

## International Journal of Remote Sensing

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tres20>

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Version of record first published: 16 Oct 2012.

To cite this article: Anders Sirén, Hanna Tuomisto & Hugo Navarrete (2013): Mapping environmental variation in lowland Amazonian rainforests using remote sensing and floristic data, International Journal of Remote Sensing, 34:5, 1561-1575

To link to this article: <http://dx.doi.org/10.1080/01431161.2012.723148>

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## Mapping environmental variation in lowland Amazonian rainforests using remote sensing and floristic data

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(Received 7 April 2011; accepted 12 December 2011)

This article describes a method for detailed mapping of ecological variation in a tropical rainforest based on field inventory of pteridophytes (ferns and lycophytes) and remote sensing using Landsat Enhanced Thematic Mapper Plus (ETM+) imagery. Previously known soil cation optima of the pteridophyte species were first used in calibration, i.e. to infer soil cation concentrations for sites on the basis of their pteridophyte species composition. Multiple linear regression based on spectral reflectance values in the Landsat image was then used to derive an equation that allowed the prediction of these calibrated soil values for unvisited sites in the study area. The predictive accuracy turned out to be high: the mean absolute error, as estimated by leave-one-out cross-validation, was just 7% of the total range of calibrated soil values. This method for detailed mapping of natural environmental variability in lowland tropical rainforest has applications for land-use planning, such as wildlife management, forestry, biodiversity conservation, and payments for carbon sequestration.

### 1. Introduction

Within the humid Amazonian forests, a few broad forest types have traditionally been separated on the basis of drainage conditions (seasonally inundated forests and swamp forests) or the presence of characteristic soils (white sand forests). The majority of forests, however, lack such obvious distinguishing traits and fall under the broad category of *terra firme* forest or ‘typical rainforest’. Due to their physiognomical uniformity, *terra firme* forests are generally treated as one or just as a few classes in broad-scale vegetation maps. For example, the relatively recent vegetation map of Brazil (IBGE 2004) only recognized two *terra firme* forest types, namely ‘dense forest’ and ‘open forest’. It is not clear whether these forest types differ in floristic composition or edaphic properties, so the classification provides little information on ecological similarity among sites.

Field surveys carried out in different parts of Amazonia have documented considerable and interlinked floristic and edaphic variation within the *terra firme* forest. Site-to-site differences in physical and chemical properties of soils (such as texture and nutrient content) are reflected in the distribution patterns of plant species, and congruent floristic patterns have been found in taxonomically unrelated plant groups. Such soil-related distribution patterns have been documented especially for pteridophytes, Melastomataceae,

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palms, and trees (Gentry 1988; Duivenvoorden 1995; Tuomisto et al. 1995, 2002, 2003a, 2003b; Ruokolainen, Linna, and Tuomisto 1997; Vormisto et al. 2000, 2004; Duque et al. 2002, 2005; Phillips et al. 2003; Tuomisto, Ruokolainen, and Yli-Halla 2003; Ruokolainen et al. 2007; Honorio Coronado et al. 2009; Zuquim et al. 2009; Higgins et al. 2011). Consequently, any one of these plant groups can be used as an indicator of soil conditions and, by inference, also of floristic patterns in the other plant groups (Ruokolainen, Linna, and Tuomisto 1997; Duque et al. 2005; Ruokolainen et al. 2007).

An improved understanding of natural environmental variability in *terra firme* rainforests has made it obvious that the forests cannot be assumed to be homogeneous, which has important practical implications. For example, terrestrial animals, especially herbivores, may perceive differences in habitat quality among sites with different kinds of soil. If primary productivity and plant species composition vary due to soil differences, the kinds and quantities of available edible plants will also vary. Furthermore, plants growing on nutrient-deficient soils seem to be generally better defended against herbivores and consequently provide lower quality food (Janzen 1974; Gartlan et al. 1980; Coley, Bryant, and Chapin 1985). There are indications that abundance and species composition of animals in *terra firme* forests is related to the fertility of soils (Salovaara 2005; Pomara et al. 2012), which has implications for hunting.

This study is aimed at producing information on environmental variability to help interpret the results of other studies in the same area. For example, it has been found that although the number of animals the hunters of a local village caught in different parts of their hunting range could largely be explained by spatial variation in the hunting effort (Sirén, Hambäck, and Machoa 2004), there were also significant deviations from this pattern, which gave rise to the hypothesis that animal abundance may also vary naturally due to habitat heterogeneity.

Because of the potential ecological importance of habitat variability in tropical rainforests, methods are needed to recognize and map such variability in an accurate and cost-effective way. Field inventories provide point data from the actual inventory localities, and remote-sensing methods can be used to map large continuous areas with high spatial resolution. However, even distinguishing secondary succession from old-growth forest by means of remote sensing is complicated in tropical rainforest areas (e.g. Lu et al. 2003; Lu, Moran, and Batistella 2003; Vieira et al. 2003; Sirén and Brondizio 2009). Distinguishing different types of old-growth *terra firme* forest from each other is even more challenging, but some recent studies have nevertheless succeeded in separating a few forest types representing soils of different geological origins (Tuomisto et al. 2003a, 2003b; Salovaara et al. 2005; Thessler et al. 2008; Higgins et al. 2011).

The difficulty in distinguishing different types of *terra firme* rainforests from each other has to do with the fact that over broad areas, the forest is relatively homogeneous in structural terms, all being multi-species broadleaf forests with closed canopy. Consequently, the forest is also spectrally relatively homogeneous at the scales relevant for mapping. Although there may be differences in terms of forest structure, species composition, or spectral reflectance, ground truthing these is difficult. Moreover, any differences between forest types may go unnoticed when they are obscured by other kinds of variability within the forest types. This is particularly the case in regions with rugged terrain, where solar illumination varies considerably between shaded and sunlit slopes. Correcting for such topographic effects is in itself a major challenge (cf. Riaño et al. 2003; Twele and Erasmí 2005; Thessler et al. 2008; Gao and Zhang 2009).

A final constraint to the use of remote-sensing methods in mapping environmental variability in *terra firme* forests is that discrete environmental or vegetation types are not

easy to either define or recognize in structurally uniformly complex, species-rich vegetation. Ground truthing of image classifications is therefore much more difficult than in less species-rich or structurally more variable forests. Describing the forests on the basis of continuous variables representing ecological characteristics, such as soils, may therefore be more practical than classifications based on discrete vegetation classes, even in remote-sensing applications (cf. Thessler et al. 2005).

The objective of this study is to develop a method to map natural environmental heterogeneity in *terra firme* tropical rainforest on the basis of floristic inventory and remote sensing. Satellites register radiation mostly from the canopy, which consists of trees and lianas, but the plants in all strata of the forest react to the same variation in the underlying soils. This is the justification for using one plant group as an indicator of both soil conditions and more general floristic patterns (Ruokolainen, Linna, and Tuomisto 1997; Tuomisto et al. 2003a, 2003b; Ruokolainen et al. 2007; Higgins et al. 2011). Therefore, we analyse the relationship between spectral signatures of the canopy and trends in plant species composition in the field and take advantage of previously known relations between the plant species and edaphic conditions to recognize a soil gradient in the study area. Finally, we produce a map, which provides an estimate of the spatial distribution of the soil gradient in the study area.

## 2. Materials and methods

### 2.1. Study area

The study was carried out in a tropical rainforest in Ecuadorian Amazonia (Figure 1). The study area is about 1300 km<sup>2</sup>, and it coincides with the study area of Sirén, Hambäck, and Machoa (2004), who studied hunting by the people of the Sarayaku community (1°44' S, 77°29' W). There are no roads in the area, so all transport is by foot or river. Mean annual temperature in the area is about 23°C, and the average annual precipitation is 3000–3500 mm. Local inhabitants recognize a major rainy season in May–June, a dry season in July–August, and a minor rainy season in December–January (Sirén 2004). Interannual variation in total rainfall, as well as variation in the timing of the seasons, is, however, high. The area is characterized by a rugged topography, which is shaped by tectonic uplift and landslides (Bès De Berc et al. 2005). The highest peaks in the north-west reach 640 m a.s.l., whereas in the southeast they do not surpass 500 m a.s.l. As the Bobonaza River flows through the area, its elevation decreases from 390 to 330 m a.s.l. Occasionally, heavy rains cause flooding of the alluvial plains of the Bobonaza as well as of smaller rivers or creeks, but the water also withdraws rapidly, so there are no seasonally flooded *varzea* forests in the area. Swamp forests with dense stands of *Mauritia flexuosa* occur only as dispersed patches, the total area of which is negligible in comparison with the total forest area. Agricultural fields and anthropogenic secondary forests (fallows) cover about 4% of the total area and are concentrated near villages and navigable rivers (Sirén 2007). Small patches of natural secondary forest also exist as a result of landslides or storms, but most of the area is covered by old-growth *terra firme* forest.

### 2.2. Field inventory

The sites for floristic transects were selected in such a way that they got fairly evenly distributed throughout the study area (Figure 1). Whenever possible, transects were located near existing hunting trails, because travel through the forest in the absence of trails was extremely slow. A total of 36 transects were established, and each transect was 2 m wide and 500 m long. In order to cover the full range of the topographic variation, two nearby



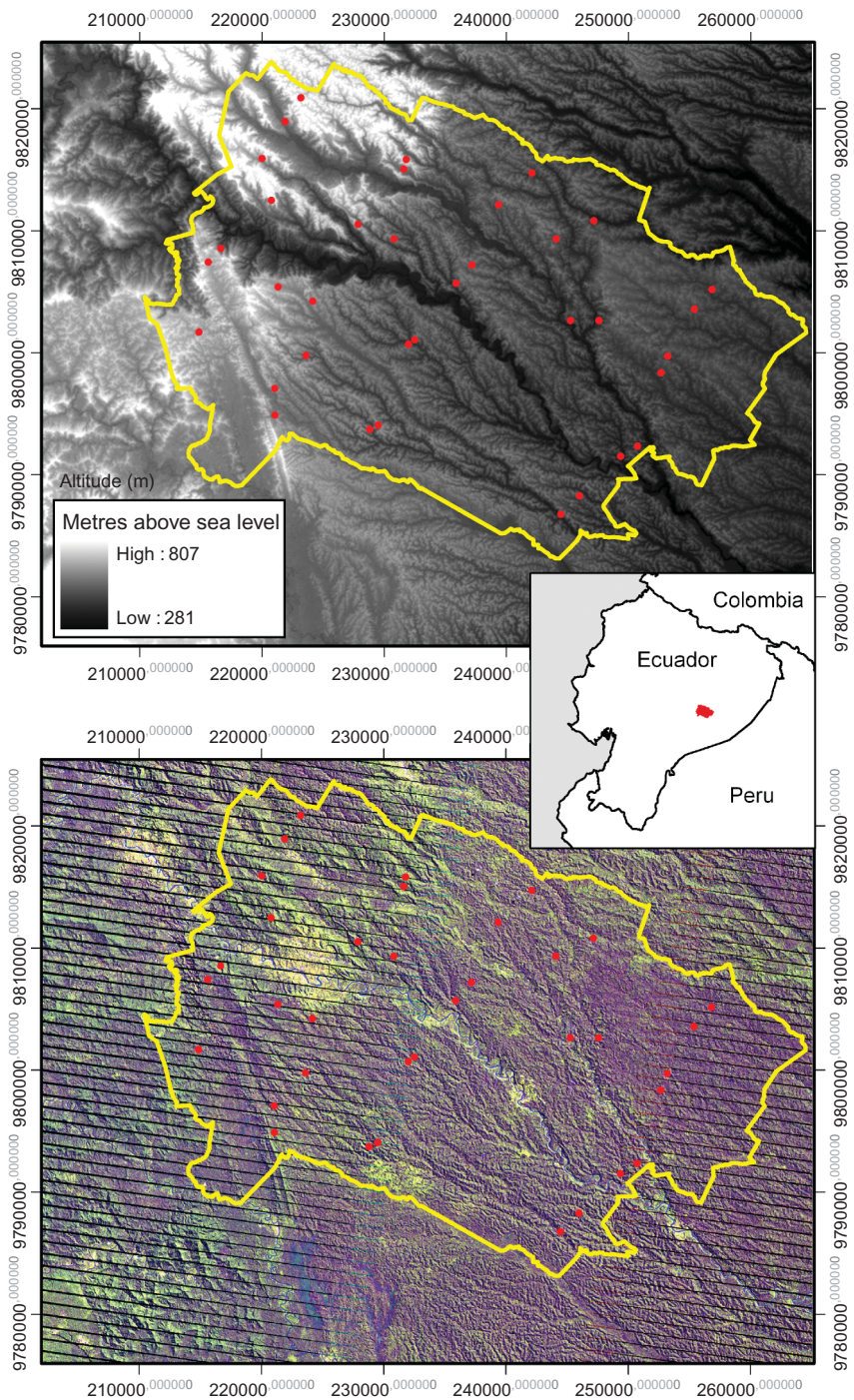


Figure 1. Top: Shuttle Radar Topography Mission (SRTM) digital elevation model of the study area in Ecuadorian Amazonia. Bottom: A Landsat ETM+ image over the study area (band 5 = red, band 4 = green, and band 3 = blue). The image shown here has not yet been corrected for topographic shade effects. The black stripes are data gaps due to the SLC-off mode as explained in the main text). The yellow line denotes the limits of the study area, and the red dots indicate the locations of the floristic transects. The location of the study area in Ecuador is indicated by the red area in the inset.

transects were always taken to represent different parts of the local topography. One transect started at a creek or a river and went upwards at an approximately right angle to the main direction of the drainage network. The other transect started 50 m behind the top of a ridge, then passed the top of the ridge and continued downwards, approximately at a right angle to the main direction of the drainage network.

Each transect consisted of a narrow straight trail opened with a machete in the selected compass bearing. Transects were at first measured with a measuring tape, taking care to measure horizontally even in steep terrain, and georeferenced with a Garmin Etrex Vista Cx GPS receiver (Garmin, Inc., Olathe, KS, USA). A Garmin Etrex Vista HCx receiver was found to be more reliable and was later used both for georeferencing and for measuring transect length.

Because floristic inventories in tropical rainforests are very laborious, pteridophytes (ferns and lycophytes) were used as indicators of floristic and edaphic patterns in the study area. Pteridophytes have three important advantages in this context. First, they are relatively easy to observe, collect, and identify, which speeds up fieldwork and makes it possible to inventory more transects. Second, they are relatively abundant but not excessively species rich, which facilitates obtaining robust sample sizes within the transects (Ruokolainen et al. 2007; Jones, Tuomisto, and Olivas 2008). Third, information on the distribution of Amazonian pteridophytes along edaphic gradients already exists from other sites, which makes it possible to use pteridophyte species composition to infer edaphic properties for a site.

For this purpose, a list of pteridophyte species was prepared for each transect. All terrestrial individuals with at least one green leaf longer than 10 cm were considered, as well as those epiphytic and climbing individuals that had such leaves below 2 m height. Although epiphytes have no direct connection with the soil, including them has been the common practice in these kinds of inventories (e.g. Tuomisto et al. 2003a, 2003b). This is because many species are able to grow both on the ground and epiphytically, and often it is difficult to establish whether a particular individual has a soil connection. All floristic surveys were done by the same person (AS) with some training in identification of herbarium specimens but without previous experience of pteridophyte inventories in the field. Therefore, voucher specimens of all observed species were initially collected for identification by an expert on Ecuadorian ferns (HN). Based on photographs of these identified voucher specimens, a simple photo guide was prepared and then used in the field for the subsequent transects. Eventually, most species could be identified in the field, but voucher specimens were nevertheless collected for verification. The time needed to survey a single 500 m transect was thus reduced from 5 days in the beginning to 2–4 h towards the end of fieldwork. All voucher specimens were finally identified by HT to ensure that the species concepts matched those used in Tuomisto, Ruokolainen, and Yli-Halla (2003). This was necessary to calculate soil cation content optima for each pteridophyte species for the purposes of calibration (to be described below).

### 2.3. Analyses of floristic data

Floristic relationships among the transects were visualized using ordination and clustering methods. Floristic similarities between transects were first quantified using the Jaccard index ( $C_J = a/(a + b + c)$ , where  $a$  is the number of species shared between two transects,  $b$  is the number of species only found in the first transect, and  $c$  is the number of species only found in the second transect).

For ordination, the Jaccard index values were converted to dissimilarities by subtracting them from unity, and the resulting dissimilarity matrix was subjected to principal

coordinates analysis (PCoA). This ordination method aims at concentrating information from the dissimilarity matrix such that the compositional dissimilarities can be visualized using just a few dimensions. Clustering of the transects was carried out using the proportional link linkage algorithm. This is a hierarchical agglomerative clustering method that joins transects into groups on the basis of their pairwise floristic similarity (here it is based on the Jaccard index). Connectedness was set at 0.5 (i.e. midway between single and complete linkages; Legendre and Legendre 1998). The clustering results provide insights into the compositional data that are complementary to those obtained by ordination. These analyses together provide the background information needed for making inferences concerning environmental variation in the study area.

Soil cation content in the transects was estimated using calibration, which is a standard method in ecology (Jongman, Ter Braak, and Van Tongeren 1995). Calibration is based on the idea that any one plant species only occurs in a part of any environmental gradient, and that its occurrence is most frequent and its abundance highest at sites that are closest to its optimum conditions. Species optima for a given environmental variable can be estimated as an average of the variable values in the sites where the species have been observed. The value of the variable at a new site can then be estimated as an average of the optima of those species that occur at the site. For this purpose, soil cation content optima for the pteridophyte species occurring in our transects were first calculated using data from 134 other transects situated in Ecuador, Colombia, and northern Peru. These transects had been established using a method similar to ours, but both pteridophyte species composition and soil cation content data were available (Tuomisto, Ruokolainen, and Yli-Halla 2003 and unpublished data). Those species observed in this study but not in the previous ones were excluded from this analysis. For each species, its soil cation optimum was calculated as a weighted arithmetic mean of the soil cation content in the transects where the species had been observed, with species abundance (number of individuals) in each transect used as the weight. The optima were then used to estimate soil cation content for each transect of this study by calculating the mean of the optima of all those species that occurred in the transect in question. This mean was unweighted because species abundance information was not collected in this study. The resulting numbers are here referred to as 'calibrated soil values'.

#### **2.4. Estimation of soil values based on image data**

For image interpretation, a Landsat Enhanced Thematic Mapper Plus (ETM+) image (path 9, row 61) acquired on 2 July 2005 was used (Figure 1). This image was in scan line corrector (SLC)-off mode, implying that there were data gaps due to a technical problem of the satellite sensor. Fortunately, the study area was at the centre of the scene, where the least number of data gaps are present. Both such SLC-off data gaps and pixels representing water or river beaches were masked out prior to image analysis. Radiometric calibration of the image data to convert digital number (DN) values to physical at-sensor radiance was done according to Green, Schweik, and Hanson (2002). A number of procedures for atmospheric and topographic correction were tested. The best performance was achieved by combining atmospheric correction using the dark object subtraction and topographic correction method and by applying the equal area normalization algorithm of Erdas Imagine (Intergraph, Corp., Huntsville, AL, USA), also called the internal average relative (IAR) reflectance (Kruse 1988; Zamudio and Atkinson 1990), to each pixel. A detailed comparison of different preprocessing procedures will be presented elsewhere.

The spectral signatures in the satellite image and the calibrated soil values for the transects were used to obtain a regression equation to estimate soil values over the entire study area. To collect spectral signatures, the GPS points of each 500 m floristic transect were displayed on screen, and a 200 m  $\times$  600 m rectangle was placed on top of each transect. An average spectral signature was registered for each rectangle using Landsat bands 1–5 and 7. Multiple regression was then performed to model the calibrated soil values as a linear function of spectral signatures in the six bands. Stepwise multiple regression was used in order to exclude from the regression equation those bands that did not have a statistically significant contribution to explaining the variation in the calibrated soil values (with criteria  $p \leq 0.05$  for entry and  $p \geq 0.10$  for removal).

Before using the regression equation to extrapolate soil values to the whole image, some additional image processing was done. Existing information on land use in the area (Sirén 2007; Sirén and Brondizio 2009) was used to mask out areas that were known or suspected to be cultivated land or anthropogenic secondary forests (fallow). The land-use mask included all land within a 50 m buffer around pixels classified as cultivated land in 1987 or as fallows in either 1987 or 2001; a 150 m buffer around pixels classified as cultivated land in 2001; and a 200 m buffer around navigable rivers. After the land-use mask, a focal mean filter was applied to the image in order to remove such variation on a small spatial scale, which is likely to represent noise rather than relevant ecological information. This filter was given a radius of 195 m, such that its area was approximately equal to that of the rectangles used to collect spectral signatures. Applying the focal mean filter also filled the data gaps caused by the SLC-off mode. A side effect was that even pixels that had previously been excluded with the land-use mask were again given DN values, but these were eliminated by a second application of the land-use mask. An estimated soil value was then calculated for each pixel in the scene using the multiple regression equation.

The error in the soil values estimated from the Landsat data in relation to the original soil values obtained by calibration was quantified by leave-one-out cross-validation. In this validation method, one transect is set aside to be used as the test set, and the remaining 35 transects are used as the training set to parameterize the regression equation. Each transect is then used as the test set in turn, and the estimated soil values obtained in this way for the test transects are compared with the original calibrated soil values. This provides a measure of the expected accuracy of the results when the regression equation is applied over the entire Landsat scene.

### 3. Results

#### 3.1. Ordination, clustering, and calibrated soil values

The total number of pteridophyte species observed in the 36 transects was 182, but some closely related species were confused in the field and were consequently lumped. The numerical analyses were therefore run with 171 broadly circumscribed species (gamma richness  $R\gamma = 171$  species). On average, the transects contained 46 species (alpha richness  $R\alpha = 46$  species/transect).  $R\gamma$  is 3.7 times as large as  $R\alpha$ , which indicates that the amount of compositional heterogeneity (beta richness  $R\beta$ ) in the data corresponds to what would be observed among 3.7 transects that share no species. The pairwise Jaccard index similarity values that were calculated between transects ranged between 0.13 and 0.65, with the average being 0.37.

PCoA showed that there is a strong compositional gradient in the floristic data. This is mainly captured along Axis 1, but there is also indication of an arch (transects at both



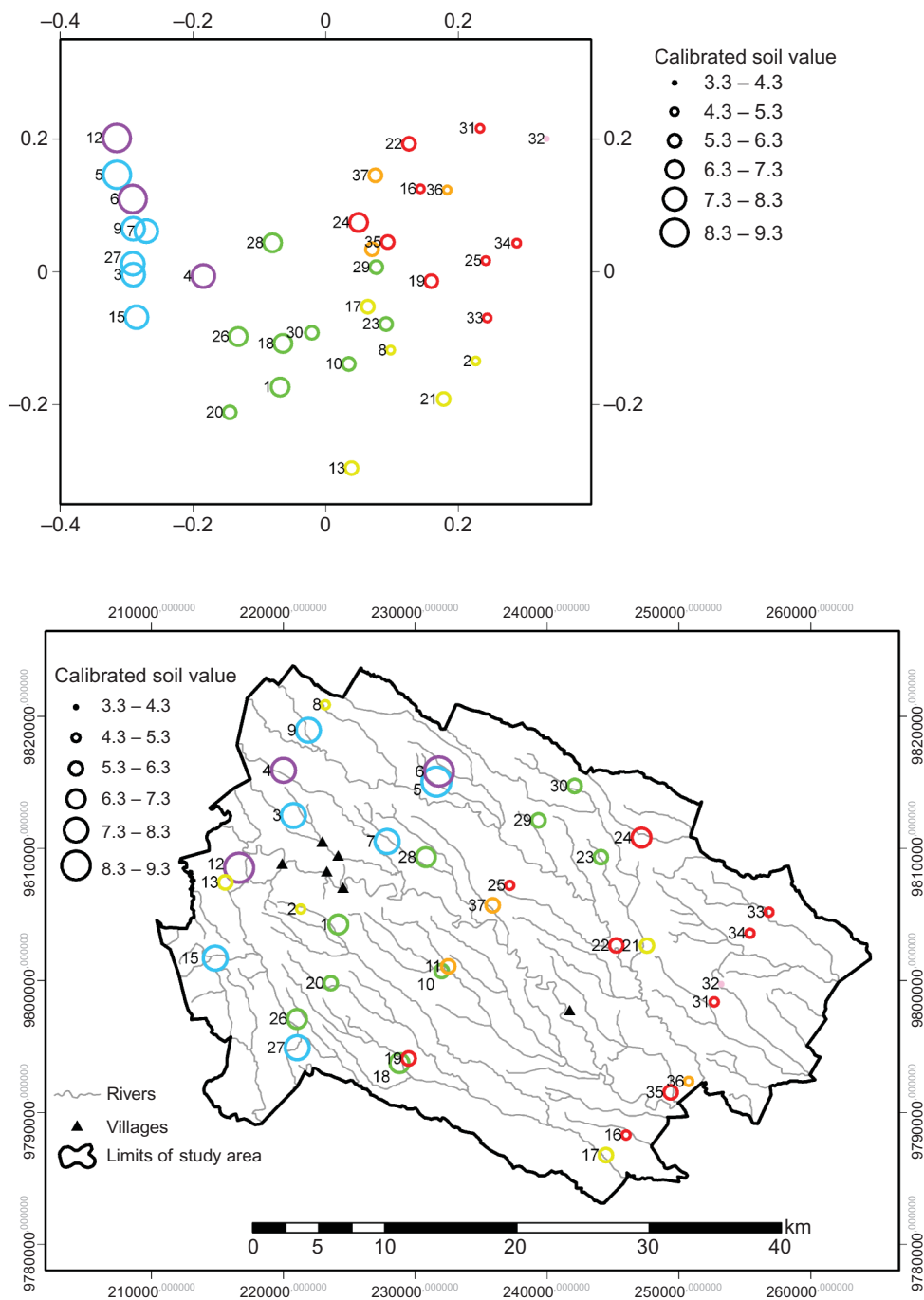


Figure 2. Top: The positions of 36 transects of 2 m × 500 m along the first two axes of PCoA based on floristic differences of pteridophytes (one-complement of the Jaccard index). Bottom: The geographical distribution of the same 36 transects in the study area in Ecuadorian Amazonia. In both panels, the size of the circle corresponding to each transect is proportional to the calibrated soil value (estimated using floristic data), and the colours indicate to which of seven recognized floristic classes each transect belongs (proportional link linkage clustering with connectedness 0.5 based on the Jaccard index).

extremes of the gradient have higher values along Axis 2 than transects at the middle of the gradient do; Figure 2, top). Seven transect classes were recognized in the clustering analysis, and each one of these is restricted to a specific part of the floristic gradient. This supports the results of the ordination and suggests that the interpretation of the main floristic gradient would not be drastically changed even if the higher ordination axes were considered.

Calibrated soil values, which approximate soil cation content values, are highest in the leftmost end of the floristic gradient and gradually decrease towards the rightmost end. The Pearson correlation between calibrated soil values and ordination scores along Axis 1 is very high (correlation coefficient,  $r = 0.95$ ,  $p < 0.001$ ), which indicates that the floristic gradient is strongly related to an edaphic gradient. Although measured soil cation contents were not available to verify this relationship, the regularity of the pattern confirms that the species found in this study associate with each other in similar ways as they do in other areas. If this were not the case, species that had high optimum values in other areas would be mixed with species having low optimum values in this study area, which would lead to all sites obtaining calibrated soil values close to the overall average. The fact that the calibrated soil gradient was tightly linked with the local floristic gradient supports the use of the obtained calibration results in the rest of the analyses.

When projected on the map of the study area (Figure 2, bottom), the clustering and calibration results suggest that there is an east–west gradient in soil fertility: the areas to the east have, in general, lower calibrated soil values than the areas to the west (Pearson correlation between longitude and calibrated soil value:  $r = -0.63$ ,  $p < 0.001$ ). Some transects, however, deviate from this general pattern. In particular, transects 2, 8, and 13 were all assigned to the same floristic cluster and have relatively low calibrated soil values, but they occur in the western part of the study area, where all other transects have much higher calibrated soil values.

### 3.2. Estimation of soil values based on spectral signatures

A linear multiple regression model was obtained to predict soil values for unvisited sites based on spectral reflectances in the Landsat ETM+ image. The stepwise regression procedure eliminated bands 2 and 4, so the final regression model used the Landsat bands 1, 3, 5, and 7 (adjusted coefficient of determination,  $R^2 = 0.85$ ). When the soil values obtained from calibration were compared with those estimated from the Landsat data using leave-one-out cross-validation, the Pearson correlation between the estimated and calibrated soil values was 0.91 ( $p < 0.001$ ). The mean absolute error of these estimates was 0.40 cmol(+) kg<sup>-1</sup> (centimoles of positive charge per kilogram of soil) corresponding to just 7% of the range between the minimum and maximum calibrated soil values (Figure 3).

The final map of spectrally estimated soil values based on the corrected image is shown in Figure 4. In general, estimated soil values increase in the upriver direction, although several local deviations from this general pattern can be seen. Some such deviations seem to be related to geological features, such as the plateau at high altitude in the northwest corner of the study area, where estimated soil values are rather low.

## 4. Discussion

### 4.1. Assessment of the methods

Our results support earlier suggestions that pteridophyte inventory in combination with remote sensing is an efficient tool for the mapping of habitat variability in tropical rainforests (Tuomisto et al. 1995, 2003a, 2003b; Salovaara, Cárdenas, and Tuomisto 2004;

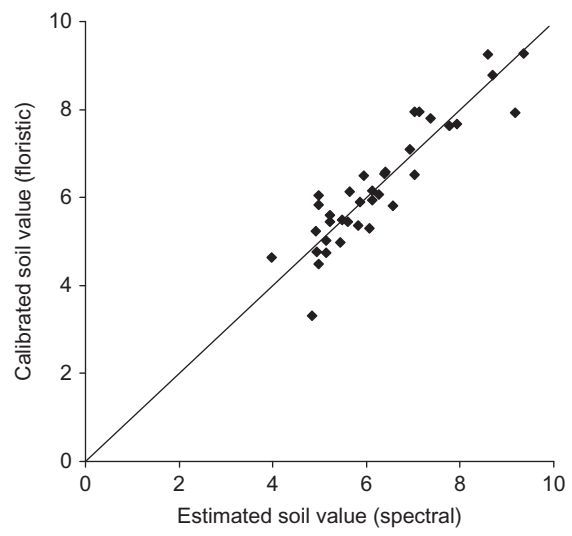


Figure 3. Calibrated soil values plotted against estimated soil values. Estimated soil values are calculated using multiple regression of calibrated soil values against spectral reflectances on an atmospherically and topographically corrected Landsat ETM+ satellite image using leave-one-out cross-validation. Each point represents one field transect site.

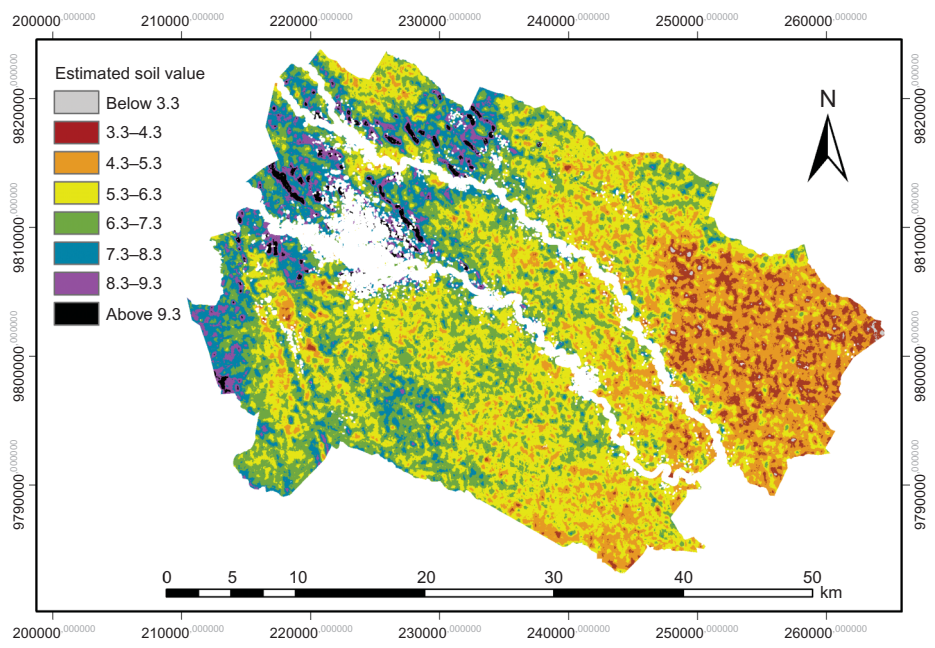


Figure 4. Map of estimated soil values in the study area in Ecuadorian Amazonia. The soil values provide an approximation of the concentration of exchangeable bases in the soil (Ca, K, Mg, and Na in  $\text{cmol}(+) \text{ kg}^{-1}$ ). Estimated values were obtained with a multiple linear regression, where spectral values of Landsat ETM+ bands 1, 3, 5, and 7 were used as the independent variables. The regression equation was parameterized with soil values obtained from calibration, i.e. on the basis of pteridophyte species composition in 36 field transects. All calibrated soil values were within the range 3.3–9.3  $\text{cmol}(+) \text{ kg}^{-1}$ , so estimated values outside this range need to be interpreted with caution.

Salovaara et al. 2005; Thessler et al. 2005; Higgins et al. 2011). Earlier studies on Amazonian pteridophytes have demonstrated a tight correspondence between pteridophyte species turnover and differences in soil cation content, which implies that the former can be used as an indicator of the latter (Ruokolainen, Linna, and Tuomisto 1997; Tuomisto et al. 2003b; Tuomisto, Ruokolainen, and Yli-Halla 2003; Ruokolainen et al. 2007; Higgins et al. 2011). We found a clear linkage between the main floristic gradient observed in the pteridophyte data and the spectral reflectance of the forest canopy. Since the inventoried pteridophytes are small understorey plants, they have no direct influence on canopy reflectance, which is determined mostly by canopy trees and lianas. The correlation arises because both understorey plants and canopy plants react to soil properties, such as cation content, which in this study was approximated by the 'soil value' inferred from pteridophyte species composition.

There is a long tradition of using indicator plant species and calibration to infer soil properties from plant species composition in boreal and temperate areas (Cajander 1926; Ellenberg et al. 1991; Jongman, Ter Braak, and Van Tongeren 1995; Diekmann 2003; Schmidtlein 2005). The high similarity between the floristic gradient obtained by ordination and the edaphic gradient reconstructed using calibration suggests that the same principle works even in high-diversity tropical forests. Since cation content is one aspect of soil fertility, the reconstructed edaphic gradient can be assumed to reflect potential primary productivity of the forests. It may also be related to other ecosystem properties, such as standing biomass, forest dynamics, or animal distributions (Quesada et al. 2009; Slik et al. 2010; Pomara et al. 2012).

The correlation between spectral signatures and calibrated soil values is very high in our data, which indicates that the latter reflect a relevant ecological property of the study sites. However, the accuracy of these calibrated values as estimates of soil cation concentration has not been tested with actual soil data, which is why we have used the less specific term 'soil value' in this article. In general, calibration can be expected to underestimate the range of soil cation content values, because the method is based on iterative taking of means. The calibrated soil cation content estimates are means of species optima, which themselves are means of the original soil cation content measurements in the background data. In both cases, the minimum value of the means will be larger and the maximum value smaller than the corresponding extreme values in the original data. As a result, calibration leads to the soil cation contents of the cation-poorest sites to be overestimated and the cation contents of the cation-richest sites to be underestimated. Nevertheless, the obtained values provide a relative measure by which environmental variability in the study area can be estimated and mapped.

The soil values obtained by calibration in our data set correspond to soil cation contents in the range 3.3–9.3 cmol(+) kg<sup>-1</sup>. The total range of soil cation content values in the background data set used to calculate soil cation optima was 0.8–27 cmol(+) kg<sup>-1</sup>. The difference in range must partly depend on the calibration process, as explained above. However, those species that were limited to the most cation-poor soils in the background data set were entirely absent from the present data set, which suggests that the cation-poorest soils were also absent. It is also noteworthy that the background data set included mostly sites with low to intermediate soil cation contents, and only a few sites with cation contents exceeding 10 cmol(+) kg<sup>-1</sup>. It is therefore likely that the soil cation optima for those species associated with the cation-richest soils were underestimated, and the maximum soil cation content estimate of 9.3 cmol(+) kg<sup>-1</sup> is an underestimate as well. In addition, about 25% of the species observed in the present data set could not be assigned an optimum value at all, because they were not present in the background data set, and could therefore not be used in calibration.

#### 4.2. Applications

To successfully protect biodiversity, conservation area networks need to include a sufficient representation of the entire range of habitat variability in all regions. Broad-scale maps of environmental and floristic variation are needed to assess how well this goal has been reached and to identify areas that should be prioritized in future conservation actions. The method used in this article provides one means to produce such maps.

The estimation of soil characteristics could also be used in land-use planning in order to direct agricultural development to fertile areas. This would help avoiding such errors as have been done in the past, when agricultural expansion has been targeted to areas where soils have been too poor for the intended crops (e.g. Fearnside 1986). At the same time, the method may be proactively used by conservationists to identify forests that may be at increased risk of conversion to agriculture due to their high soil fertility.

Since general forest productivity is affected by soil properties, understanding the heterogeneity in soils is also important for estimating sustainable levels for the harvesting of forest products such as timber or game animals. Earlier studies have found that game animal abundance (as estimated from catch per unit of hunting effort) is spatially variable in our study area (Sirén, Hambäck, and Machoa 2004 and unpublished data). Human hunting effort itself explained much of this variability for all important game species, but other factors seemed to complicate the picture. This study was motivated by the need to find out whether mammal abundance varies naturally in response to variability in soil productivity, not just as a result of human hunting pressure. The map of estimated soil values produced here (Figure 4) will provide the means to test this hypothesis. The local community is concerned about the sustainability of hunting in its territory and has set aside no-take areas for wildlife in order to ensure long-term sustainability of hunting (Sirén 2006). Even when intentions are good, however, failure to recognize spatial variability of wildlife habitats may lead to suboptimal harvest strategies and put sustainability at risk (Jonzén, Lundberg, and Gårdmark 2001). Spatial information on environmental variability, and on how game populations react to this variability, may be useful when deciding about the location and size of no-take areas, as well as when evaluating their performance.

The United Nations Reduced Emissions from Deforestation and Degradation (REDD) programme aims to establish mechanisms for monetary compensation for maintaining carbon stocks in forests. In the southern part of Peruvian Amazonia, it has been found that carbon stocks vary considerably both among and within 25 mainly topographically defined forest types (Asner et al. 2010). Soil properties can be expected to be among the ultimate determinants of carbon stocks, but the exact relationships are not yet well understood (Laurence et al. 1999; Clark and Clark 2000; Quesada et al. 2009). Including information on edaphic characteristics, either directly by soil chemical analyses or indirectly by floristic inventory of indicator species, can therefore be expected to improve the accuracy of the models used to estimate carbon stocks over large areas.

#### Acknowledgements

During the early planning phase of the project, Anders Sirén was funded by the Academy of Finland. During further planning, as well as fieldwork and preliminary data analysis, he was funded by a postdoc grant from the Swedish International Development Authority (SIDA) and a postdoc grant from the Swedish Research Council for Environment, Agricultural Sciences, and Spatial Planning (FORMAS). During the final analyses and writing the manuscript, Sirén was funded by Akademikernas Erkända Arbetslöshetskassa, the Swedish Cultural Fund in Finland, the Oscar Öflund Foundation, and by a grant awarded to Professor Risto Kalliola by the Kone Foundation. Saul Malaver, Alex Machoa, and Angel Gualinga assisted with fieldwork. We thank the Government Council of the



Sarayaku Community for facilitating fieldwork and Dra. Laura Arcos Terán, Dean of the Natural and Exact Sciences, Faculty of the Pontificia Universidad Católica del Ecuador, for institutional support to the development of the project.

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