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Global assessment of the effects of terrestrial acidification on plant species richness

Ligia B. Azevedo [a,*], Rosalie van Zelm [a], A. Jan Hendriks [a], Roland Bobbink [b], Mark A.J. Huijbregts [a]

[a] Department of Environmental Science, Institute for Water and Wetland Research, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands
[b] B-WARE Research Centre, Radboud University Nijmegen, P.O. Box 6558, 6503 GB Nijmegen, The Netherlands

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ABSTRACT

This study estimates the potential losses of vascular plant species richness due to terrestrial acidification for different world's biomes. We used empirical occurrence data of 2409 species from 140 studies and estimated the relative species richness – pH response curves using logistic regressions. The regressions were then used to quantify the fraction of species that are potentially lost due to soil pH changes. Although we found considerable variability within biomes, out results show that the pH at which species richness was maximized was found to be the lowest in (sub)tropical forests (pH = 4.1) and the highest in deserts (pH = 7.4). We also found that (sub)tropical moist forests are highly sensitive to decreases of in soil pH below 4.1. This study can be coupled with existing atmospheric deposition models to quantify the risk of species richness loss following soil acidification.

1. Introduction

Terrestrial acidification is a global threat to plant diversity and is mainly caused by atmospheric deposition of acidifying compounds (Dentener et al., 2006a). Soils of low pH or with low acid neutralizing capacity are generally characterized by increased mobilization and toxicity of aluminum and other metals, leaching of base cations, and decreased nitrification and organic matter decomposition rates (Bobbink et al., 2010; Knoepp and Swank, 1994; Matson et al., 1999).

As a result of changes in nutrient regulation, plants may suffer from a decrease in phosphorus and magnesium content in tissue, an increase in tissue yellowing, a reduction in biomass, coverage, and root growth, unsuccessful germination and regeneration, and competitive exclusion by acid-tolerant species (Falkengren-Grerup, 1986; Roem and Berendse, 2000; Zvereva et al., 2008). Consequently, decreased occurrence of plants in unsuitable, acidified soils has been reported in areas subjected to soil pH reductions in the past (Falkengren-Grerup, 1986; Roem and Berendse, 2000).

Here we focus on soil pH as an indicator of soil acidity since it is an important predictor of plant occurrence and it is correlated to many soil nutrients, e.g. base cations, and acidifying pollutants, e.g. aluminum and sulfur (Kozlov and Zvereva, 2011; Peppler-Lisbach and Kleyer, 2009; van Zelm et al., 2007).

Up to now, studies that relate soil pH with species richness have included only a limited number of ecosystems, most of which are in mid to high latitudes (Chytrý et al., 2010; Olsson et al., 2009). Recently, climate has been shown to be an important predictor of the sensitivity of vascular plants to various pollutants (Kozlov and Zvereva, 2011). In warmer climates, for example, higher temperatures may increase the mobility of toxicants and the year-round production of tissue may enhance sensitivity to pollutants (Zvereva et al., 2008). In addition, larger plants or plants consisting of woody tissue appear to be more sensitive to acidifying pollution than small, soft tissue ones (Zvereva et al., 2010, 2008). To identify large regions according to their climate and ecological interactions and similarities (Orians, 1993), this study categorized the world into terrestrial biomes delineated by Olson et al. (2001). Classification on a biome level highlights the influence of soil pH while accounting for main climatic differences such as temperature, precipitation, or sunlight.

The objective of our paper is to develop response relationships of vascular species richness along the pH gradient for different world's biomes. The response relationships were attained for the acidic pH gradient, up to levels where vascular species richness is maximized. Here we define species richness as the total number of vascular species (trees, herbs, shrubs, etc) occurring on a soil of a given soil pH. Vascular plants are important not only because they comprise a vast number of species of plants but also due to their contribution to a considerable portion of primary production in the terrestrial system. Response relationships of species richness and

* Corresponding author.
E-mail address: l.azevedo@science.ru.nl (L.B. Azevedo).

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pH can be used for predictions of the potential reductions of biodiversity due to soil property changes (van Zelm et al., 2007). Connecting pH response curves to pollutant transport models, including their impacts on soil properties, may give insight into the impact of acidifying pollution at large spatial scales, help identify sensitive areas, and indicate where acidifying pollution reduction efforts should be concentrated (Mac Nally and Fleishman, 2004; van Zelm et al., 2007).

2. Material and methods

In order to estimate the relative vascular plant species richness–pH patterns, we first gathered field observational data from the literature relating individual species occurrence and soil pH to derive empirical relationships of species richness along the soil pH gradient. Second, we performed a logistic regression analysis to arrive at pH–response functions for the different biomes. The steps of gathering literature data to finally determining response functions are described below and illustrated in Appendix 1 of the Supporting Information.

2.1. Data gathering

We collected peer-reviewed studies available up to September 2010 consulting Web of Science with the following keywords: (1) pH; and (2) either soil, ground, land, or terrestrial; and (3) either cover, abundance, species richness, species frequency, extinction, presence, absence, diversity, biodiversity, community, occurrence, or biomass; and (4) either plantation, plant, plants, vegetation, vegetative, flora, forest, tree, or trees. This keyword combination allowed the retrieval of approximately 4000 peer-reviewed studies that were considered for our data inventory. We then manually selected the studies that fulfilled the following criteria.

We excluded croplands or urban studies as they do not reflect the natural vegetation of the area and included studies based on abandoned, restored, re-vegetated areas, and semi-natural grasslands since they are also subjected to biodiversity losses due to terrestrial acidification. Additionally, we only included exploratory, survey studies that reported a specific quantitative relationship between pH and vascular plant species. We only considered species and not higher taxonomic groups (e.g. family, class, etc). An exception was made for genus-level records when those did not accompany any other species belonging to that genus. Lower taxonomic level records (i.e. subspecies, variety) were also included and were considered equal to a species record.

2.2. Data handling

First, pH values were standardized to a representative soil depth and to water extracted pH (pH-H_2O). When more than one pH was reported for a given soil (e.g. multiple horizons), we used the value that was closest to either the B horizon or to 50 cm of soil depth. This is the soil horizon where there is accumulation of clay minerals such as iron and aluminum and the approximate depth at which roots are present in all biomes (Canadell et al., 1996). For the studies reporting soil pH by KCl or $CaCl_2$ and not by H_2O extraction (fifteen in total), we converted pH-KCl and pH-$CaCl_2$ values to pH-H_2O using data from the ISRIC-World Soil Information database (Batjes, 2009), Appendix 2.

Second, we standardized the species name records using The Plant List (2010) so as to correct for synonyms. Since species occurrence was reported in different ways (i.e. biomass, percent cover, abundance) we adapted the data to a presence or absence format by transforming any number higher than zero to species presence and any zero value to species absence.

Subsequently, we allocated each of the selected studies to one of the biomes based on the vegetation coverage described by their authors. Studies describing a vegetation pattern that either did not fit the biome classification system described by Olson et al. (2001) or that were described as a transition zone between two biomes were excluded.

Following this, we derived the pH range at which each plant species can occur within the biome. We considered a species to be absent at pH values outside its reported pH range. The soil pH range obtained from each study was set equal to the mean pH $\pm$ 1.645 times the reported standard deviation (i.e. 90% of sample population) following Latour et al. (1994). For forty studies that did not report mean and standard deviation values, but the minimum–maximum pH ranges were used instead, e.g. Karim and Mallik (2008). Finally, we determined the range between the minimum and maximum pH of each specific plant species per biome as the pH occurrence range for that species. If a species was reported in more than one study within the same biome, we used the lower and upper pH boundaries as the overall species occurrence range. From the pH occurrence ranges of the species within each biome, we excluded the species that were reported at a single mean pH value (273 of 3311 species–biome combinations) because these data are not representative of the tolerance pH range where a species is found in the environment.

2.3. Response curves

We computed the species richness (S) as the sum of present species at each 0.1 pH unit i value within each biome j as

$$S_{i,j} = \sum_{\mathrm{pH}_{i,j}} O_{i,j} \quad (1)$$

where O is the occurrence of each species at pH i in biome j. O is 0 when the species was reported absent and 1 if the species was reported present.

In a subsequent step, so as to compare biomes with dissimilar species richness, e.g. temperate vs. (sub)tropical forest, the species richness results in each biome were transformed into a zero-to-one measure described as the empirical potentially not occurring fraction (ePNOF, equation (1)) of species following Struijs et al. (2011) as

$$\mathrm{ePNOF}_{i,j} = 1 - \frac{S_{i,j}}{S_{\mathrm{opt},j}} \quad (2)$$

where $S_{i,j}$ is the number of species present at pH i and $S_{\mathrm{opt},j}$ is the highest species richness along the pH gradient of biome j. An ePNOF of zero represents the optimum pH condition ($\mathrm{pH_{opt}}$) or optimum pH conditions (range of $\mathrm{pH_{opt}}$), where species richness equals $S_{\mathrm{opt},j}$; while an ePNOF of one represents the complete absence of species.

We calculated logistic functions of PNOF (cPNOF) by fitting them to the empirical ePNOF data. The use of logistic functions follows the calculation procedure commonly adopted in ecotoxicology to arrive at species sensitivity distributions for toxic chemicals and population modeling studies (De Zwart, 2001). They are represented as

$$\mathrm{cPNOF}_{i,j} = \frac{1}{1 + e^{-\frac{\left(\alpha_j - \mathrm{pH}_{i,j}\right)}{\beta_j}}}, \quad \text{for } \mathrm{pH}_{i,j} \le \mathrm{pH}_{\mathrm{opt},j} \quad (3)$$

or

$$\mathrm{cPNOF}_{\mathrm{opt},j} = 0, \quad \text{for } \mathrm{pH}_{i,j} = \mathrm{pH}_{\mathrm{opt},j} \quad (4)$$

where $\mathrm{cPNOF}_{i,j}$ is the calculated PNOF at pH i of biome j below $\mathrm{pH_{opt}}$ (equation (3)) or at the optimum pH (equation (4)). At pH levels above $\mathrm{pH_{opt}}$, species richness is not affected by acidic soil conditions but by other stressors, which we do not account in this study, such as sodium toxicity, etc. Coefficient α represents the pH at which 50% of plant species potentially do not occur and β represents the relative change in species richness with pH. Biomes with low β values comprise the ecosystems with the steepest slope in the logistic function. We fitted the α and β coefficients using logistic regression in SAS 9.2. The sample size for cPNOF is given by the number of cPNOF–pH datapoints (with a 0.1 pH interval) observed from the lower end of the pH gradient up until the pH optimum. The confidence intervals were reported at a 95% confidence level.

2.4. Sensitivity analysis

In order to evaluate the uncertainty in the pH-response curves within biomes, we performed a sensitivity analysis for two additional levels of spatial aggregation: Ecoregion and individual sites (study) within each biome. That was attained by allocating the studies to ecoregions instead of biomes (Olson et al., 2001). Ecoregions are biogeographical subunits of specific biomes thus they offer a higher resolution of the existing vegetation. We then used the same methodology as described above and derived ecoregion-specific and site-specific logistic functions.

3. Results

A total of 140 studies fulfilled our selection criteria (Appendix 3) which, in total, comprised 2409 vascular plant species (see Appendix 4 for their respective pH range within each biome). The number of studies within biomes varied from 2 (i.e. flooded grasslands and savanna, mangrove, and montane grassland and shrubland) to 55 (temperate broadleaf mixed forest), Table 1. The location of each study is shown in Fig. 1.

In (sub)tropical moist broadleaf forests, the optimum pH was the lowest (4.1) while in desert and xeric shrublands and mediterranean forests, woodland and scrub, the optimum pH was the highest (7.4–7.8). Biomes within the temperate zone have rather similar optimum pHs, i.e. broadleaf mixed and coniferous forests, and grassland, savanna, and shrubland (4.7–5.1). The logistic regressions for all biomes indicate an association between increasing PNOF and pH decreasing (Fig. 2).