Improving estimates of tropical peatland area, carbon storage, and greenhouse gas fluxes

I.T. Lawson

Department of Geography and Sustainable Development, University of St Andrews, Irvine Building, North Street, St Andrews KY16 9AJ, UK

T.J. Kelly

School of Geography, University of Leeds, Leeds LS2 9JT, UK

P. Aplin

School of Geography, University of Nottingham, University Park, Nottingham NG7 2RD, UK

A. Boom

Department of Geography, University of Leicester, Leicester LE1 7RH, UK

G. Dargie

School of Geography, University of Leeds, Leeds LS2 9JT, UK

F.C.H. Draper

School of Geography, University of Leeds, Leeds LS2 9JT, UK

P.N.Z.B.P. Hassan

Department of Geography, University of Leicester, Leicester LE1 7RH, UK

J. Hoyos-Santillan

School of Biosciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK

J. Kaduk

Department of Geography, University of Leicester, Leicester LE1 7RH, UK

D. Large

Department of Chemical and Environmental Engineering, University of Nottingham, University Park, Nottingham NG7 2RD, UK

W. Murphy

Department of Geography, University of Leicester, Leicester LE1 7RH, UK

S.E. Page

Department of Geography, University of Leicester, Leicester LE1 7RH, UK

K.H. Roucoux
Department of Geography and Sustainable Development, University of St Andrews, Irvine Building, North Street, St Andrews KY16 9AJ, UK
S. Sjögersten
School of Biosciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK
K. Tansey
Department of Geography, University of Leicester, Leicester LE1 7RH, UK
M. Waldram
Department of Geography, University of Leicester, Leicester LE1 7RH, UK
B. M. M. Wedeux
Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK
J. Wheeler
Department of Geography, University of Leicester, Leicester LE1 7RH, UK
Corresponding author: I.T. Lawson, School of Geography, University of Leeds, Leeds LS2 9JT, UK
Email: itl2@st-andrews.ac.uk
Telephone: +44 (0) 1334 464 023
Fax: +44 (0) 1334 463 949

Abstract

Our limited knowledge of the size of the carbon pool and exchange fluxes in forested lowland tropical peatlands represents a major gap in our understanding of the global carbon cycle. Peat deposits in several regions (e.g. the Congo Basin, much of Amazonia) are only just beginning to be mapped and characterised. Here we consider the extent to which methodological improvements and improved coordination between researchers could help to fill this gap. We review the literature on measurement of the key parameters required to calculate carbon pools and fluxes, including peatland area, peat bulk density, carbon concentration, above-ground carbon stocks, litter inputs to the peat, gaseous carbon exchange, and waterborne carbon fluxes. We identify areas where further research and better

coordination are particularly needed in order to reduce the uncertainties in estimates of tropical peatland carbon pools and fluxes, thereby facilitating better-informed management of these exceptionally carbon-rich ecosystems.

Keywords

Peat, greenhouse gases, remote sensing, tropical ecology, carbon cycle.

I Introduction

Most peat in the tropics is located in the lowland humid forests of Southeast Asia, Amazonia, Central America and equatorial Africa (Figure 1). Page et al. (2011b) estimated the extent of tropical peatlands at 441,000 km^2 and their carbon (C) pool at 81.7–91.9 Gt C. This carbon pool is susceptible to climate change as well as local human impacts. Some peatlands in inland regions of Kalimantan have lost carbon due to increasing El Niño intensity and changing sea levels during the late Holocene (Dommain et al. 2011, 2014), suggesting that these peatlands may also respond to future (anthropogenic) climatic change. More recently, peatlands throughout Southeast Asia have been degraded by logging and plantation development (Miettinen et al. 2012). Drainage to improve growing conditions for crops such as oil palm and *Acacia* (for pulpwood) leads to peat subsidence and enhanced CO_2 emissions persisting over decades (Jauhiainen et al. 2012; Hooijer et al. 2012). Accidental burning, due mainly to small-scale land clearance fires getting out of control, can lead to very large peat losses over weeks or months (e.g. in the exceptional El Niño year of 1997, CO_2 emissions from Southeast Asian peatland fires were equivalent to 13–40% of total global fossil fuel emissions: Page et al. 2002). Crucially, whilst a large proportion of lost tropical forest biomass can be recovered within decades in secondary-growth forest (Letcher and Chazdon 2009), restoration of peatland carbon stocks to pre-disturbance levels would take thousands of years.

Despite their importance, basic information on carbon storage in tropical peatlands is lacking. This is not just a problem in the tropics. Reviewing estimates of the size of the boreal peatland carbon pool, Vasander and Kettunen (2006) showed that they vary by an order of magnitude (from 41.5 Pg C for all histosols globally: Buringh 1984, to 455 Pg C for boreal and subarctic peatlands: Gorham 1991) due mainly to substantial variation in estimates of peat dry bulk density (DBD) and thickness. The same problem applies in the tropics but with the additional difficulty that, unlike in boreal peatlands, the area of peat is also very poorly known in some regions.

Most research in the tropics has focused on Southeast Asian peatlands, and their distribution is comparatively well known, yet large uncertainties still exist in estimates of the amount of carbon stored in them. For example, published figures for Indonesia include 37.2 (Wahyunto et al. 2003, 2004, 2006), 55 ± 10 (Jaenicke et al. 2008), and 57.4–58.3 Pg C (Page et al. 2011b), based on differing methodologies. New field data can make a substantial difference: Dommain et al. (2014) estimated the peatland carbon pool in western Indonesia (excluding Papua) at 23.1 Pg C, a substantial downward revision of the 33.3 Pg C estimate for the same area by Wahyunto et al. (2003, 2004) due mainly to new data on DBD and peat thickness, even though the area of peat estimated by the two studies (which are based on similar GIS datasets) was almost identical (131 500 and 129 700 km^2 respectively). Peatlands in other tropical regions are less well mapped. For example, although wetlands in the Cuvette Centrale of the Congo Basin, the fourth- or fifth-largest wetland on Earth (Campbell 2005), have been mapped using remote sensing techniques (e.g. Bwangoy et al. 2010; Betbeder et al. 2014), the extent of peat within these wetlands is essentially unknown; published estimates of the size of the peatland carbon pool in the Congo basin are based on very few field data (Joosten et al. 2012). In Amazonia, the existence of c. 40 000 km^2 of peat in the Pastaza-Marañón basin, Peru, has only recently been confirmed by fieldwork (Lähteenoja et al. 2009a,b, 2012). The uncertainty in this peat carbon pool is very large (0.8–9.5 Gt: Lähteenoja et al. 2012). Limited surveys have been carried out in parts of Brazil (Lähteenoja et al. 2013) and French Guiana (Cubizolle et al. 2013), but remain to be conducted elsewhere in the Amazon basin. A substantial revision of the global estimate of the size of the tropical peatland carbon pool is therefore likely over the next few years. Data on carbon fluxes, especially of the important greenhouse gas (GHG) methane, are likewise extremely scarce, especially outside Southeast Asia.

The high carbon density of tropical peatlands makes them an obvious focus for emissions-management schemes such as the UN REDD+ (United Nations Reducing Emissions from Deforestation and Forest Degradation) programme (Murdiyarso et al. 2010). This will require precise inventories of peatland carbon stocks and fluxes to be carried out for specific regions in order to provide accurate estimates of baseline carbon pools and fluxes against which projected reductions in carbon emissions can be measured, verified, and translated into carbon credits.

Therefore two fundamental research priorities are (1) to quantify the amount of carbon stored in tropical peatlands accurately at a range of scales, and (2) to quantify fluxes of carbon to and from the tropical peatland carbon pool. More broadly, a better understanding of the present distribution of tropical peatlands, the processes of peat accumulation and decay, and the development of peatlands over time is relevant to other important research questions, including:

- What determines the distribution of peat in the tropics?
- How will tropical peat stocks change in the future?
- How do tropical peatlands influence biogeography and biodiversity?
- How should tropical peatlands be managed?

In this paper we aim to encourage better and more consistent methodologies for producing carbon inventories and budgets, principally at a regional scale. The value of a coordinated approach is clear: for example, where long term, repeated and systematic carbon inventories of tropical forest biomass have been coordinated by the RAINFOR (Malhi et al. 2002) and AFRITRON networks (among others), many new insights into long- (Baker et al. 2004) and short-term (Lewis et al. 2011) carbon dynamics have emerged, generating over 100 carbon-focused publications by more than 200 collaborators.

The paper is divided into three parts, 1) mapping peat distribution, 2) estimating the size of the carbon pool, and 3) estimating carbon fluxes. In part 1, we focus on emerging remote sensing technologies which, alongside appropriate measurements on the ground, can improve our ability to map peatland extent. In part 2 we discuss the measurement of peat thickness, peat bulk density and carbon concentration. In part 3 we discuss carbon fluxes into and out of peatland ecosystems, specifically, long-term carbon accumulation rates, litter inputs and decomposition, gaseous and waterborne fluxes, and above-ground carbon stocks. We focus on forested tropical lowland peatlands, although we recognize that many of the issues we discuss also pertain to other types of peatland in the tropics and beyond.

II Mapping peat distribution

Field mapping of peatlands is a considerable challenge, especially at regional, national and global scales. However, a combination of field measurements and inferences from remote sensing can provide an optimal balance, where realistic programmes of fieldwork can yield map-based products that cover a region comprehensively, are reasonably accurate and reliable, and with robustly quantified uncertainties.

Tropical peatlands are often distinct from surrounding *terra firme* (dry-land) forests in four ways that are observable in satellite and airborne data. Firstly, their vegetation is often low in diversity. In South and Central America, some parts of Africa, and on the island of New Guinea, palms are often more abundant than in upland forests, sometimes forming mono-dominant stands (e.g. Lähteenoja and Page 2011; Wright et al. 2011). However, diversity in some peatland forests can be high (e.g. Sumatran swamps: Brady 1997). Secondly, vegetation structure is often (but not always) distinctive, often with more open canopies and low-stature or thin-stemmed trees, or no trees at all (e.g. Anderson 1983; Page et al. 1999; Phillips et al. 1997). Thirdly, their topography can be distinctive. Tropical peatlands typically occupy a specific topographic or geological setting, for example the subsiding Pastaza-Marañón basin in Peru or the peats forming along dendritic drainage channels in the Tasek Bera basin, Malaysia (Wüst and Bustin 2004); blanket peats that are indifferent to topography only occur rarely in upland settings (Gallego-Sala and Prentice 2012). Many tropical peatlands are also detectably dome-shaped (e.g. Phillips et al. 1997; Jaenicke et al. 2008; Lähteenoja et al. 2009b). Finally, peatland water tables often lie close to, at or above the surface throughout the year (e.g. Lawson et al. 2014). Whilst any one of these four features alone is insufficient to characterise an area of forest as potentially peat-forming, the combination of two or more presents a much stronger case (Draper et al. in press).

These properties can be mapped using a number of different remote sensing products. Compositional and structural features of peatland vegetation have been distinguished using optical sensors such as Landsat (Phua et al. 2007; Jaenicke et al. 2010; Li et al. 2010; Lähteenoja and Page 2011), SPOT (Systeme Pour l'Observation de la Terre; Lee 2000; Miettinen and Liew 2010), and MODIS (Moderate Imaging Spectrometer; Langner et al. 2007; Wijedasa et al. 2012). Figure 2 presents an example of vegetation classification of the Changuinola peat dome in San San Pond Sak, Panama, using multi-scale Landsat Thematic Mapper (TM) image analysis supported by aerial photography and field data to characterise the main vegetation gradient. To date, optical imagery from medium spatial resolution sensors such as the Landsat series (30 m multispectral imagery) has been the primary and most successful tool for mapping peatlands. The new generation of VHR (very high resolution) products, such as IKONOS (4 m multispectral) or WorldView-2 (2 m multispectral) imagery, potentially brings new opportunities for detailed and accurate vegetation mapping. One key difficulty in the tropics is the infrequent temporal coverage of these sensors, which makes cloud-free images difficult to obtain. RapidEye (5 m multispectral) products, derived from a constellation of five satellites with consequently more frequent image acquisition, can be a more reliable source of cloud-free imagery (e.g. Franke et al. 2012). Opportunities are likely to grow further as new sensors are launched (e.g. 1.24 m resolution WorldView-3) and future missions become operational (e.g. the EU's Sentinel-2 10 m resolution twin satellites),

Active sensors such as radar and LiDAR (Light Detection And Ranging) which penetrate the canopy can be used to detect the distinctive forest structures (e.g. combination of low canopy, thin stems, high stem density in pole forest) or patterns in structure (e.g. concentric zonation of vegetation communities) that characterize some peatlands. Radar and LiDAR are also able to provide topographic data which can help to distinguish between peatland and *terra firme* forests, but few attempts have been made to identify tropical peatlands using these tools. One useful exception is the use of an orbital LiDAR instrument onboard the ICESAT satellite to measure peat topography and forest biomass at a study site in Kalimantan (Ballhorn et al. 2011; other examples include Hoekman and Vissers 2007; Rakwatin et al. 2009; Jaenicke et al. 2008; Jubanski et al. 2013). A limitation of LiDAR products is that they are generally available as discrete point measurements (orbital sensors) or thin strips of data (aerial sensors) rather than a full coverage. Other data sources (e.g. L-band radar data and ground-based measurements of forest structure) are usually needed to interpolate between LiDAR measurements (Mitchard et al. 2012).

The presence of standing water below a forest canopy can produce a distinctive radar backscatter signal, particularly at longer radar wavelengths. L-band radar has been used extensively in tropical contexts to map standing water (de Grandi et al. 1998, 2000; Hess et al. 2003; Hoekman 2007; Bwangoy et al. 2010), to track changes in floodwater extent (Rosenqvist and Birkett 2002; Alsdorf 2003; Jung et al. 2010; Lee et al. 2011; Betbeder et al. 2014), and, using time series of radar data, to distinguish areas that are constantly wet from those that are only seasonally wet (Waldram 2014).

Remote sensing therefore already provides effective tools for extrapolating from field measurements to map peatlands over large areas, but there is scope for further methodological research. The use of optical sensors to define peatland extent has been widely and successfully implemented, but the less commonly used active sensors may discriminate between peatland and *terra firme* more effectively in many circumstances. We recommend that wherever possible, multiple remote sensing products (including both optical and active sensors) should be used in combination. Some of the data types discussed here, such as airborne LiDAR, are too expensive to obtain for many projects. However, suitable products for mapping peatlands based on vegetation structure and composition, topography and inundation at a coarse scale (c. 30 m) are freely available from Landsat, SRTM (Shuttle Radar Topography Mission) and ALOS PALSAR. A combined approach using these products is a highly feasible starting point for future mapping projects.

It remains the case, however, that interpretations of peatland distribution based on remote sensing need to be validated with ground reference data. Ground reference points are often difficult and expensive to install and therefore require careful planning in order to maximise their usefulness. They need to meet many criteria: they should be widely distributed across the study region, encompassing the full range of spatial heterogeneity; they need to span the full range of environments present in the landscape (including anthropogenic ones such as rice fields and oil-palm plantations: Miettinen et al. 2012), not just those associated with peat; and the reference dataset should be sufficiently large both to develop and validate a classification using different subsets of the data. Typically, hundreds of points are required to develop a reliable classification for a particular region, so it would clearly be desirable if researchers visiting new sites could collaborate in generating suitable data. In Table 1 we recommend a set of measurements that are needed for synoptic mapping and ground reference, and which can easily and quickly be collected as part of the basic site description for any kind of research on tropical peatlands. More extensive and specialized measurements (e.g. detailed vegetation composition, water table depth variation) may be necessary for more specific applications of remote sensing, but wherever possible they should be carried out in a way that preserves the compatibility of measurements between studies, in line with Table 1.

III Carbon stocks

The quantity of carbon stored by peatlands in a region (M_c, in kg) can be calculated as:

$$M_c = AD\rho c \tag{1}$$

where A is the area of peatland (m^2), D represents its mean thickness (m), ρ is the mean DBD (kg m^{-3}) and c is its carbon concentration (dry mass proportion; Gorham 1991). The area of peatland can be determined by a combination of remote sensing and ground survey, as discussed in Section II. The remaining three variables on the right hand side of equation (1) are each susceptible to considerable uncertainty, which in combination can lead to very large uncertainties in M_c.

1 Peat thickness

In carbon inventory research it is usually convenient to treat peat as a separate, particularly carbon-rich category of soil, but a long-standing problem in peat research, unlikely to be resolved any time soon, is how to define 'peat'. Most workers define a peat soil as one that contains more than a certain proportion of organic matter, but the critical value varies widely, between about 30 and 65 wt% organic matter (Joosten and Clark 2002:41; Wüst et al. 2003), hindering data synthesis (Page et al. 2011b). Some peat units have a clearly-defined contact with the underlying, less organic material, but others change in composition more gradually. In such cases it can be impossible to judge peat thickness consistently in the field, and unfortunately, core samples are not always taken for laboratory analysis of organic matter content, resulting in unreliable data. Researchers must acknowledge that 'peat' is *de facto* a flexible term, and circumvent definitional issues by collecting objective data on the properties of the material they are studying. One way forward, and our recommendation, is to build on past efforts such as the CARBOPEAT project (http://www.geog.le.ac.uk/carbopeat) to compile the necessary data (core location, sample depth, and sample loss-on-ignition and carbon concentration) to allow reanalysis using a standardized definition of 'peat'.

Estimates of peat thickness for a region are usually based on limited numbers of measurements, which may be biased by over-reporting of the thickest deposits. The geometry of peatlands is such that thick peats are often restricted to quite small areas (the centre of domed mires or basin-filling swamps) surrounded by much more extensive areas of shallow peat. Simply taking the mean of a series of measurements from the edge to the centre of a single peatland is likely to result in an overestimate of the mean peat thickness. A much more robust approach is that taken by Dommain et al. (2014), building on existing detailed GIS maps of Indonesian peatlands by Wahyunto et al. (2003, 2004, 2006). By interpolation between field measurements, they defined GIS polygons of small areas of peat of different mean thicknesses. The total volume of peat was then derived by multiplying the area of each polygon by its specific thickness. This provides a useful template for future work, not least because the link between field data and estimates of carbon storage is explicit, facilitating revisions as further data emerge. GIS datasets can also be readily shared and assimilated into larger-scale mapping or reanalysis projects, and are thus a very desirable form of research output.

There are few detailed studies of the geometry of individual tropical peatlands, but the exceptionally detailed survey using a dense grid of 194 depth estimates across a 235 ha swamp, the CICRA peatland in southern Peru (Householder et al. 2012), demonstrates that useful insights can be gained that can guide more representative sampling of other peatlands in the region. In this case, comparison of the peatland volume estimate derived from the entire network of points showed that less detailed estimates of the volume of the same peatland based on short transects tended systematically to overestimate the total peat volume. This 'calibration' was then used to adjust volume estimates based on transect data only from other sites in the region.

Ground penetrating radar (GPR) could also be used alongside manual coring to determine peat thickness and stratigraphy, and may be especially useful for studying features such as voids which can be important in volume terms in forested peatlands (e.g. Slater and Reeve 2002; Parry et al. 2014). There are, however, considerable practical difficulties associated with deploying relatively bulky GPR over large distances in forested peatlands, though smaller instruments are currently in development.

Few attempts have so far been made in the tropics to derive peat thickness by remote sensing, and they are exceptional cases. For example, Jaenicke et al. (2008) integrated Landsat Enhanced Thematic Mapper (ETM+) and SRTM data, a network of 750 field measurements of peat thickness, and a three-dimensional peatland development model to estimate the volume of domed peatlands in Kalimantan; the success of this project depended on the rather special properties of the mires in question (regular shape, very thick peats). Ballhorn et al. (2009) also used LiDAR measurements to estimate *changes* in peat thickness over time due to burning on Indonesian peatlands. A more generally applicable method for measuring peat thickness remotely is perhaps unlikely to emerge but there is scope for further investigation on a site-by-site or region-by-region basis. Peat thickness can sometimes correlate with other properties that are visible by remote sensing. For example, thick peats often occur towards the centre of ombrotrophic peat domes. Field observations suggest that these deep, nutrient-poor peats are frequently (but not always) associated with specialized and structurally distinctive vegetation communities in, for example, Kalimantan (Page et al. 1999), Panama (Sjögersten et al. 2011), Peru (Kelly et al. 2013; Draper et al. in press), and the Republic of Congo (G. Dargie unpublished data). These plant communities are often distinctive in Landsat TM, ALOS PALSAR and other imagery. However, apparent relationships between remote sensing data and peat thickness must be confirmed using empirical data because many factors other than peat thickness may be equally or more important in controlling vegetation composition and structure (Draper et al. in press), as is the case in temperate/boreal peatlands (Wheeler and Proctor 2000).

2 Bulk density

Measured values of dry bulk density (DBD) for individual peat samples from Indonesia vary by almost an order of magnitude, and the few available data from undisturbed sites in Amazonia vary by a factor of two (all in peats with ash contents <10%; Figure 3). This variability, which arises from factors including the botanical composition of the peat, consolidation of deeper peats, drainage history, and measurement method, is a major source of uncertainty in estimates of the size of the peatland carbon pool because calculations of carbon stocks at individual sites, or even across regions, are frequently based on the mean of a very small number of DBD measurements (e.g. Page et al. 2011b; Householder et al. 2012).

Frequently, the number of samples taken may be too small, and/or the spacing between samples may be too large to capture the spatial variability of peat DBD. Within-site lateral variation in DBD has not been explored systematically in tropical contexts and more work is needed to establish whether there are any predictable patterns. Sometimes the stratigraphic profile of DBD is quite consistent at sites within a region (Hooijer et al. 2012), but DBD can also vary systematically between peatland types within a region (e.g. floodplain peatlands, domed peatlands; Shimada et al. 2001). The converse has been shown in boreal peatlands (i.e. DBD varies between regions within the same peatland type; Sheng et al. 2004; Yu 2012; there are insufficient data to know if this also applies in the tropics). Site-specific measurements are therefore always desirable, and in general more data are needed to determine whether DBD varies spatially in a predictable way.

A further complication is that tropical peatlands can show considerable stratigraphic variation in DBD (Figure 4) due to fluvial mineral inputs (Lähteenoja et al. 2009b), long-term vegetation succession and related variations in peat structure (Phillips et al. 1997; Roucoux et al. 2013), peat decomposition, post-drainage consolidation (Hooijer et al. 2012), and water- or gas-filled voids. This stratigraphic variation can only be addressed through field measurements and ample down-core sampling. A greater palaeobotanical insight into the origins of variation in DBD in tropical peats would also be a useful line of research.

A second potential source of error in DBD estimation is that peat samples of known volume must be recovered, which is difficult to achieve reliably. One method for collecting volumetric samples is to dig a pit into the peat and extract a monolith from the pit wall (Hooijer et al. 2012; Couwenberg and Hooijer 2013), but this may entail continuously pumping water out of the pit which can be impractical, is limited to shallow sections, and, by analogy with what is known of the effects of seasonal changes in water table on peat volume in undisturbed peats (Price 2003), may lead to compaction and over-estimation of DBD. Various specialised corer designs have been proposed to improve the collection of volumetric samples from shallow peats (Wright et al. 1984; Givelet et al. 2004; van Asselen and Roosendaal 2009; see De Vleeschouwer et al. 2010 and Glaser et al. 2012 for discussion of the relative merits of different devices). At present, most workers use a Russian-type corer which is suitable for use in shallow and deep peats; as a side-sampling device it offers better control over sample depths than a piston corer and a low risk of sample contamination than a Hiller corer, which is especially important if the peat is to be radiocarbon dated (cf. Glaser et al. 2012), but can be less effective at cutting through woody peats than a corer with a serrated barrel. The volume of the *in situ* peat sample is usually assumed to be identical to the internal volume of the corer. In reality, core recovery is often imperfect, especially in fibrous or woody peat that cannot be cut cleanly, or where the peat is structurally weak and is not retained within the corer, or (in the case of piston corers) it fails to fill the barrel (Wright 1991; Dommain et al. 2011; Lähteenoja et al. 2013). Thus, DBD measurements are probably often subject to large errors stemming from erroneous volume estimations. Russian-type corers in particular may yield systematic underestimates of DBD (Clymo 1983). In general, large-volume corers (including wide-diameter Russian corers) are to be preferred over smaller devices because they will more likely retrieve a representative sample, but they can be impossible to use in stiff or woody peats and are more logistically problematic compared with a smaller, lighter device. As yet, there have been few systematic comparisons of different methods to assess the extent of the uncertainty in volume measurements (Pitkänen et al. 2011), especially in fibrous and woody peats. More research on this topic could help to quantify and, perhaps, compensate for any differences between datasets that are due to the use of different sampling devices.

A third way in which DBD measurements made by different research groups may vary stems from variation in laboratory methods, for example in the temperature at which the peat samples are dried. Chambers et al. (2011) proposed a protocol for measuring DBD and other basic variables (including drying at 100°C) which we recommend and which, if followed, will minimize this uncertainty.

3 Carbon concentration

Two principal approaches are used to estimate carbon concentration in peats. The more accurate and direct technique is elemental analysis (Nelson et al. 1996; Chambers et al. 2011). In peats with low ash content the carbon concentration calculated by this method typically varies between about 52 and 58% (Figure 5). However, many workers use mass loss-on-ignition (LOI; Heiri et al. 2001) as a cost-effective way to estimate organic matter concentration. The LOI at (typically) 450°C is assumed to be attributable to combustion of organic material; the remainder, the 'ash', is typically composed of sedimentary mineral material and biogenic silica. Carbon concentration can then be estimated by assuming that the organic material contains (e.g.) 50 wt% C (Turunen et al. 2002).

On the basis of available data, applying the LOI-based approach described by Turunen et al. (2002) could apparently systematically underestimate carbon concentration by c. 8 wt% in tropical peats with very low ash contents (Figure 6). This disparity is principally attributable to the varying abundance of carbon-rich compounds, such as lignin or charcoal, in the organic matter fraction of peat. However, at least at some sites, the paired measurements show a strong linear relationship, albeit with some scatter. There may even be a strong linear relationship between DBD and carbon density (the product of carbon concentration and DBD, measured in e.g. kg C m^{-3}), sufficient to support the suggestion that DBD measurements alone may be sufficient for a first-order estimate of carbon concentration (Warren et al. 2012; Farmer et al. 2013). However, the strength of this relationship varies and it has not been tested for tropical peats outside a few locations in Southeast Asia.

Therefore, for inventory purposes, and especially when undertaking work for the first time at a new site, in our view it remains important to measure carbon concentration as accurately as possible, i.e. using an elemental analyser following Chambers et al. (2011). LOI remains a useful tool in its own right because it provides a direct measure of the organic matter content of the peat, which is valuable in understanding the developmental history of a site. As with DBD, systematic studies of within- and between-site variation in carbon concentration are lacking in tropical contexts.

The question of the number of samples to take, both horizontally and vertically, for DBD and carbon concentration in a peatland is inevitably constrained by the resources available for a given project. One approach to designing a sampling strategy is to assess the way in which the variation in different measurements (DBD, carbon concentration, peat thickness) contributes to the overall uncertainty in the estimate of the carbon pool. For example, peat thickness is usually much more variable across a region than DBD or carbon concentration, suggesting that a rational use of research effort would be to focus on measuring peat thickness. Resampling techniques can be used to estimate the confidence interval around an estimate of the regional carbon pool for a given region (Manly 2007; Draper et al. in press). Chimner et al. (2014) discussed the relative merits of different core sub-sampling approaches in terms of attempting to encompass stratigraphic variation in DBD and carbon concentration in Canadian peats and found that, in Canada, (a) several different approaches gave similar results and (b) analysis of the DBD and carbon concentration of a single core section, from 25–75 cm depth at each site, gave estimates of the total peat carbon stock that were within 15% of estimates based on exhaustive sampling of entire cores from the same sites, suggesting that even a single (admittedly large) sample from each core site may be adequate for inventory purposes. This conclusion must be tested before being applied in other regions where, for example, frequent admixture of clay in deeper peats may give very different results. In general we would recommend a more conservative approach, taking several discrete subsamples throughout the full thickness of the peat (the "intermittent peat sampling method" described by Chimner et al. 2014).

4 Biomass

A widely-used set of standard protocols has been developed for measuring above-ground biomass (AGB) in *terra firme* tropical forests (e.g. Phillips et al. 2009). These protocols are, with modification, applicable in forested peatlands. They should be used wherever possible because using the same protocols on peat and *terra firme* enables biomass, productivity, diversity, and other key vegetation parameters to be compared, which means that peatland vegetation can be understood in the broader context of tropical vegetation as a whole, and can be integrated into regional assessments of AGB across all ecosystems.

Modifications, or rather additions, to *terra firme* protocols for use on peatlands are necessary because peatland vegetation is frequently dominated by plants that are usually regarded as negligible in a standard forest census, for example, thin-trunked trees with diameter at breast height (DBH) < 10 cm (the cut-off used in most AGB inventories), or grasses and sedges. An example of a modified protocol that remains compatible with standard RAINFOR protocols is provided by Roucoux et al. (2013) at Quistococha, Peru: a nested sampling design was used to record small trees with DBH between 2.5 and 10 cm in a series of sub-plots within their main census plot.

Another consideration is that peatland forests are often dominated by species (such as trunkless palms) to which standard allometric equations for calculating biomass do not apply (e.g. Chave et al. 2005; Feldpausch et al. 2011; Gehring et al. 2011). Outside Southeast Asia, the allometric equations used for AGB calculation of tropical peat swamp forests in recent literature (e.g. Kronseder et al. 2012; Englhart et al. 2013) were originally developed for "moist tropical forests" in general (Chave et al. 2005), and the performance of these models in the distinctive pole and palm forests often found on peatlands needs to be tested. Recently, species-specific equations have been developed for the most important peatland palms in South America including *Mauritia flexuosa* and *Mauritiella armata* (Goodman et al. 2013). Similar work remains to be carried out on many other species. The long history of economic exploitation of peat swamp forest in Southeast Asia means that allometric equations there are better established (Krisnawati et al. 2012).

New tools for assessing AGB on large spatial scales by remote sensing of canopy structure are rapidly developing (e.g. in Southeast Asian peatlands: Jubanski et al. 2013; Kronseder et al. 2012). Airborne LiDAR (Asner et al. 2013) and satellite-based LiDAR and L-band radar (e.g. Saatchi et al. 2011; Ballhorn et al. 2011; Mitchard et al. 2012; Baccini et al. 2012) have been widely used to estimate AGB, mainly in *terra firme* forests. As with mapping, more ground-reference data are needed to allow these approaches to be applied confidently to peatland forest AGB assessments (Table 1).

Below-ground biomass (BGB: living roots, as opposed to the necromass or dead material contributing to peat) has hardly been studied in tropical peats, but existing research shows that root inputs can be more important to peat accumulation than leaf and stem litter, i.e. these are 'replacement peats' (Brady 1997; Chimner and Ewel 2005; Dommain et al. 2011). Measuring BGB is fraught with methodological problems even in *terra firme* forests, but it would be of great interest to know (in the context of understanding carbon balance and rates of carbon sequestration – see below) how much of the peat at various depths is made up of live or recently dead root material. However, for the purposes of estimating the size of carbon pools, the live and dead components of the peat do not need to be separated explicitly.

IV Carbon fluxes

In peatlands, carbon enters the peat in the form of litter and leaves it as dissolved organic carbon (DOC), particulate organic carbon (POC), and as the greenhouse gases CH_4 and CO_2. Comprehensive carbon flux measurements have been made for several well-studied northern peatlands (Roulet et al. 2007; Nilsson et al. 2008; Koehler et al. 2011), but a complete carbon budget has only been attempted once in tropical peat swamp forest (Chimner and Ewel 2005). The limited available data suggest that tropical peatland carbon sequestration rates are towards the upper end of the range for peatlands globally (Mitsch et al. 2010; Dommain et al. 2011; Glaser et al. 2012) due to a combination of high net primary production (NPP) and low decomposition rates (Dommain et al. 2011; Sjögersten et al. 2014).

The annual change in organic carbon for a peatland (ΔC_{org}) can be expressed as follows, following Roulet et al. (2007):

$$\Delta C_{org} = NPP - F_{CO_2} - F_{CH_4} - netDOC_{EX} - netPOC_{EX} \qquad (2)$$

where ΔC_{org} is equivalent net primary production (NPP) minus F_{CO_2} (the gaseous flux of CO_2), F_{CH_4} (the gaseous flux of CH_4), $netDOC_{EX}$ (the waterborne DOC flux), and $netPOC_{EX}$ (the waterborne POC flux).

None of the quantities on the right hand side of equation 2 are easy to measure in any peatland, but in the tropics, NPP is especially difficult to quantify due to the large size of the plants on forested peatlands. The carbon flux can perhaps more easily be estimated using (i) the observed change in peat surface height, caused by accumulation and/or subsidence, relative to a fixed stake (e.g. Nagano et al. 2013; Couwenberg and Hooijer 2013); (ii) dating the basal peat to establish the apparent long term rate of carbon accumulation (LORCA: Clymo et al. 1998; Turunen et al. 2002; 'long term' in this context means centuries to millennia) as a direct measure of carbon sequestration over a given period of time (although this can differ substantially from present rates of carbon accumulation: Joosten and Clarke 2002:34); or (iii) measured rates of litter production and carbon losses through decomposition (Chimner and Ewel 2005). Our discussion below focuses on the prospects for the direct measurement of litter input and decomposition, greenhouse gas fluxes (chiefly CO_2 and CH_4), and waterborne carbon fluxes, all of which are needed both to quantify the carbon flux in tropical peatlands and in order to develop a fuller mechanistic understanding of the controls on their carbon balance and greenhouse gas fluxes.

1 Litter inputs

The transformation of different types of litter in tropical forested peatlands – roots, non-woody leaf and stem litter, and woody debris ranging from twigs and small branches to whole tree trunks – into peat is poorly understood (Tie and Esterle 1992; Brady 1997; Sulistiyanto 2004; Chimner and Ewel 2005; Shimamura and Momose 2005). The quantity of litter inputs and the rate at which each litter type decomposes determine their contribution to the peat carbon pool. Leaves can comprise the bulk of above-ground litterfall in peat swamp forests (Sulistiyanto 2004) but they typically decompose much more rapidly than woody debris and roots and therefore contribute little to the overall accumulation of peat (Chimner and Ewel 2005), except perhaps where leaves accumulate in ponds on the peat surface (Gastaldo and Staub 1999).

Above-ground litterfall can be collected and weighed using nets of e.g. 1×1 m, depending on the size of the litter, although the logistics of the necessarily frequent sampling (due to high litter decomposition rates in the traps) can be restrictive. Suitable protocols have been developed by the CTFS Global Forest

Carbon Research Initiative (www.ctfs.si.edu) and Harrison (2013); comparable sampling schemes have also been used in lowland tropical rainforest (Chambers et al. 2000; Nepstad et al. 2002). The contribution of large woody debris is harder to measure, and is almost unexplored in tropical peatlands. The frequency and relative importance of branch- and tree-fall events can be estimated by repeated litter surveys along transects (Waddell 2002) or in census plots (Chimner and Ewel 2005; Woodall and Monleon 2008; Baker and Chao 2011), although no standard method has yet been agreed upon (Larjavaara and Muller-Landau 2011); further methodological research is needed.

Equally, very few data on root dynamics are available for tropical peatlands. Root growth, especially of fine roots, can be measured using the ingrowth core or bag method (e.g. Symbula and Day 1988; Neill 1992; Brady 1997; Finér and Laine 1998; Metcalfe et al. 2008), though this can be problematic: important considerations are the linearity of root growth over the study period and temporal variation in root production, e.g. between dry and wet seasons (Metcalfe et al. 2008), as well as changes in soil structure caused by the removal of roots from the soils during preparation of the ingrowth core, which may affect later root growth. Root mortality (i.e. root litter input to the necromass) is extremely difficult to determine and involves differentiating between live and dead root material (Finér and Laine 1998). Alternative approaches, such as the use of minirhizotrons which allow *in situ* measurements of root growth and mortality (Iversen et al. 2012), have been used successfully in lowland tropical rainforest (Metcalfe et al. 2007) but not yet in tropical peatlands.

2 Litter decomposition

Potential *in situ* litter decomposition rates in tropical peatlands appear higher than in temperate/boreal peatlands (Brady 1997; Chimner and Ewel 2005; Yule and Gomez 2008), presumably due mainly to the year-round higher ambient temperatures, although other factors including litter composition, water table depth, and pH may also be involved (Qualls and Haines 1990; Chimner and Ewel 2005; Yule and Gomez 2008). Few systematic studies have been carried out, especially outside Southeast Asia.

Standard techniques for measuring the decomposition rate of fine litter are readily applied in tropical peatlands, in which rapid decomposition allows meaningful results to be obtained over sampling periods as short as two years (Yule and Gomez, 2008; Hoyos 2014). Mesh bags containing known dry weights of litter are firmly anchored to the ground to prevent them being washed away during floods, or are buried in the peat and collected at regular intervals to calculate weight loss (Chimner and Ewel 2005; Wright et al. 2013a; Hoyos 2014). Decomposition of large woody debris such as fallen trees or large branches is also presumably important in forested peatlands, but sampling is more difficult, usually requiring repeated surveys over long intervals, and data are lacking. One approach would be to follow (or build on) RAINFOR protocols to establish permanent forest census plots, which include a protocol for measuring coarse woody debris (Baker and Chao 2011). Census plots that are part of a network such as RAINFOR, where the data are relevant to many research questions, are more likely than not to be revisited over many years and hence to generate the necessary long-term datasets.

3 Greenhouse gas fluxes

To date, most data on GHG fluxes from tropical peatlands have been collected during daylight hours using static sampling chambers placed on the peat surface (Jauhiainen et al. 2005, 2008, 2012; Melling et al. 2005a, b; Sjögersten et al. 2011; Wright et al. 2011, 2013b). Automated sampling has not yet been widely adopted but is becoming more common (Sundari et al. 2012; Hirano et al. 2014). Measured GHG fluxes from peat swamp forests vary greatly both across the tropics (Sjögersten et al. 2014) and within sites (Wright et al. 2013b), often correlating with mean annual water table depth (Couwenberg et al. 2010).

Substantial temporal variation (diurnal and seasonal) poses a major challenge to obtaining reliable estimates of GHG emissions. Current data suggest that temporal variation exceeds the spatial variation between forest types (Wright et al. 2013b), and that there is frequently a strong correlation between GHG efflux and temporal variation in water table depth (Jauhiainen et al. 2005; Hirano et al. 2009, 2014; Sundari et al. 2012). Long-term data (e.g. over more than a year) obtained at regular (e.g. monthly) intervals are scarce, so the magnitude of intra- and inter-annual variation in fluxes is unclear. Strong diurnal variation in CO_2 and CH_4 efflux (e.g. Hirano et al, 2009; Wright et al. 2013b; Hoyos 2014) means that measurements intended for estimating net GHG fluxes need to include measurements at 2–4 hourly intervals or better. The effect of weather (e.g. rainfall events) and seasonality (e.g. dry/wet season contrasts) on GHG emissions, and the importance of ebullition in methane emission, also remain to be thoroughly investigated. Automated samplers capable of frequent (sub-hourly) measurements over long periods (many months; e.g. Goodrich et al. 2011) can help to resolve these issues.

Alternatively, the eddy-flux correlation approach can be used to acquire gas flux data with high temporal resolution, spatially integrated over hundreds of metres. Eddy-flux systems are currently under-used in tropical peatlands, with data presently only available from sites in Narathiwat Province, Thailand (Suzuki et al. 1999) and Kalimantan, Indonesia (Hirano et al. 2009, 2012). Additional systems will shortly become operational in Brunei, Sarawak (Malaysia), and Peru.

Additional uncertainty in estimates of peat decay rate arise because most CO_2 flux data from tropical peatlands do not separate autotrophic (from roots) and heterotrophic respiration (from decomposing peat) which makes it difficult to use peat surface measurements of GHGs to assess peat decay rates (Page et al. 2011a). In plantations with regularly spaced trees and little ground cover, attempts have been made to distinguish between soil and root respiration by measuring CO_2 release within and between rows of trees (Jauhiainen et al. 2012). Alternative approaches to separating autotrophic and heterotrophic respiration are (i) to compare the CO_2 release from buried mesh collars which restrict in-growth of roots, with collars which allow roots to grow in (Nottingham et al. 2011), or (ii) using a trenching approach (Mäkiränta et al. 2008), which involves isolating a patch of ground from root influences by cutting/digging through the roots around the plot (Mäkiränta et al. 2008), although this may affect the peat moisture status in trenched plots, with implications for CO_2 fluxes.

A further uncertainty regarding net GHG emissions is related to the pathway for CH_4 emissions through tree stems, which a study by Pangala et al. (2013) at a peatland in Borneo found to account for a very large proportion (62–87%) of ecosystem CH_4 emissions. The extent to which this pathway is generally important needs to be established by comparable studies at other sites.

4 Waterborne carbon fluxes

Waterborne carbon fluxes (DOC and POC) from tropical peatlands represent a major source of uncertainty in their overall carbon balance. In temperate peatlands, waterborne carbon typically accounts for c. 10% of total carbon export (Limpens et al. 2008). In the few studies in which DOC and POC fluxes from tropical peatlands (all in Southeast Asia) have been measured (Yoshioka et al. 2002; Baum et al. 2007), they have been found to be approximately double those from temperate peatlands (IPCC 2014). Moore et al. (2011) estimated that the peat-covered part of Indonesia alone was responsible for 10% of global fluvial DOC export to the ocean. Waterborne fluxes may be especially significant in degraded peatlands where the forest vegetation has been removed and the peat has destabilised (cf. Moore et al. 2013), and in floodplain peatlands where fluvial erosion can remove large blocks of peat *en masse* during floods. Further quantification of these processes is needed.

Total export of waterborne carbon can most easily be estimated for peatlands which have a clear hydrological boundary and discrete outflows, by measuring DOC and POC concentrations in drainage streams regularly during annual or longer periods, along with the total water discharge (Billett et al. 2004; Moore et al. 2011, 2013). The achievable temporal resolution of measurements is a critical limitation. Woody tropical peats often have high saturated hydraulic conductivity in their near-surface layers, but below-ground flow is frequently insufficient to shed the large and sporadic inputs from rainfall (Kelly et al. 2013); evapotranspiration and, especially in the wet season, surface runoff play a large role in the hydrological budget. The pathway taken by water as it leaves a peatland affects its DOC and POC load. Water which is shed rapidly through surface runoff may have a low DOC concentration due to its shorter residence time, but equally, especially in degraded peatlands, rapid runoff may cause peatland erosion and carry a greater POC load. In such hydrologically dynamic peatlands, discreet pulses of DOC and POC losses may be missed unless monitoring is carried out very frequently. In a recent study, Moore et al. (2013) focused sampling effort on the peak of the dry season and wet season, taking measurements every week during these periods. For the rest of the year, they took samples every fortnight. We recommend this as a minimum sampling resolution for future studies, taking into account the difficulty of regular sampling in many tropical peatlands; where sampling can be undertaken more intensively (for example, using automated samplers) then this should be attempted. Further research on tropical peatland hydrology (e.g. Kelly et al. 2014) leading to more reliable hydrological models would also help in estimating waterborne carbon fluxes.

V Conclusions

Tropical peatland research with a focus on their role as carbon stores, sinks and sources is becoming an increasingly active field, and an important one in relation to management of the global carbon cycle. In this review we have identified many research needs, including methodological problems, and have suggested some approaches to tackling them. In our view, however, the overarching need is for a more coordinated approach to data collection and sharing. This is necessary to allow us to address the most fundamental, large-scale questions about how much peat exists in the tropics, and where it is; and about the role of tropical peatlands in the global carbon cycle, today and in the future. Our main conclusions and recommendations are as follows:

1. Tropical peatland research would benefit from a network of sites where basic measurements have been made using identical methodologies. A precedent exists in the well-organised, extensive networks of permanent tropical forest census plots (e.g. RAINFOR and AFRITRON). Where practical, methods should be compatible with those used for peatland research outside the tropics, but perhaps more importantly, they should be compatible with methods used in other tropical ecosystems (particularly *terra firme* forest), in recognition of the fact that effective management depends primarily on being able to compare the relative costs and benefits of managing peatlands and other ecosystems in the same region for carbon storage and other ecosystem services. Table 1 proposes a set of measurements which are cheap and practical to implement as part of basic site description, and which would help to build a pan-tropical dataset that would put regional and global estimates of tropical peatland carbon stocks and fluxes on a firmer footing.

2. Concerted effort to focus research on particular sites, drawing on both the social and the natural sciences, has proven successful at one tropical peatland (Allen et al. 2005; Chimner and Ewel, 2005; Drew et al. 2005). We would like to see the research community continue to build on this collaborative

and interdisciplinary approach by establishing a small number of keystone sites where a rich body of knowledge can be accumulated over time. This would facilitate the testing of conceptual and numerical models of peatland processes, and would help to build long-term datasets that can be used to analyse temporal variability in peatland behaviour.

3. As in many other fields, it would be helpful if data were routinely published in full, in tabular form in papers (as supplementary data if necessary) or in appropriate data repositories such as the Carbon Dioxide Information Analysis Center (http://cdiac.ornl.gov/) or the UK Environmental Information Data Centre (http://www.ceh.ac.uk/data), in order to facilitate reanalysis and synthesis. Full publication of data is increasingly required by grant funding bodies. The fact that this so rarely happens at present suggests that mechanisms are needed to incentivise sharing of data between researchers. Again, existing networks such as RAINFOR (Malhi et al. 2002) offer precedents to follow, in terms of 'ground rules' that incentivise data sharing by guaranteeing opportunities for co-authorship of any publications that result.

4. There is, separately, a need for a community-wide data synthesis project to build a GIS-compatible database on carbon storage in tropical peatlands (and indeed, peatlands globally) that would facilitate inter-site comparisons.

5. Throughout this review we have identified research priorities which, if addressed, would improve our ability to make reliable measurements and to extrapolate from point measurements to regional and global assessments of peatland carbon stocks and fluxes. These include:

a. Studying the relationships between peat properties, the overlying vegetation, and their remote sensing signatures;
b. Developing radar/LiDAR techniques for mapping tropical peatlands and measuring AGB;
c. Investigating the use of multiple remote sensing methods in combination in mapping tropical peatlands;
d. Collaboratively developing large ground reference point datasets to support remote sensing;
e. Investigating further the potential for inferring peat thickness by GPR and remote sensing;

f. Systematically comparing different volumetric peat sampling methods;
g. Investigating the spatial and stratigraphic variation in peat DBD and carbon concentration;
h. Investigating the relative importance of different litter inputs (including coarse woody debris and roots) to peat formation/C flux;
i. Improving our understanding of the spatial and, especially, temporal variation in greenhouse gas fluxes from peatlands;
j. Investigating further the importance of vegetation (especially trees) as conduits for greenhouse gases in tropical peatlands.

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Table

Variable	**Method(s) and key references**
Location	± 10 m precision of good quality consumer-grade handheld GPS or GPS/GLONASS units is adequate.
Peat thickness	Measurement by coring or augering, taking care to define the base of the 'peat' using reproducible criteria, i.e. taking ample samples for carbon concentration and loss-on-

	ignition measurements: e.g. Parry et al. (2014).
Peat carbon concentration	Measured by elemental analysis, including samples from the full range of peat depths: Chambers et al. (2011); Chimner et al. (2014).
Peat dry bulk density	Each carbon concentration measurement should have an associated dry bulk density measurement: see Chambers et al. (2011).
Canopy height	Height of the ten tallest trees within 20 m of the core site, measured using a clinometer and tape measure, or a laser rangefinder: Phillips et al. (2009).
Vegetation composition/structure	Ideally, installation of a permanent 0.5–1 ha vegetation sampling plot following RAINFOR protocols (Malhi et al. 2002), extended where appropriate (e.g. to include small trees, shrubs and herbs where these are important, and coarse woody debris). Where this is impractical, a general description of the vegetation structure and dominant species within 20 m of the core site is sufficient for most remote sensing studies.

Table 1. A suggested protocol for site description which facilitates basic data comparison, and development/testing of remote sensing techniques for peatland mapping and characterization.

Figure captions

Figure 1. Distribution of the peat carbon pool in the tropics, based on country-scale estimates from Page et al. (2011b; dotted regions indicate no data). In Australia, the estimate refers to the state of Queensland only. Examples of lowland peatlands discussed in the text are indicated as follows: SSPS:

San San Pond Sak, Panama; PMF: Pastaza-Marañón Foreland, Peru; CC: Cuvette Centrale, Republic of Congo/Democratic Republic of Congo; TB: Tasek Bera, Malaysia; K: Kalimantan, Indonesia.

Figure 2. Vegetation classification of the Changuinola peat dome in the San San Pond Sak tropical peatland, Panama, using Landsat Thematic Mapper imagery, supported by both aerial photographs and field data as sources of reference.

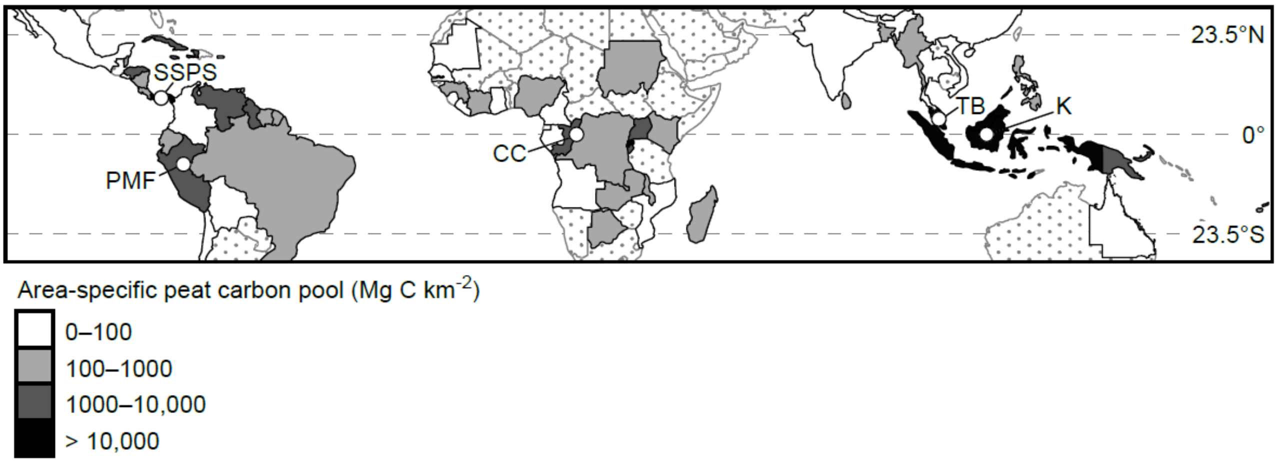
Figure 3. Dry bulk density (DBD) values from published peat sequences. The box plots show the range of the data (dashed bars) and the lower, middle and upper quartiles (horizontal lines); the width of the bars is proportional to the square root of the size of each dataset (the total number of samples is 90); outliers are shown as circles. Only data from peats with <10% ash are shown. Note that the Sebangau peatland is in Indonesia; all other peatlands are from the Peruvian Amazon. Data sources: Wüst et al. 2002, 2003; Page et al. 2004; Lähteenoja et al. 2009a; Lähteenoja and Page, 2011.

Figure 4. Dry bulk density and ash content from core SA6.5, Kalimantan, Indonesia (Page et al. 2004), illustrating stratigraphic variation in DBD values.

Figure 5. Organic carbon values from published peat sequences (references and symbols as for fig. 2). Only data from peats with <10% ash are shown. Note that all records are from the Peruvian Amazon, except Tasek Bera (Malaysia) and Sebangau (Indonesia). Data sources: Wüst et al. 2002, 2003; Page et al. 2004; Lähteenoja et al. 2009; Lähteenoja and Page, 2011.

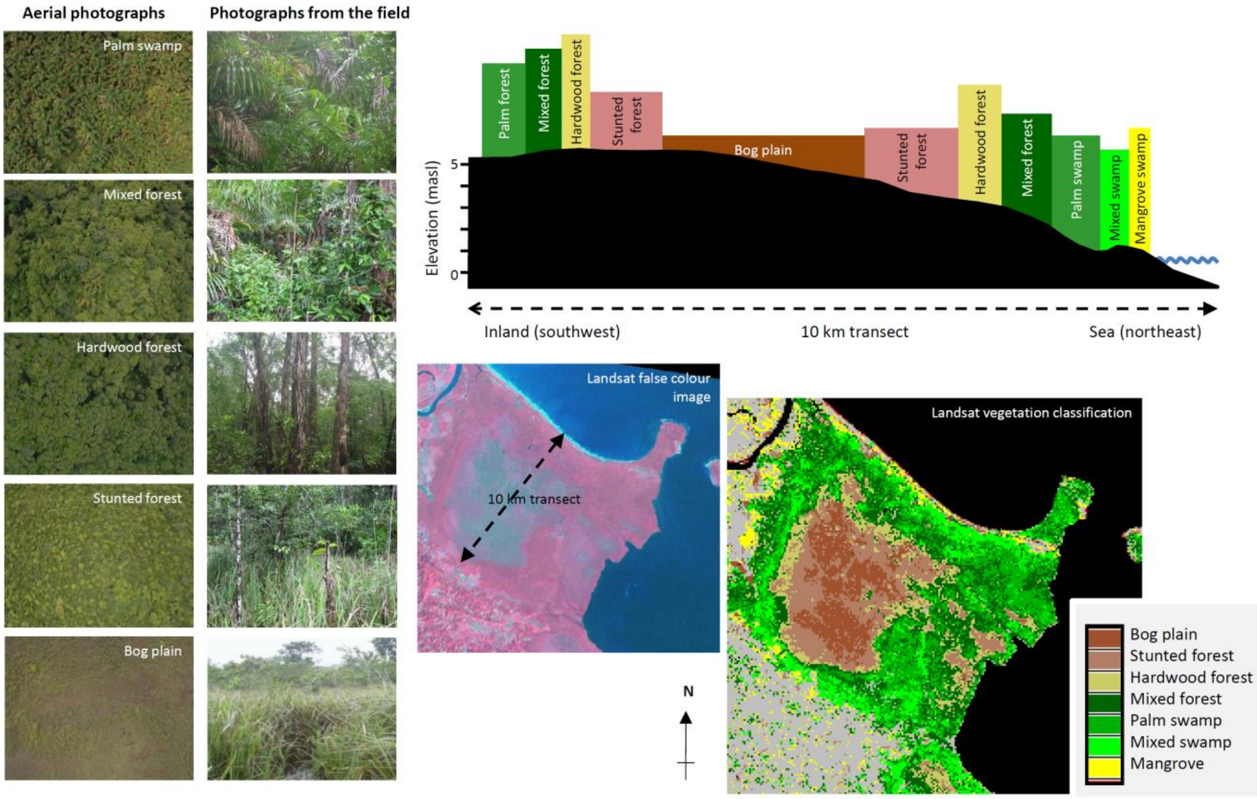
Figure 6. Carbon density measured using an elemental analyser plotted against ash content determined by loss-on-ignition (LOI) for some tropical peats. The straight line indicates the relationship used by Turunen et al. (2002) to estimate carbon content from LOI data. Only data from peats with <10% ash are shown. Data sources: Wüst et al. 2002, 2003; Page et al. 2004; Lähteenoja et al. 2009a; Lähteenoja and Page, 2011.

Fig. 1



23.5°N
0°
23.5°S
SSPS
PMF
CC
TB
K
Area-specific peat carbon pool (Mg C km^{-2})
0–100
100–1000
1000–10,000
> 10,000

1069 Fig. 2



1070

1071

Fig. 3

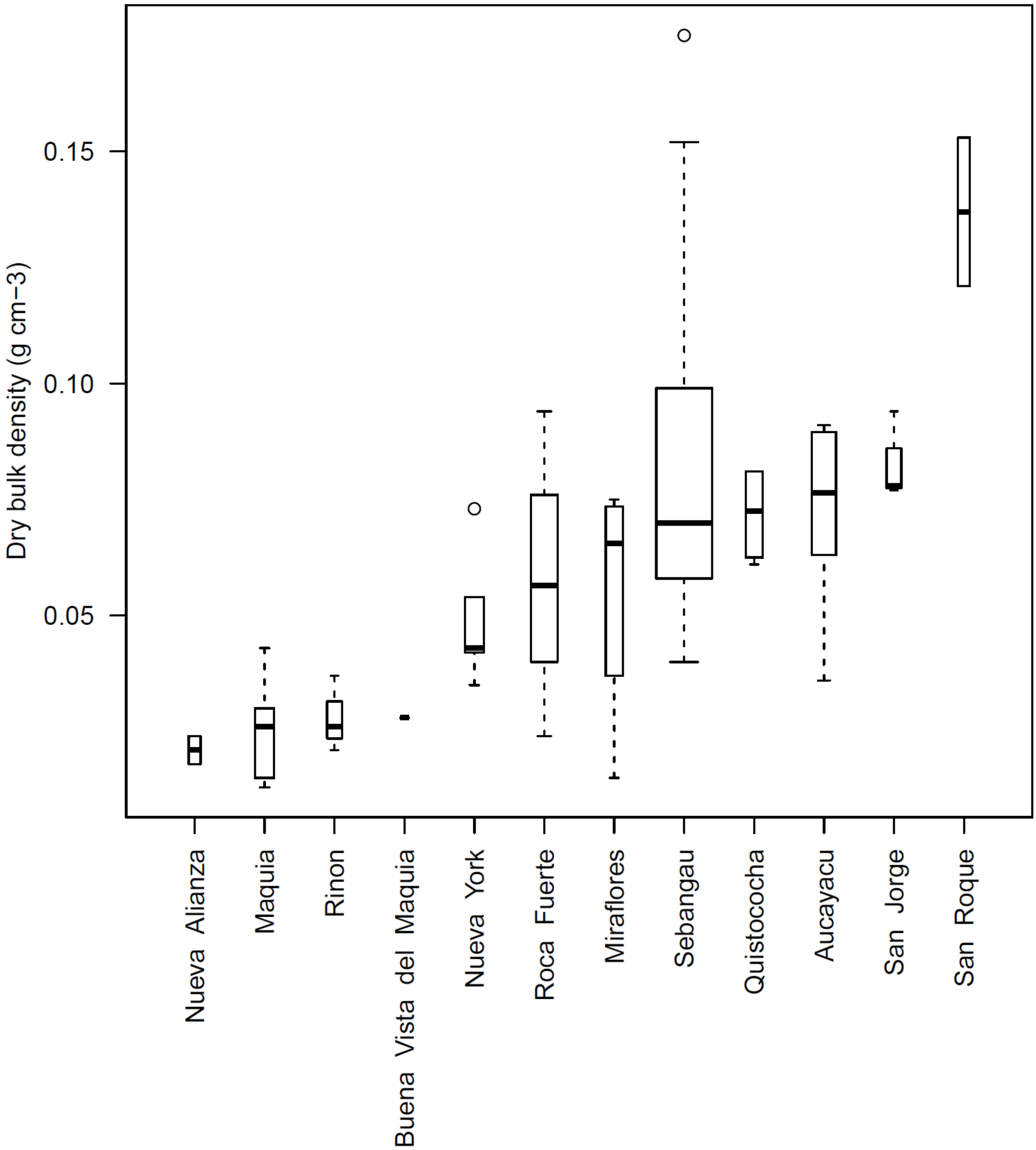
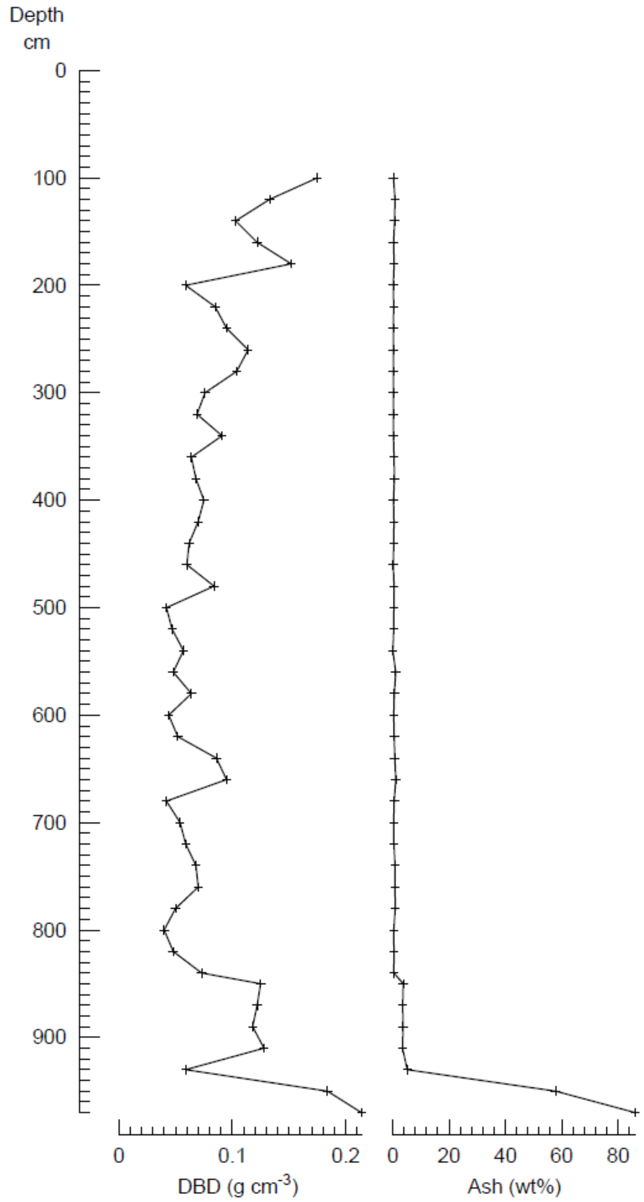
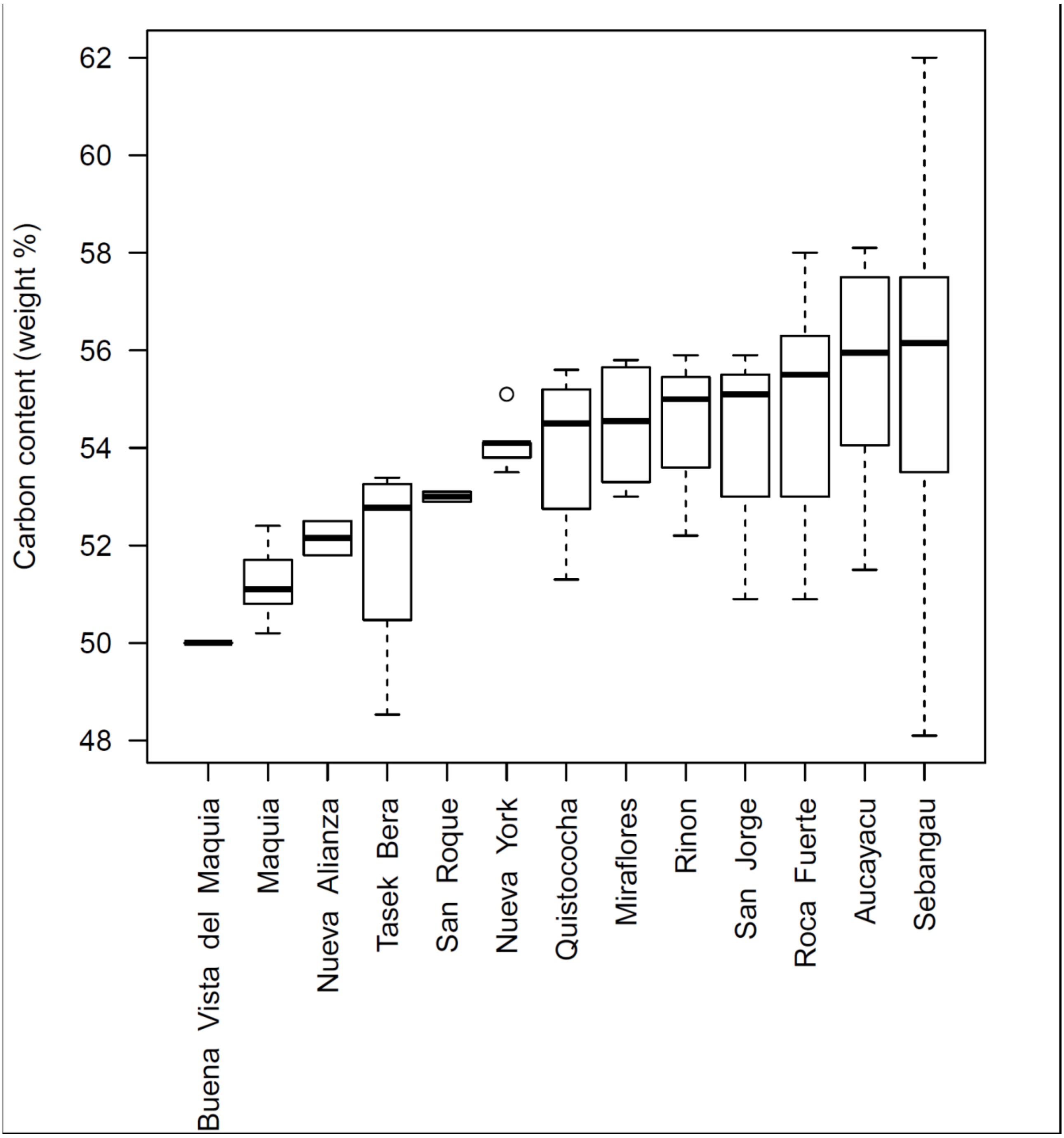

Dry bulk density (g cm−3)
0.05
0.10
0.15
Nueva Alianza
Maquia
Rinon
Buena Vista del Maquia
Nueva York
Roca Fuerte
Miraflores
Sebangau
Quistococha
Aucayacu
San Jorge
San Roque

Fig. 4

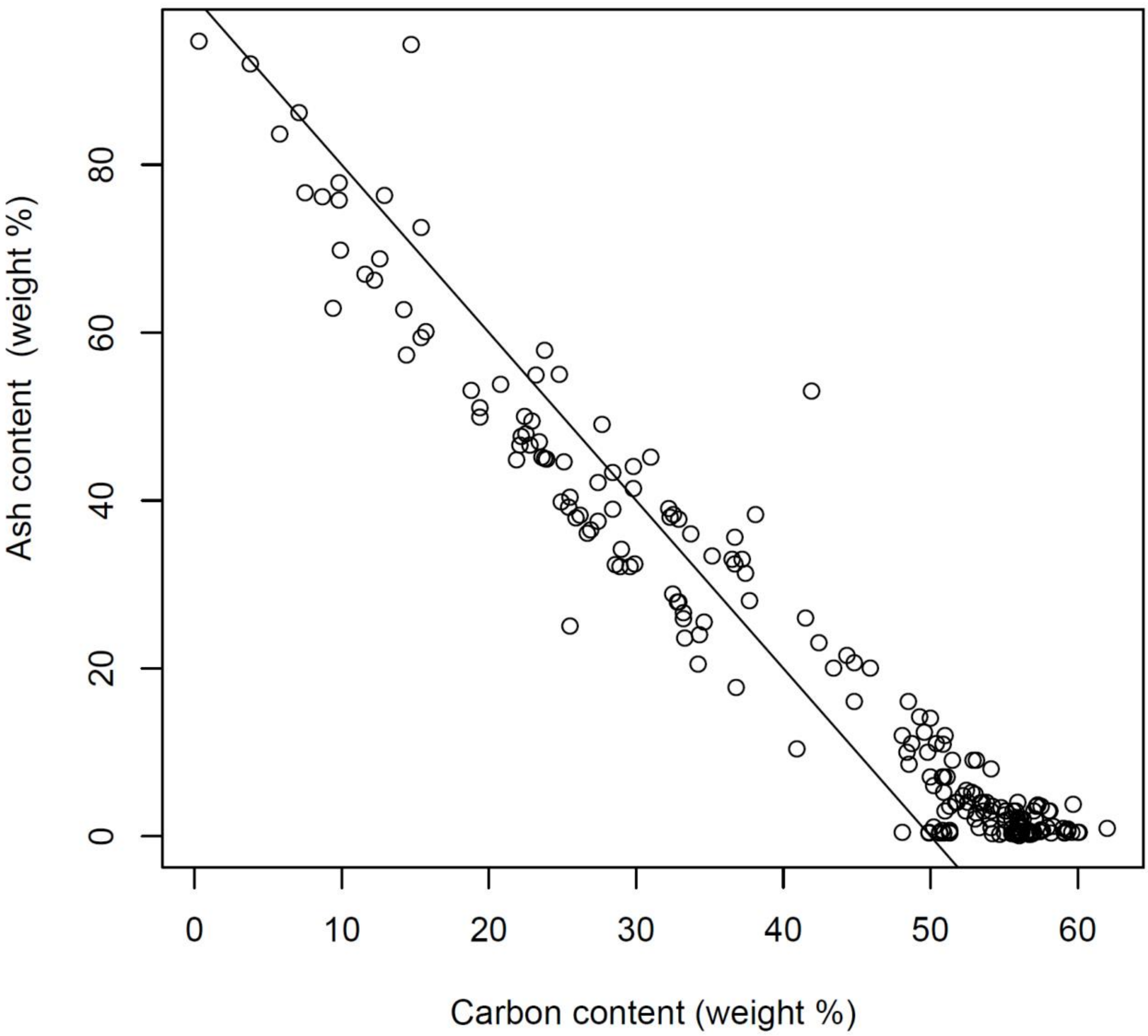


Depth
cm
0
100
200
300
400
500
600
700
800
900
0
0.1
0.2
DBD (g cm-3)
0
20
40
60
80
Ash (wt%)

Fig. 5


Carbon content (weight %)
62
60
58
56
54
52
50
48
Buena Vista del Maquia
Maquia
Nueva Alianza
Tasek Bera
San Roque
Nueva York
Quistococha
Miraflores
Rinon
San Jorge
Roca Fuerte
Aucayacu
Sebangau

1081 Fig. 6



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