

Effects of Climate Change on the Potential Species Richness of Mesoamerican Forests

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ABSTRACT

The realized species richness of tropical forests cannot yet be reliably mapped at a regional scale due to lack of systematically collected data. An estimate of the potential species richness (PSR), however, can be produced through the use of species distribution modelling. PSR is interpretable as a climatically determined upper limit to observed species richness. We mapped current PSR and future PSR under climate change scenarios for Mesoamerica by combining the spatial distributions of 2000 tree species as predicted by generalized additive models built from herbaria records and climate layers. An explanatory regression tree was used to extract conditional rules describing the relationship between PSR and climate. The results were summarized by country, ecoregion and protected area status in order to investigate current and possible future variability in PSR in the context of regional biodiversity conservation. Length of the dry season was found to be the key determinant of PSR. Protected areas were found to have higher median PSR values than unprotected areas in most of the countries within the study area. Areas with exceptionally high PSR, however, remain unprotected throughout the region. Neither changes in realized species richness nor extinctions will necessarily follow changes in modelled PSR under climate change. However model output suggests that an increase in temperature of around 3°C, combined with a 20 percent decrease in rainfall could lead to a widespread reduction of around 15 percent of current PSR, with values of up to 40 percent in some moist lower montane tropical forests. The modelled PSR of dry forest ecoregions was found to be relatively stable. Some cooler upper montane forests in northern Mesoamerica, where few species of tropical origin are currently found, may gain PSR if species are free to migrate.

Key words: ecoregion; Mesoamerica; natural protected areas; regression tree; species distribution modelling; tree species richness; tropical forests.

IT IS NOW WIDELY ACKNOWLEDGED THAT ANTHROPOGENIC CLIMATE CHANGE HAS HAD A SIGNIFICANT IMPACT on global biodiversity in recent decades, and that these effects are likely to intensify in the future (MEA 2005, Lovejoy & Hannah 2006, Rosenzweig *et al.* 2007). Recent reviews of such impacts have revealed consistent responses to warming trends in terrestrial species, including poleward and elevational range shifts of flora and fauna, phenological changes, changing migration patterns and lengthening of the growing season (Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003, Parmesan 2006, Rosenzweig *et al.* 2007, Cheung *et al.* 2009). In addition to altered distribution patterns, some species have declined in abundance, leading to fears that climate change could result in the widespread decline and loss of species (Thomas *et al.* 2004, Deutsch *et al.* 2008). Species turnover and migration are generally accepted as likely responses, leading to the development of novel communities (Keith *et al.* 2009). The extent to which climate change will lead to extinction, however, has been controversial (Thuiller *et al.* 2004, Willis & Bhagwat 2009). For example, Hole *et al.* (2009) recently modelled the potential changes in distribution of sub-Saharan Africa's breeding bird fauna, and found that

persistence of suitable climate space across a network of protected areas was remarkably high, with 88–92 percent of species retaining suitable climate space within the network.

Conflicting evidence regarding the potential impacts of climate change on biodiversity may reflect inadequacies in either the data or the modelling approaches used (Thuiller *et al.* 2008, Willis & Bhagwat 2009). Forecasting the potential impacts of climate change on areas of high species richness represents a particular challenge due to the need for accurate data for large numbers of species. Speciose regions, such as tropical forest biomes, are at high risk of biodiversity loss as a result of climate change (Huntingford *et al.* 2008). Coincidentally, it is these same regions where information regarding the distribution and ecological characteristics of individual species is most often lacking (Cayuela *et al.* 2009). In such circumstances, modelling approaches that are relatively undemanding in terms of data requirements may be preferred. Niche-theory models are simplistic, as they incorporate no demographic information. They have the advantage, however, of allowing the modelling of numerous individual species simultaneously, enabling the impacts of climate change on species richness to be explored (Thuiller *et al.* 2008). Studies that have combined the results of species distribution modelling for large numbers of species include analyses of 1350 plant species in Europe (Thuiller

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et al. 2005), 108 reptile and amphibian species in Europe (Araújo *et al.* 2006), 122 tree species in Europe (Thuiller *et al.* 2006), 975 endemic species in southern Africa (Broennimann *et al.* 2006), 330 species of Proteaceae in South Africa (Midgley *et al.* 2002), 176 amphibian species in Mexico (Ochoa-Ochoa *et al.* 2009), 285 bird and 114 mammal species in northeastern Mexico (Ortega-Huerta & Peterson 2004), 354 bird species in central Mexico (Lira-Noriega *et al.* 2007), 35 large-bodied mammal and bird species in the Mexican Yucatán peninsula (Urquiza-Haas *et al.* 2009), and 300 species of Mexican tropical trees (Pennington & Sarukhán 2005). The spatial patterns of diversity that have been produced have been used for setting conservation priorities in Mexico (Ortega-Huerta & Peterson 2004), for modelling β diversity at the watershed scale (Lira-Noriega *et al.* 2007) and as input for GAP analysis (Urquiza-Haas *et al.* 2009). To date, however, no published study has combined models of tree species over the entire Mesoamerican region with the aim of comparing potential richness with respect to large scale climatic variability.

Tropical tree species diversity correlates with both net ecosystem productivity and other measures of biological diversity such as bird and insect species richness (Acevedo & Currie 2003, Hurlbert & Haskell 2003, Seto *et al.* 2004, Simmons *et al.* 2004). This makes tree species richness a particularly important indicator of overall conservation value. Although species richness of a few well studied forest plots has been accurately documented, systematic regional survey data are not available from tropical regions such as Mesoamerica. Studies on the distribution of tropical tree species therefore rely on data from museum collections and herbaria (Barry & Elith 2006, Elith & Leathwick 2007). The paucity of systematically collected data (Feeley & Silman 2011) prevents the reliable mapping of true, realized species richness of tropical trees at a regional scale. Computer algorithms that produce predictive species distribution models (SDM) are therefore needed in order to map distributions (Engler *et al.* 2004, Broennimann *et al.* 2006, Stockwell *et al.* 2006, Thuiller *et al.* 2008). The interpretation of the output of SDMs when data shortages prevent truly independent validation, requires considerable care and discretion. In particular the difference between potential and realized distributions must be made explicit. Both traditional climate envelope based approaches and the numerous contemporary variations that use algorithms to fit SDMs using climatic variables as input lead to maps of potential, not realized distributions. The result of combining the potential distribution maps for multiple species can therefore be defined as potential species richness (PSR). For any grid square or pixel, the climatically determined PSR represents the total number of species that have been found within an area with a similar climate to that of the focal pixel. PSR is interpretable as a climatically determined upper limit for observed species richness. A species list based on an inventory of any particular site would consist of a subset of this climatically determined potential species pool. PSR therefore has a simple interpretation that is derived from the model output. Despite this, we are unaware of previous studies in which PSR is defined and interpreted as a response variable, although the term modelled species richness has been used. We prefer the use of the term

potential species richness as it has an explicit link to ecological theory. In effect PSR is a measure of climatically determined gamma diversity.

The aim of the current study was to map the PSR of tree species using available data on known species occurrence and current and future climate. Models were used to address the following specific questions: (1) How is the variability in PSR distributed between countries and ecoregions at a regional scale? (2) Does the current network of recognized protected areas adequately cover areas with currently high values of PSR? (3) Which features of the current climate are most closely associated with high PSR; and (4) How will the spatial distribution of PSR be affected by climate change over the next century assuming that (a) species are free to migrate to new areas of suitable climate, and (b) species cannot migrate to areas with a suitable climate.

METHODS

STUDY SITE.—Mesoamerica is one of the world's major centres of plant diversity (Davis & Heywood 1995, Raedig *et al.* 2010) and is of global conservation importance (Myers *et al.* 2000, Olson *et al.* 2001, Myers 2003). Conservation of this diversity through linked regional networks of protected areas has been identified as a high priority (Bennett 2004). The species diversity of the region is threatened by land use change and the effects of anthropogenic climate change (Peterson *et al.* 2002). A reliable map of realized tree species diversity that covers the entire Mesoamerican region is not currently available. Because of extensive anthropogenic forest disturbance throughout the region it may be assumed that realized species richness is most likely to be attained within the network of protected areas. It can also be assumed that if protection from anthropogenic disturbance as a result of protected status is effective, climate change will become the most important long-term threat to species richness within protected areas. We restricted our study to the region comprising the Central American countries and the area of southern Mexico below 21.5° N. The area was chosen in order as lying below the tropic of cancer (23.5° N) and included the entire Yucatan peninsula and the Mexican states of Chiapas, Tabasco, Oaxaca, Veracruz, Guerrero and Jalisco. Some high elevation areas of central Mexico were included in this area. Although these high elevation areas have been described as having a temperate, rather than tropical climate the validity of purely temperature driven phenology models has been found to terminate at 30° N, well above the cut off latitude of this study (Borchert *et al.* 2005). Annual mean monthly temperature range is much lower than is typical for temperate forests. For the purposes of the study we therefore regarded these forests as tropical montane forests, although they may have current species composition of mainly temperate origin.

BIOLOGICAL DATA.—Presence-only data were obtained for 2995 species of Mesoamerican trees and shrubs from the Missouri Botanical Garden (MOBOT) VAST database (MOBOT 2009, available at: <http://www.mobot.org/>). Free-standing woody species with maximum diameter at breast height above 5 cm were

selected for downloading from the data base using the criteria of known occurrence in well-sampled study sites spread across the region from Veracruz in Mexico to Panama. Only specimens with recorded geographical coordinates were used. Records that had clearly been rounded to the nearest degree were discarded. Elevational range was investigated for all species. Points more than three standard deviations from the mean elevation were discarded. We used species with a minimum number of occurrence points of eight. This resulted in the retention of 2000 species. The maximum number of occurrence points per species was 1239 (*Casearia sylvestris*). The total number of records for all species used was 131,780.

CLIMATE DATA.—Climate data were derived from the WorldClim data set (Hijmans *et al.* 2005). After analysis of co-linearity using principal component analysis (PCA), we selected seven original and derived variables based on the criteria of orthogonal properties through reference to the rotated PCA weightings and biological interpretability. These variables differed slightly from the derived BIOCLIM variables provided with the data set and were designed to capture the key elements of regional climatic variability: (i) maximum temperature in June (tmax6); (ii) minimum temperature in January (tmin1); (iii) the difference between the maximum monthly maximum temperature and the minimum monthly minimum temperature (AMTD); (iv) the maximum difference between maximum and minimum temperature for any single month (DMTD); (v) mean monthly precipitation in January (prec1); (vi) mean monthly precipitation in June (prec6); (vii) number of months with over 100 mm precipitation (GM). The layers were resampled to a 3 arc second grid through nearest neighbor resampling.

PREDICTING AND INTERPRETING PSR.—In order to determine potential species richness we ran generalized additive models (GAM), recursive partitioning (rpart), random forests and neural nets using the R statistical environment (R Development Core Team 2010). We also used the program Maxent (Phillips *et al.* 2006) which we integrated with R through a customized script. Initial trials with a subset of 200 species showed that the predictions from Maxent, random forests and GAMs using identical input were highly correlated with each other (mean $R^2 > 0.94$). Given that predictions of potential distribution are not directly testable, even with truly independent data, we decided to apply a single modelling method in order to simplify interpretation. We therefore report results from GAMs with pseudo-absences derived from a sample of 5000 background pixels using the 'gam' package (Hastie 2008). The degree of smoothness was selected by cross validation. A stepwise procedure was used to select the most parsimonious model using the Akaike information criterion (AIC). A similar technique has been found to be the most effective means of optimizing predictions of distributional change for European plants (Thuiller *et al.* 2005). Receiver operator characteristics were calculated and visualized using the 'PresenceAbsence' package (Freeman 2007). This allowed us to evaluate the ability of the model to discriminate between back-

ground pixels with no records of the species and pixels where the species was found using area under the curve (AUC) analysis. For the purposes of this study, we relied on a measure of discrimination using a subset of the original data rather than independent validation. Such a measure is sensitive to the relative area of the species distribution with respect to the study area. Although the AUC suggested good (>0.8) to excellent (>0.95) discrimination for all of the species modelled, these values should not be interpreted in terms of a model true predictive power. The predictive power of models of realized distribution can only be fully established through the use of inventory data with confirmed absences, which are incomplete for the tree species modelled here. Formal validation of potential distribution is still more challenging and will usually require experimental techniques. In order to produce binary maps, we required a consistent threshold value (Jiménez-Valverde & Lobo 2007). The AUC is often used as a criteria to set thresholds. However when modelling relies on pseudo-absences, specificity is based on the 'correct' prediction of pseudo-absence, rather than true absence. This leads to inflated AUC values for species with narrow distributions (Lobo *et al.* 2008). We therefore discounted specificity when setting the threshold and used only the measure of sensitivity, which we set at 0.8 for all species. This conservative, sensitivity based threshold, was chosen in order to prevent outliers that may have arisen as a result of coordinate imprecision unduly affecting the distribution maps. All 2000 binary maps were summed at the pixel level in order to calculate the total PSR for the climatic conditions at each pixel.

In order to interpret the relationship between climate and PSR, we fitted a recursive partitioning model to the combined output of the 2000 individual species models. This used the same climatic variables as were used for fitting the 2000 individual species models.

PSR UNDER CLIMATE CHANGE SCENARIOS.—Global circulation model (GCM) outputs were downloaded from the World Database for climate model data (WDCC 2009) and analyzed using climate data operators (CDO 2009). The downscaled climate scenarios were used as input when fitting models for each species. GCMs suggest increased temperatures for the region ranging from 2 to 6°C by the end of the century and a reduction of up to 20 percent in annual rainfall, depending on the scenario chosen. There is more variability between GCMs in predictions of changes in rainfall patterns than temperature. We used climate change scenarios based on an analysis of the results of the HADCM2 global circulation model using the IPCC SRES A2 and B2 scenarios for the years up to 2100. We found a strong linear correlation between the pattern of change produced for the two scenarios ($R^2 = 0.95$). For brevity, here we only reported the results from the A2 scenario. This may be viewed as a 'worst case' scenario with the greatest change in climate setting an upper limit of credible change. The results from other scenarios lie between this upper limit and the present value.

We then used the fitted models for each species to predict PSR under climate change scenarios. Under a 'complete migra-

tion' scenario the results of individual models using altered climatic variables as input were summed as for the present climate model. A 'no migration' scenario was produced by summing over the pixels in which the species was predicted to be present in both time intervals. To evaluate the percentage of species lost by pixel, we summed the predicted number of species lost by pixel and divided by the predicted current species richness. The procedure was also used to assess the percentage of species gained by pixel. Gain can only occur under the assumption of migration.

PSR CHANGE.—Pixels were classified by country, ecoregion (Olson *et al.* 2001) and protected status. Protected areas with known IUCN status were downloaded from the World Database of protected areas (WDPA 2009). We presented the results as boxplots conditioned on combinations of classifications by country, ecoregion and protected status in order to show both the median PSR and the variability of PSR in each section of the map. All the analyses were performed with the R environment for statistical computing (R Development Team 2010).

RESULTS

The overall pattern of PSRs under the current climate shows a pronounced a north-south gradient in tree species richness (Fig. 1). Potential climatically associated tree species richness was found to reach peak values of 1100 species (drawn from the total of 2000 that were included in the study) in Panama. PSR values declined toward the north, although considerable local variability was also shown.

Forest ecoregions with the highest PSR occur in the southern part of the study area, where the warm lowlands are both moist and aseasonal (Fig. 2). Cooler, moist, montane ecoregions were found to have higher PSR than nearby dry, warm ecoregions. In the northern area most of the lowland ecoregions have pronounced seasonal rainfall and a greater annual temperature range. Northern lowland forests can support notably fewer

species of trees than either southern lowland forests or northern lower montane forests. The largest area with continuous forest cover in southern Mexico occurs in the Yucatan peninsula. The PSR for these forests, with highly seasonal rainfall, was found to be comparatively low. PSR in the northern part of the study area was found to reach its highest levels in moist lower montane forest ecoregions.

When PSR was analyzed by country and protected status, southern Mexico was found to have the lowest median PSR both within and outside the protected area network (Fig. S1). The results showed considerable variability, however, across the region. Exceptional areas in Mexico, Guatemala, El Salvador and Honduras have values of PSR that are comparable or even above the median value within countries further south. High tree species diversity in the more northerly part of the study range occurs in naturally fragmented areas with unusually moist and aseasonal climatic conditions. This has important implications for conservation.

Median current PSR was found to be higher within protected areas than unprotected areas in all countries, with the exception of Guatemala (Fig. S1). There is thus a clear positive association between tree species diversity and the selection of areas for protected status. However the overlap in the variability of PSR within protected areas and outside showed that a large proportion of the region with potentially high tree species richness remains unprotected (Fig. 1. and Fig. S1). El Salvador was found to have the highest discrimination between protected and unprotected areas. This result can be attributed to the small size of the country and the limited area under formal protection according to the WCMC/IUCN data base. In the cases of southern Mexico and Guatemala, the highest tree species diversity is predicted for moist montane forests that currently fall outside formally protected areas.

Nonlinear interactions between rainfall and moisture were distinguishable as determinants of tree species richness by the recursive partitioning analysis (Fig. S2). A key cut-off point was identified when the number of months with over 100 mm rainfall

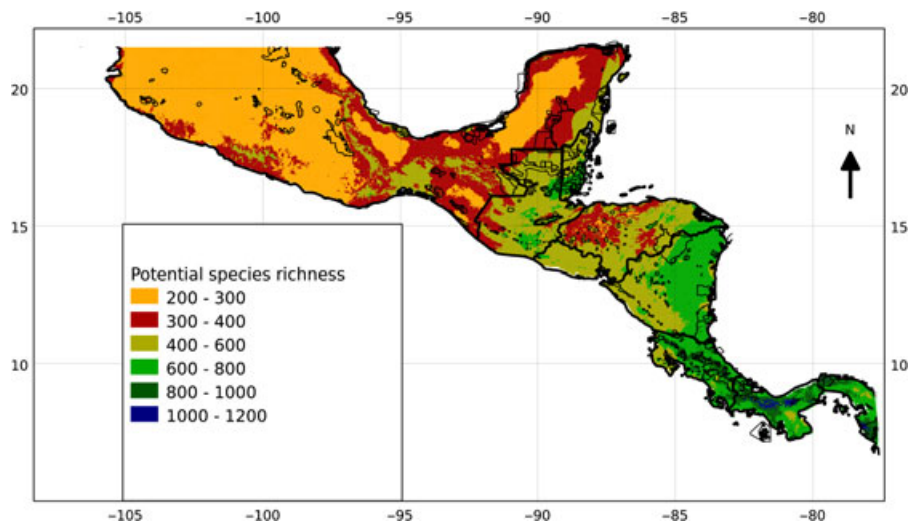


FIGURE 1. Spatial pattern of potential tree species richness over the study area. Values range from 259 to 1150 species.

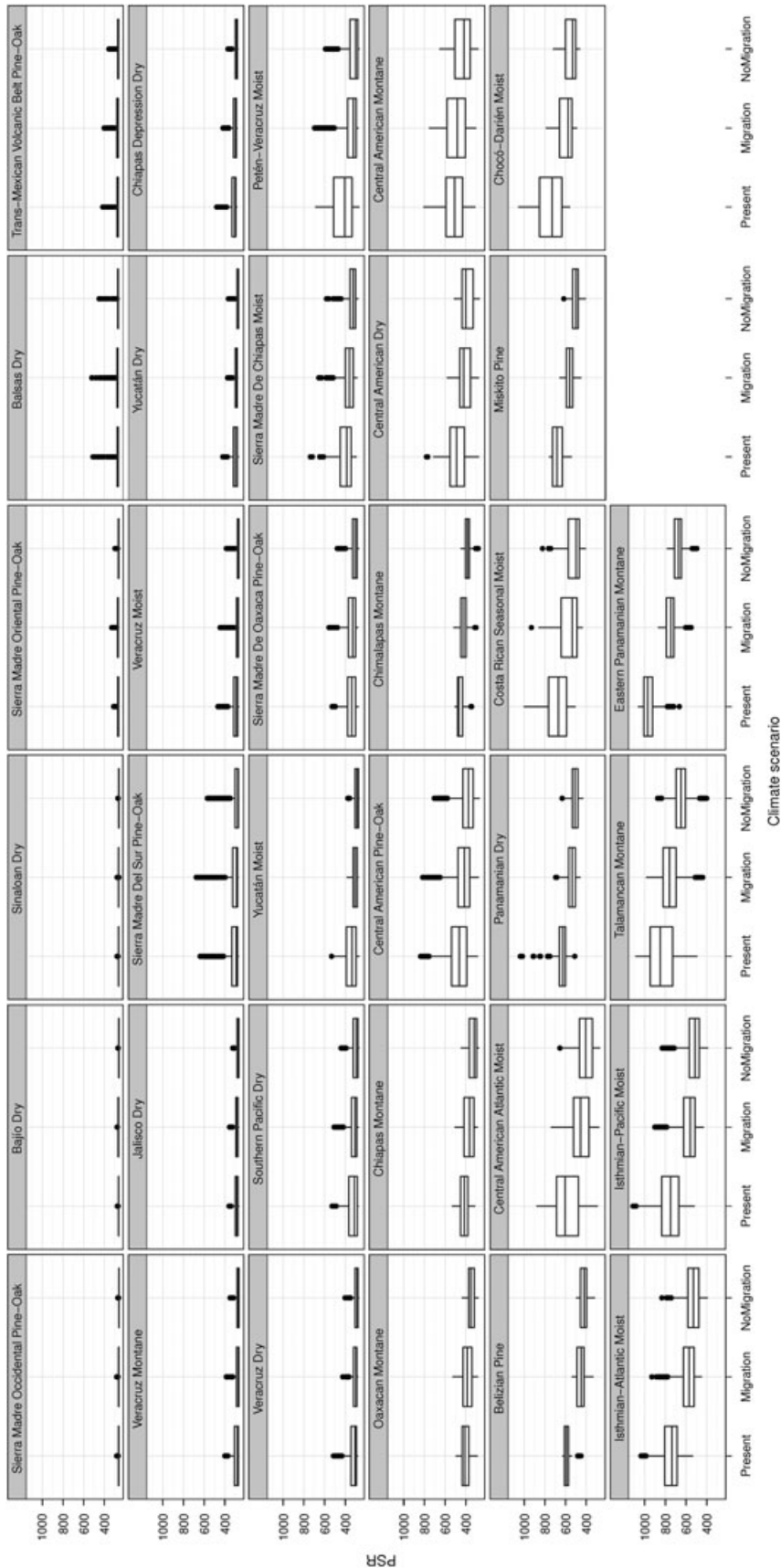


FIGURE 2. Conditional boxplots of current and projected potential tree species richness (PSR) by forest ecoregion. The panels are ordered from lowest current median PSR (top left) through to highest current PSR (bottom right). Migration and no-migration PSR is based on downscaled HADA2 GCM scenario, suggesting an increase in temperature of around 3°C and a decrease of rainfall of around 20 percent.

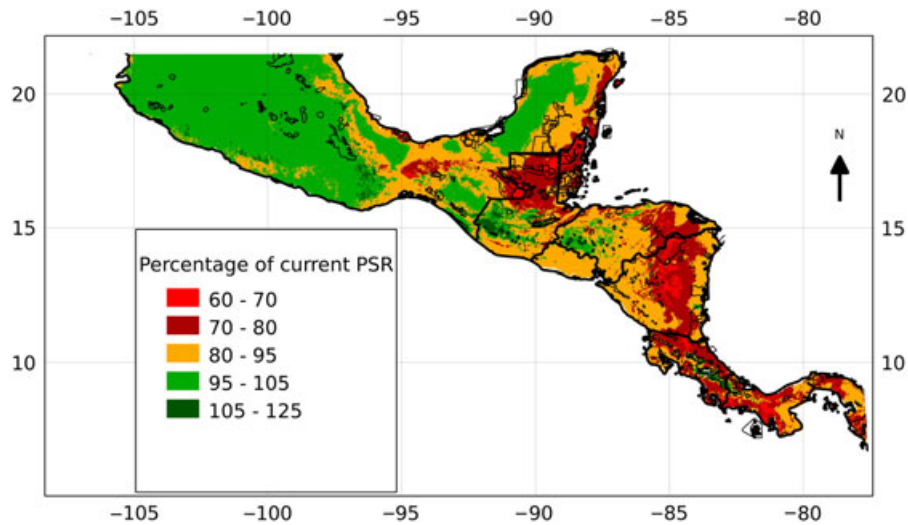


FIGURE 3. Predicted changes in tree species diversity by 2100 under the HADA2 scenario assuming migration. Values are the percentage of current potential species richness.

falls below six. In these drier conditions a rise in temperature results in lower predicted tree species richness. When the number of months with rainfall above 100 mm are greater than eight (aseasonal rainfall), potential species richness increases when minimum temperatures are over 15°C. Nevertheless the PSR under these conditions also increases if maximum temperatures in June are low. Thus, in general terms, narrow annual temperature range and aseasonal rainfall are associated with the highest values of PSR.

Areas with high current values of PSR were predicted to suffer a higher proportional reduction in PSR under climate change than areas with lower current PSR (Fig. S3). This result may be explained through reference to the recursive partitioning model (Fig. S2). A small change in the maximum temperature in June for areas with relatively aseasonal rainfall is associated with a large change in species richness. An interesting spatial pattern emerges when change in PSR assuming migration is analyzed (Fig. 3). This shows that the northerly part of the study area could potentially gain species under climate change if species are free to migrate. Nevertheless, most moist montane cloud forests would experience major losses in PSR throughout the study region as a result of a decrease in rainfall.

Extensive areas with particularly high PSR that are still not formally protected include the northern highlands of Chiapas and the comparatively cool and moist 'cañadas' between the highlands and the Lacandon, the Chimalapas region and the cloud forests of Oaxaca, Veracruz and Guerrero in Mexico. Although these areas retain relatively intact forest cover, these unprotected areas may be amongst the most vulnerable to species loss through climate change if rainfall is reduced.

DISCUSSION

There are some caveats that must be considered when interpreting these results. The intrinsic limitations of all methods based on associative species distribution models are very well

documented (Jiménez-Valverde *et al.* 2008, Lobo *et al.* 2008, Pineda & Lobo 2009). This study was explicitly limited by properties of the available data. Reliable distribution models cannot be produced for rare species with few occurrence points (Papes & Gaubert 2007) and we did not attempt to do so. The challenges involved are documented and discussed in detail with reference to this data set by Cayuela *et al.* (2009). We chose AUC as the best available tool to describe the discriminatory ability of the models, even though this approach has known weaknesses (Lobo *et al.* 2008). In particular, the restricted geographical distribution of some species within a large study region will have resulted in very high AUC values which have been inflated as a result of correctly predicting absence outside a species true climatic envelope (Lobo *et al.* 2008). AUC values should be interpreted in their specific context and cannot be compared directly across studies. One of the key limitations in any study of tropical forests is the shortage of independent data that may establish the known absences that are required to formally validate the predictive ability of models (Feeley & Silman 2011). Because of data limitations some of the potential distributions predicted for individual species will have inevitable errors. In our context, we expect GAMs with pseudo-absences to produce some unreliable predictions for species with widespread distributions as random pseudo-absences land inside the true occupied area. The realized distributions of species with narrow ranges tend to be better modelled than that of widely distributed species, although their potential climatic tolerance may remain unknown. This may lead to overfitting. Thresholds were needed in order to give the results a clear interpretation in terms of numbers of species predicted, but setting thresholds involves applying some arbitrary criteria. However, our aim was to trace robust spatial patterns in PSR rather than accurately map realized distributions for each species. As the results from 2000 separate models were combined, individual errors will tend to even out, thus making the pooled result more robust than any of the individual models taken separately. Species turn-

over along an environmental gradient (β diversity) is not explicitly shown by the results here. Nonetheless, further exploration of such patterns would help contribute to the evaluation of alternative protection systems (Lira-Noriega *et al.* 2007).

The study provides an additional confirmation of the extremely high conservation value of moist tropical forests in general and moist lower montane forests in particular. The strong association between rainfall and species richness matches that reported at a global level (Francis & Currie 2003) and at a local level within the study region (González-Espinosa *et al.* 2004, Golicher *et al.* 2008). Climate change will not only alter the spatial distribution of current climate types, but will also introduce novel climatic regimes (McMahon *et al.* 2009). The rate of change could possibly exceed the potential of biota to migrate and change their geographic range. Under scenarios in which species are free to migrate to areas that match their climatic preferences, overall species richness might be expected to remain unchanged. In fact the models show a widespread decline in species richness even given this unrealistic assumption. This occurs as a result of the concentration of tree species richness in a comparatively small fraction of the total area.

The finding that species diversity is highest where seasonal variation in rainfall and temperature is lowest provides further support for the theory that biological diversity is favored by stable climatic conditions (Huston 1979, Huston & Wolverton 2009). Biogeographical effects and historical contingency may also have played a role. In the more northerly area of the study region montane forests are composed mainly of genera of temperate origins, such as *Abies*, *Pinus*, and *Quercus* species. They currently share few species with the truly tropical forests found in the lowlands and southern montane forests. The pool of species of temperate origin is smaller than that of tropical origin so this alone may account for the low current PSR. The southern area of the study region may have been enriched through biotic interchange with South America. The migration of tree species with origins in South America was facilitated by the formation of the isthmus of Panama around three million years BP (Burnham & Graham 1999), although the interchange of plant species may have begun earlier (Cody *et al.* 2010). Speciation has continued throughout the region during the Pleistocene (Pennington *et al.* 2004) along with several episodes of range contraction and expansion as a result of climate variability. Rapid anthropogenic climate change will pose a threat to diversity regardless of the underlying mechanism behind the current richness pattern. Species are equally likely to be lost under climate change if they are either slow to migrate or associated with previously stable climates.

Some contemporary conservation initiatives have tended to shift the focus toward avoiding extinction, rather than protecting high levels of biodiversity *per se*. This study did not attempt to quantify extinction risk as such. Extinction risks for Amazonian species have recently been calculated based on very simple assumptions regarding the relationship between rarity and geographical range (Hubbell *et al.* 2008). Such models have been criticized as not taking into account full geographical distributions, as many Amazonian species extend their range into Central

America (Feeley & Silman 2008). The same effect occurs in this study region. Many species have extended ranges that include South America. Thus it would be misleading to imply that a reduction in PSR equates directly with extinction. Change in PSR, however, is partly due to reduction in the area available to species with already reduced geographical ranges. Thus the results are suggestive regarding the magnitude of the risk of species loss, rather than directly predictive. At least 20 percent of the tree species may be threatened as a direct result of climate change alone, without taking into account effects of land use change. A more detailed assessment with an explicit focus on endemic species is needed in order to accurately quantify the threat of extinction.

The results suggest that the current network of reserves provides only partial coverage for species rich forests. A moderate amount of overlap between protected areas and regions with high potential species richness has also been reported in comparable studies in the region. For example Ochoa-Ochoa *et al.* (2009) found that most amphibian species have some proportion of their potential ecological niche distribution protected, although 20 percent are not protected at all within governmental protected areas. Shortfalls in the current pattern of protected areas are clearly identifiable in the results presented here. These are particularly apparent in southern Mexico and Guatemala. In these regions most of the pixels with highest potential species richness fall outside protected areas. In Guatemala, moist warm lower montane areas with high PSR coincide with high human population density. Although some species diversity has been retained within productive agricultural systems and in forest fragments, much of the potential diversity has already been lost in the areas where human pressure is most intense. Anthropogenic disturbance may continue even within formally protected areas throughout the region. Conversely, the amount of area under some form of protection may be underestimated in our study. UNEP-WCMC data base only includes areas that have been reported through national agencies. Forested areas in Mexico and Central America are increasingly being brought under sustainable management schemes that serve to at least partially protect species richness. There is a growing recognition of the role of indigenous and private protected areas in regional conservation (Ochoa-Ochoa *et al.* 2009). Although such areas may be of comparatively limited extent they play a vital role in promoting landscape connectivity. The human modified tropical landscape as a whole is also being increasingly seen as offering new opportunities for conservation (Chazdon *et al.* 2009). These additional conservation measures that act outside the limits of formal reserves may be particularly important mechanisms that allow tree species to migrate in the face of climate change.

The results should not be interpreted as implying that areas with high climatically associated species richness should be prioritized for conservation without taking into account other factors. In addition, it could be argued that exogenous climate change is a global threat that can not be addressed through locally acting protection. The results of this study, however, suggest both a proximate mechanism through which biodiversity loss is likely to occur and some actions that may be taken to reduce the rate of

loss. Lower rainfall and higher temperatures will tend to result in loss of species that rely on moist conditions for reproduction and survival. Anthropogenic disturbance of forests results in canopy opening that accelerates the process of change through preventing regeneration of sensitive species. However, trees are long lived organisms that may survive for many years even in areas where they can no longer reproduce. Thus extending the protection of existing forests may allow time for communities and ecosystems to adapt. Outside protected areas the moister conditions found along riparian belts and on north facing slopes may be specifically targeted for local conservation initiatives. The selection of areas with high local tree species diversity could allow the high potential species richness associated with moist climates to persist locally in suitable forest fragments under climate change. These refugia may act as nuclei for natural restoration if anthropogenic climate change is eventually slowed through appropriate action over the course of the next century.

CONCLUSIONS

Climatically determined potential species richness (PSR) can be predicted by modelling, although realized species richness remains unknown for most of the region and extinctions under climate change scenarios cannot be predicted directly using modelled projections of PSR.

The spatial pattern of PSR is complex, although a clear north–south gradient is apparent. Length of the dry season appears to be a key climatic determinant of current PSR. Non-additive interactions between rainfall and temperature also affect potential species richness.

Areas with exceptionally high PSR remain unprotected throughout the region. Model output suggests that an increase in temperature of around 3°C, combined with a 20 percent decrease in rainfall could cause a widespread reduction of around 15 percent in PSR. Change is also spatially heterogeneous with losses of up to 40 percent concentrated in moist forests with high diversity of rare species. The PSR of dry forests appears rather stable under the moderate climate change scenario. Some cooler montane forests, particularly in northern Mesoamerica, where few species of tropical origin are currently found, may gain in potential species richness if species are free to migrate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Conditional boxplots of current Potential Tree Species Richness split by country and protected status.

FIGURE S2. Rules for determining current PSR derived using recursive partitioning.

FIGURE S3. Change in PSR as a percentage of current value.

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