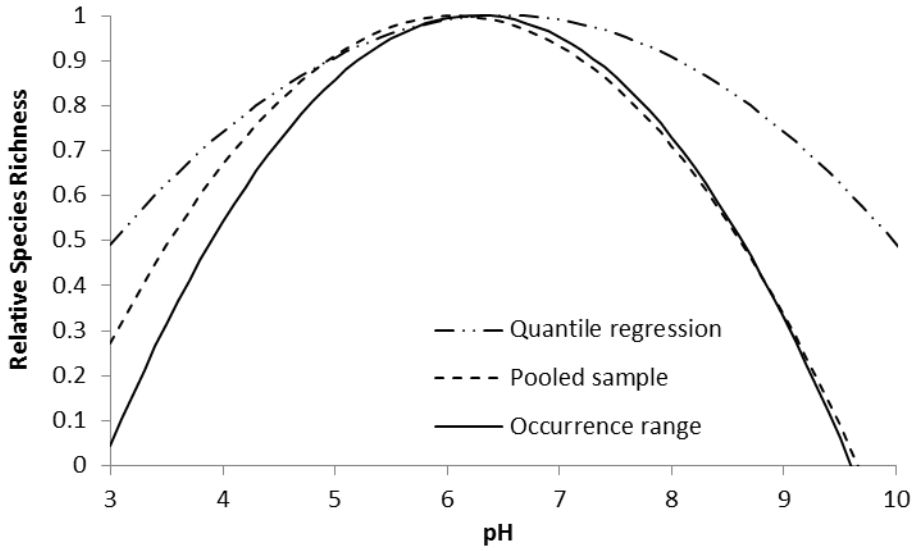

Figure 3. f-SSDs for the relative species richness (r-SR) along the pH gradient for the quantile regression (y = -0.75(-1.13- -0.31)+0.54(0.32-0.74)x-0.04(-0.06- -0.03)x^2), pooled sample (y = -1.94(-2.32- -1.22)+0.94(0.65-1.12)x-0.08(-0.10- -0.05)x^2), and occurrence range methods (y = -2.55(-3.16- -1.89)+1.12(0.94-1.32)x-0.03(-0.10- -0.01)x^2). The 95th percentile confidence intervals of the regression coefficients are given between brackets.

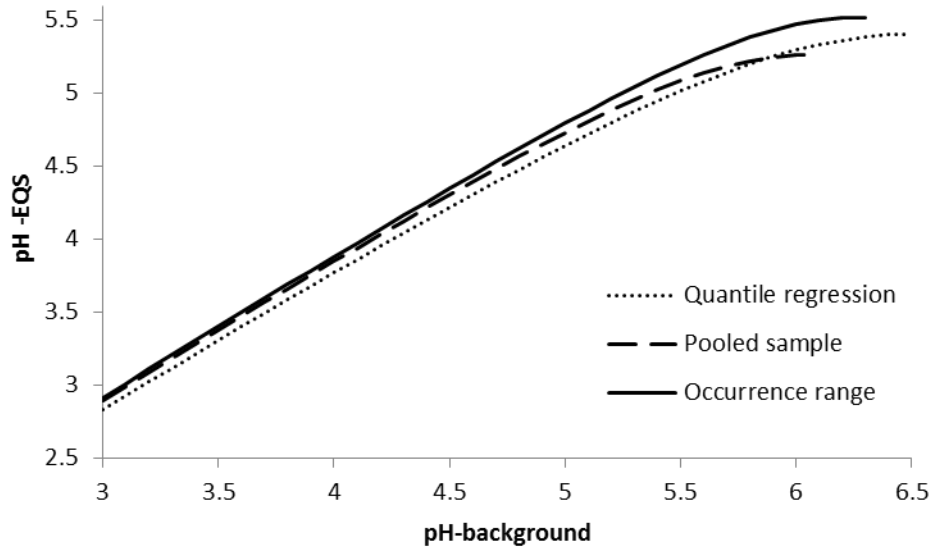

Figure 4. Environmental quality standards for pH (pH-EQS) corresponding to the respective background levels (pH-natural background) for each method.