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Coincident scales of forest feedback on climate and conservation in a diversity hot spot

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The dynamic relationship between vegetation and climate is now widely acknowledged. Climate influences the distribution of vegetation; and through a number of feedback mechanisms vegetation affects climate. This implies that land-use changes such as deforestation will have climatic consequences. However, the spatial scales at which such feedbacks occur remain largely unknown. Here, we use a large database of precipitation and tree cover records for an area of the biodiversity-rich Atlantic forest region in south eastern Brazil to investigate the forest–rainfall feedback at a range of spatial scales from *ca* 10^1–10^4 km^2. We show that the strength of the feedback increases up to scales of at least 10^3 km^2, with the climate at a particular locality influenced by the pattern of landcover extending over a large area. Thus, smaller forest fragments, even if well protected, may suffer degradation due to the climate responding to land-use change in the surrounding area. Atlantic forest vertebrate taxa also require large areas of forest to support viable populations. Areas of forest of *ca* 10^3 km^2 would be large enough to support such populations at the same time as minimizing the risk of climatic feedbacks resulting from deforestation.

Keywords: vegetation–climate feedbacks; land-use change; Atlantic forest; vertebrates; conservation

1. INTRODUCTION

The Atlantic forest of the East coast of Brazil is the focus of considerable conservation concern due to its extraordinary levels of diversity and endemism (Harcourt & Sayer 1996; Goerck 1997; Machado & Da Fonseca 2001; Morellato & Haddad 2001) as well as the drastic reduction in its area since European settlement (figure 1). Intensive cultivation, ranching, mining and other industrial activities and urban expansion have all taken their toll (Dean 1995; Harcourt & Sayer 1996; Brannstrom & Oliveira 2000) and now probably less than 10% of the original forest remains, in thousands of fragments (Da Fonseca 1985; Harcourt & Sayer 1996; Ranta *et al.* 1998; Morellato & Haddad 2001; Oliveira-Filho & Fontes 2001). Compared to similar areas of undisturbed forest, the remaining fragments support an impoverished fauna at reduced population sizes (Chiarello 1999; Marsden *et al.* 2001). The climatic consequences of such forest fragmentation are, however, less appreciated.

It is evident that the distribution of vegetation is strongly influenced by climate (Woodward 1987); less clear is the role that changing patterns of vegetation may have upon the climate. Although the idea that vegetation feeds back to affect climate has been around for centuries (e.g. Bonan 2002; Williams 2003; Webb *et al.* in press), it received little serious scientific attention for much of the twentieth century until the emergence of studies showing, for instance, the predicted climatic consequences of complete Amazonian deforestation (e.g. Shukla *et al.* 1990). This coupling between vegetation and climate is

now firmly established, and the various biophysical and biogeochemical feedbacks between the land surface and the atmosphere which drive it have been well studied (Bonan 2002; DeFries *et al.* 2002; Moorcroft 2003). This understanding has led to predictions that land-use change will have climatic consequences (DeFries *et al.* 2002), with deforestation often leading to a regionally drier climate. Such consequences are likely to be especially detrimental in rainforest systems where many species are particularly sensitive even to small decreases in rainfall (Condit 1998). In the extreme, deforestation may significantly reduce the area over which rainforest could potentially re-establish (Hilbert *et al.* 2001) such that the habitat alteration is irreversible.

Although the potential significance of vegetation–climate feedbacks is widely recognized, the spatial scales at which these occur remain largely unknown. Yet, this question of scale is of crucial importance for conservation. For instance, a well protected forest fragment may be deemed large enough to support viable populations of species of conservation concern; yet its local climate may differ from that of a similar sized area of a larger forest, and it may be doomed to degradation as better adapted species encroach (Laurance *et al.* 2002). This concern has previously received little attention; indeed, empirical evidence even for a relationship between vegetation and climate at any scale is surprisingly scarce, particularly for the biodiversity rich tropics (Webb *et al.* in press; but see Durieux *et al.* 2003; Nair *et al.* 2003; Fisch *et al.* 2004; Machado *et al.* 2004).

We have shown elsewhere that there is a strong positive relationship between tree cover and rainfall in the Atlantic forest region (Webb *et al.* in press) which is most parsimoniously interpreted as a climatic response to forest

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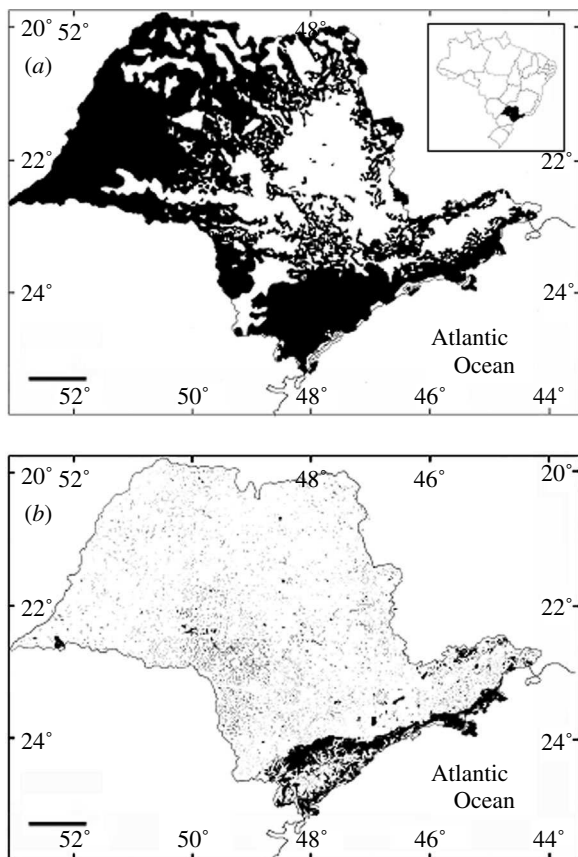
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Figure 1. Forest cover in São Paulo state in (*a*) 1907 (total coverage *ca* 145 000 km^2; redrawn from Victor 1975) and (*b*) 1993 (total coverage less than 30 000 km^2; redrawn from Instituto Florestal de São Paulo 1993). Prior to European settlement, which commenced in 1500, forest covered the majority of the state (204 500 km^2, or greater than 80% of the land area; Victor 1975). The inset in (*a*) shows the position of São Paulo state in southeast Brazil. The scale bar in each panel is 100 km.

clearance (see below). Here, we use remotely sensed data on tree cover measured at spatial scales varying from *ca* 10^1 to 10^4 km^2 surrounding each climate station in our dataset to assess the scale at which this vegetation–climate feedback is most pronounced. We compare this result with estimates of the minimum area of suitable habitat (MASH) required to support viable populations of a range of Atlantic forest vertebrate taxa, an issue that has received considerably more attention from conservation planners. MASH estimates were derived from population density estimates obtained from the literature. Comparison of these two approaches provides valuable information on the spatial scales most relevant for tropical forest conservation, both in terms of vertebrate populations and climatic stability.

2. MATERIAL AND METHODS

(a) *Study area*

We concentrate our analyses on São Paulo state, a typical Atlantic forest state covering some 250 000 km^2 in SE Brazil (figure 1). São Paulo presents an ideal (if rather depressing) system for our study because land-use change here has been essentially climate-independent: the wholesale destruction of its forest is well documented (e.g. Victor 1975; see figure 1) and clearly occurred 'with broadax and firebrand' (Dean 1995) rather than as a response to climatic change. By

considering remaining tree cover in previously forested areas (see below), we can, therefore, separate differences in land cover due to deforestation from natural, climate-driven differences. In addition, precipitation records have been collected across the state for some time. Finally, although deforestation has been extreme, substantial areas of forest (about 20% of all remaining Atlantic forest; Fundação SOS Mata Atlântica/Instituto Nacional de Pesquisas Espaciais 2002) still remain. Thus, previously forested areas which now differ substantially in forest cover exist.

(b) *Rainfall and forest cover analyses*

Precipitation records for São Paulo state processed under guidelines from the Departmento de Aguas e Energia Electica de São Paulo were provided by Mirian R. Gutajahr and Renato Tavares of the Instituto Geologico/SMA, São Paulo. Data for a given climate station in a given year were included only if they were complete (records for every day) and marked in the dataset as having been validated (i.e. checked against neighbouring stations for unusual observations). From these records we obtained estimates of annual rainfall (mm) and annual number of rain days at several hundred climate stations for as many years as possible over the period 1982–1992. We retained for analysis those climate stations for which we had at least five annual rainfall estimates during this period. We took the mean of each measure to give an estimate of annual rainfall that was more or less contemporaneous with the tree cover estimates (see below), but which was not overly influenced by unusually wet or dry years.

Measures of percentage tree cover in 1992–1993 were derived from the global land cover facility (GLCF) of the University of Maryland's Continuous Fields Tree Cover Project, which gives percentage tree cover globally at 1 km resolution. The measurement is continuous over the range 10–80% tree cover, and there are also classes for unvegetated land and open water (for a full description see DeFries *et al.* 2000). Mean tree cover for each climate station was obtained by averaging the tree cover measurements (excluding water) over 12 different scales centred on the 1 km grid square in which the station was located, from 3×3 (the minimum possible given the precision to which the location of the climate stations was known) to 97×97 km^2.

The distribution of natural vegetation over an area the size of São Paulo is likely to vary with climate, potentially confounding attempts to attribute differences in rainfall to a response to changes in tree cover. We therefore considered only climate stations that had substantial tree cover in the recent past, i.e. those that were classed as either forested or wooded in 1962 according to our digitized versions of historical vegetation cover maps (Borgonovi & Chiarini 1965; Victor 1975). In other words, we considered only sites at which a lack of trees at the time of the GLCF tree cover estimate can be attributed to a reduction in tree cover since the 1960s. The final sample size, considering only climate stations that both met the precipitation data requirement, and which were forested or wooded in 1962, was 237 (figure 2).

Since we considered only sites at which any changes in tree cover between the historical and the GLCF estimates are likely to have resulted from human activity, rather than to have been driven by changes in rainfall patterns, we designate rainfall as the response variable and tree cover as a predictor in our models (see also §4). Of course, even considering only sites that were climatically suitable for forest growth in the
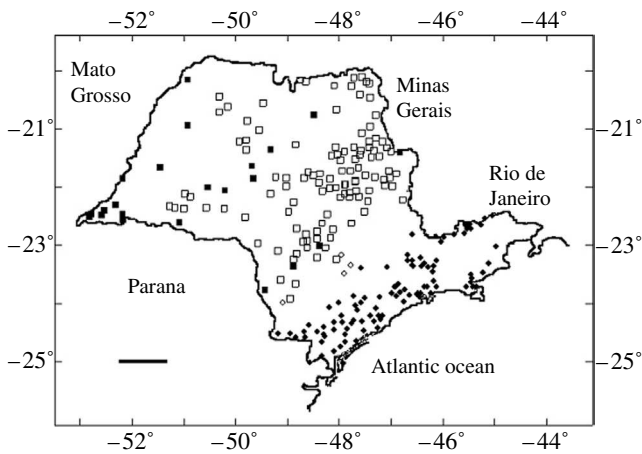
Figure 2. Locations within São Paulo state of the 237 climate stations used in this study. Filled symbols are those stations classed as forested in 1962, open symbols are stations that were wooded in 1962. Diamonds represent stations falling broadly into the coastal, mountainous region, squares are in the interior, plateau region. See text for details. Scale bar, 100 km.

recent past, rainfall will vary over an area as large as São Paulo state for reasons other than tree cover. We reduce these other sources of variation to three general geographical predictor variables included in all models: latitude, longitude and altitude. In fact, we generated three composite variables from a PCA of the longitude, latitude and altitude of the climate stations. Using all three PCA-derived variables retained all of the variation in latitude, longitude and altitude between climate stations, while reducing collinearity in the models (Quinn & Keough 2002). We then estimated the relationship between mean annual rainfall and mean percentage tree cover (arcsine-square root transformed), controlling for latitude, longitude and altitude, over all 12 spatial scales for the included climate stations, using simple linear models fitted in R (R Development Core Team 2004). Previous analyses have shown that such relationships are stronger and more consistent when rainfall was measured as rain days, rather than total rainfall (Meher-Homji 1980, 1991; Wilk *et al.* 2001; see §4). We therefore focus on results from models with mean annual rain days (ln-transformed) as the response variable, although results from models using total annual rainfall are also presented.

From each of the linear models, we recorded the partial regression coefficient associating tree cover and rainfall; a significant positive value of this coefficient means that higher rainfall was observed in areas of higher tree cover, independent of latitude, longitude and altitude. We also recorded the R^2 value of the model, i.e. the proportion of total variation in annual rainfall that was explained by a combination of latitude, longitude and altitude together with tree cover measured at the appropriate scale.

We tested the robustness of our results in three ways. First, we ran the same analyses, but on two subsets of the climate stations (figure 2). The first subset consisted of only those climate stations that were classed as forested in 1962 (i.e. not including the 1962-wooded stations; $N=120$); the second subset was those that fall approximately into the mountainous coastal region of the state ($N=102$), where the forest is generally moister and less seasonal than that on the plateau in the interior of the State (Oliveira-Filho & Fontes 2001), and where rather more forest remains (figure 1). Even in this

coastal region, however, estimates of percentage tree cover remaining vary widely, even at large spatial scales. For example, the mean forest cover in the 1369 km^2 centred on these coastal stations varies from 5.3 to 78.7%.

For our second test, we relaxed the assumption that the relationship between rainfall and tree cover, latitude, longitude and altitude was linear by using generalized additive models (GAMs; Hastie & Tibshirani 1990). GAMs allow a response variable to be modelled as a non-specified smoothed function of one or more predictors; the degree of smoothing selected by the smoothing procedure for each variable indicates how far the relationship departs from linear. Here, smooths were based on penalized regression splines, and were selected using an automated procedure based on generalized cross validation, implemented using the mgcv package in R (Wood 2003, 2004). We fitted separate smooth functions for each predictor, but in practice, with rain days as the response variable tree cover was almost always identified as a linear (i.e. infinitely smooth) predictor in the full and reduced datasets. We therefore re-ran these models with tree cover included as a parametric predictor and the three PCA-derived latitude, longitude and altitude variables as optimal smooths. This enabled us to compare the coefficient associating tree cover with rainfall across scales, while allowing the relationship between rainfall and the geographical variables to depart from linearity. We discuss below the few individual cases where the estimated function associating tree cover and rainfall departed markedly from linearity.

Finally, we performed a further analysis on a small subset of the climate stations to address the problem of non-independence of the tree cover estimates at large scales. A potential problem will arise if the climate stations are sufficiently close to each other that substantial areas of land used to estimate mean tree cover overlap between adjacent stations. Although the mean pairwise distance between all climate stations in our dataset is *ca* 300 km, most (97%) climate stations are within 50 km of their nearest neighbour which suggests that a certain degree of overlap will occur in the areas used for tree cover estimates, particularly at spatial scales greater than or equal to 19×19 km^2. To assess the importance of this effect, we took random subsamples of climate stations all of which were at least 100 km from each other, and re-ran the analysis at all 12 spatial scales with ln(mean annual rain days) as the response variable. We performed 25 such sets of analyses, with sample sizes of between 20 and 24 climate stations in each; in each analysis we recorded the partial regression coefficients associating tree cover with rainfall at each spatial scale.

(c) *Vertebrate analyses*
A recent analysis (Reed *et al.* 2003) of 102 vertebrate species has suggested that *ca* 7000 adult individuals are required to maintain minimum viable populations (MVPs, less than 1% probability of extinction in 40 generations); variability between taxa was not strongly related to habitat or life history. Estimates of population densities (individuals×km^{-2}) for Atlantic forest primates, ungulates and passerine and non-passerine birds were taken from the literature (Guix *et al.* 1999; Marsden *et al.* 2000, 2001; Cullen *et al.* 2001; González-Solis *et al.* 2001). All estimates were from surveys within the Atlantic forest region. For most species, several density estimates were available, often from study areas of different sizes and of differing habitat quality, which will thus
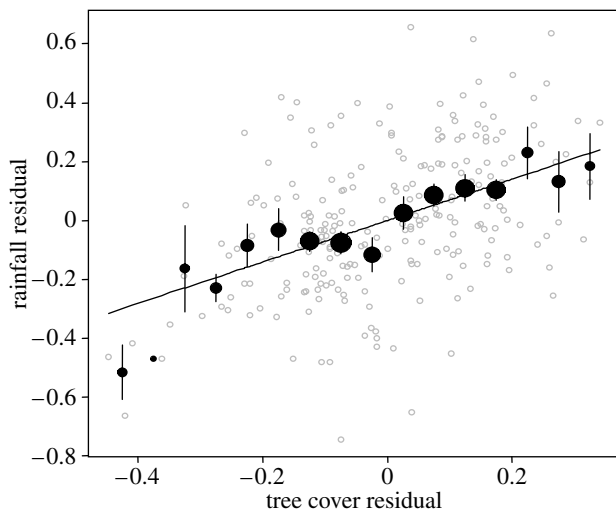
Figure 3. The relationship between rainfall (mean annual rain days) and tree cover measured at the 1369 km² scale for 237 climate stations in São Paulo state, after controlling for longitude, latitude and altitude. The values plotted (open symbols, light grey) are the residuals from a regression of rainfall on the three PCA-derived geographical variables (*y*-axis) and those from a regression of tree cover on the three PCA-derived geographical variables (*x*-axis). For clarity, the filled symbols show the mean of the rainfall residuals falling into each 0.05-unit tree cover residual bin, with vertical lines showing standard errors of the rainfall residuals in each bin; the size of each point is proportional to the number of observations in that bin. Analyses were performed on the ungrouped data, and the regression line shown is that from the analysis of all data. Its slope (0.703 ± 0.092 s.e.) is equal to the partial regression coefficient linking tree cover to rainfall in the model including tree cover and the three geographical variables as predictors, and is highly significantly positive (d.f. = 232, $t = 7.66$, $p < 0.00001$).

span the range of densities likely to be observed. In such cases, the arithmetic mean population density was used. Mean ± s.e.m. densities were obtained for each taxonomic group; these were converted to estimates of the MASH (km²) required to support a population of 7000 individuals simply by dividing 7000 by the relevant density.

3. RESULTS
(a) *Rainfall and forest cover analyses*
Considering all climate stations, and with annual rain days as the response variable, in simple linear models rainfall is significantly ($p < 0.00001$) positively associated with tree cover independently of latitude, longitude and altitude at all spatial scales. An example is shown in figure 3: for a given latitude, longitude and altitude, higher tree cover is associated with higher rainfall.

The relationship between tree cover and rainfall is not independent of the scale at which tree cover was measured, however. Tree cover measured at larger scales explains more of the variation in the number of annual rain days (table 1), at least up to scales of around 1000 km², and the partial regression coefficient associating tree cover and rainfall more than doubles over the same range of scales (table 1; figure 4). Not only were these patterns consistent for different measures of effect size (e.g. total regression R^2, partial regression coefficients associating tree cover with rainfall; see table 1), they were also observed in both of the subsets of data analysed (table 2),

and they hold when the assumption of linearity is relaxed (table 1). In all cases where rainfall was measured as rain days, the relationship between tree cover and rainfall was always positive and became stronger with increasing spatial scale, either across all scales or to a maximum around 625–1369 km². In addition, the mean of the partial regression coefficients from the 25 models including only *ca* 20 climate stations, all greater than 100 km from each other, increases almost uniformly with spatial scale ($r > 0.99$), from 0.29 ± 0.056 at 9 km² to 0.76 ± 0.087 at 9409 km².

When total rainfall was the response variable, relationships were consistently weaker, although significant positive relationships ($p < 0.05$) between tree cover and total rainfall were observed at all spatial scales less than 2401 km². Again, there was a tendency for the strength of the tree cover-rainfall relationship to increase with increasing spatial scale, at least up to a scale of several hundred km². For instance, the partial regression coefficient increased from 0.10 ± 0.043 at 9 km² to 0.17 ± 0.059 at 361 km², before declining at larger scales to 0.07 ± 0.078 at 9409 km². The reduction in explanatory power at the largest scales may be explained in part by increasing nonlinearity of the relationship at these large scales: tree cover was identified in GAMs as a linear predictor of total rainfall at scales less than 1369 km², but as a highly nonlinear (although still significant) predictor at the four largest scales.

(b) *Vertebrate analyses*
Estimates (mean ± s.e.m.) of the MASH required for the four example Atlantic forest vertebrate taxa are shown in figure 4. These estimates vary between taxa, being larger for ungulates than for passerines, for example. However, estimates for most of the species considered span the range 10^2–10^4 km² (figure 4). They tend to be somewhat larger than the 200 km² considered to be the minimum area required to support a reasonably intact Atlantic forest vertebrate fauna (Chiarello & de Melo 2001). However, the scales at which the relationship between tree cover and rainfall is strongest (*ca* 10^3 km²) would be large enough to encompass viable populations of most of the vertebrates considered.

4. DISCUSSION
We confirm here the existence of a strong positive relationship between tree cover and rainfall in the Atlantic forest of São Paulo state, SE Brazil. This relationship is observed when tree cover is measured at scales varying from 10^1 to 10^4 km². The fact that we considered only areas which were forested in the recent past, and where subsequent changes in forest cover have been overwhelmingly anthropogenic in origin, leads us to conclude that this result is most parsimoniously explained as a response of climate to land-use change (see also Webb *et al.* in press). The directionality of this relationship can be inferred from the fact that changes in tree cover between the dates of the two estimates that we consider (historical: 1960s and GLCF: 1990s) can be directly attributed to human action (e.g. Dean 1995). The relationship between rainfall and GLCF tree cover can therefore readily be explained only if rainfall has responded to changes in tree cover, or if deforestation

Table 1. Parameters from linear and generalized additive models associating mean annual rain days with mean percentage tree cover measured at each of the 12 spatial scales, for all of the climate stations in the dataset. The partial regression coefficient ($\pm$ s.e.) associating rainfall with tree cover is shown; for linear models only so too is the R^2 of the model. Bold type indicates the scale at which the largest value of a particular parameter was observed. Linear models were of the form RAIN = TC + LLA1 + LLA2 + LLA3, where RAIN is log(mean annual rain days), TC is arcsine square root transformed percentage tree cover and LLA1–3 are the three variables generated from a PCA of longitude, latitude and altitude (see text for details). GAMs took the form RAIN = TC + s_1(LLA1) + s_2(LLA2) + s_3(LLA3), where RAIN, TC and LLA1–3 are as before, and s_i indicates an optimally derived smooth function of the variable in question (see text for details).

scale of tree cover measurement (km^2)	linear model		GAM
	tree cover coefficient $\pm$ s.e.	model R^2	tree cover coefficient $\pm$ s.e.
9	0.36 $\pm$ 0.063	0.64	0.19 $\pm$ 0.068
25	0.40 $\pm$ 0.069	0.64	0.22 $\pm$ 0.076
49	0.45 $\pm$ 0.073	0.65	0.26 $\pm$ 0.081
81	0.50 $\pm$ 0.076	0.66	0.30 $\pm$ 0.086
121	0.54 + 0.078	0.66	0.34 $\pm$ 0.090
225	0.58 $\pm$ 0.081	0.67	0.37 $\pm$ 0.097
361	0.62 $\pm$ 0.083	0.67	0.41 $\pm$ 0.103
625	0.66 $\pm$ 0.087	0.67	0.46 $\pm$ 0.112
1369	0.70 $\pm$ 0.092	**0.67**	0.51 $\pm$ 0.125[a]
2401	0.70 $\pm$ 0.097	0.67	0.50 $\pm$ 0.136[a]
5329	0.72 $\pm$ 0.103	0.66	0.54 $\pm$ 0.155
9409	**0.77 $\pm$ 0.109**	0.66	**0.62 $\pm$ 0.173**

[a] At these two scales only, the optimal GAM suggested a nonlinear relationship between tree cover and rainfall (i.e. the estimated degrees of freedom for the tree cover parameter were greater than 1). However, EDFs did not greatly exceed 1, and models in which tree cover was included as a linear predictor did not have a significantly higher residual deviance than models which included the optimal smooth function of tree cover (F-test of deviance, $p > 0.05$ in both cases). The coefficient from GAMs in which tree cover was included as a linear predictor is therefore shown for all scales.

has favoured drier areas. The latter explanation seems reasonable, for instance if farmers find it easier to clear (by burning) drier forests. However, farmers in this region have in fact often preferred to farm in wetter, more fertile areas (Dean 1995). In addition, it is not clear how this biased-deforestation hypothesis could generate a systematic trend in the strength of the tree cover–rainfall relationship with increasing spatial scale. For these reasons, a relationship between contemporary tree cover and rainfall at sites that were recently forested can most parsimoniously be explained by rainfall responding to changes in tree cover, as predicted by mechanistic models coupling vegetation and climate (e.g. Lawton *et al*. 2001; Bonan 2002; Bounoua *et al*. 2002; DeFries *et al*. 2002; Moorcroft 2003).

We have also shown that this relationship between tree cover and rainfall varies systematically with spatial scale: local rainfall is more tightly associated with tree cover averaged over large areas (*ca* 10^3 km^2) surrounding the climate station than it is at smaller scales. In other words, local climate will be influenced by deforestation occurring at rather large scales (*ca* 10^3 km^2); small areas of forest, even if well protected, will exert little feedback on rainfall; and the effects of forest fragmentation are detected as a disruption of the forest–rainfall feedback for fragments less than about 10^3 km^2 in area. This effect can be quantified to a certain extent by using a model, which includes tree cover measured at both small and large scales to predict rainfall when tree cover is modified at one or other scale. We therefore fitted a GLM with normal errors and a log-link with mean annual rain days as the response variable, and the three geographic variables (the latitude–longitude–altitude principal components) as predictor variables together with mean tree cover at two scales, 9 km^2 and 1369 km^2. All predictor variables except for
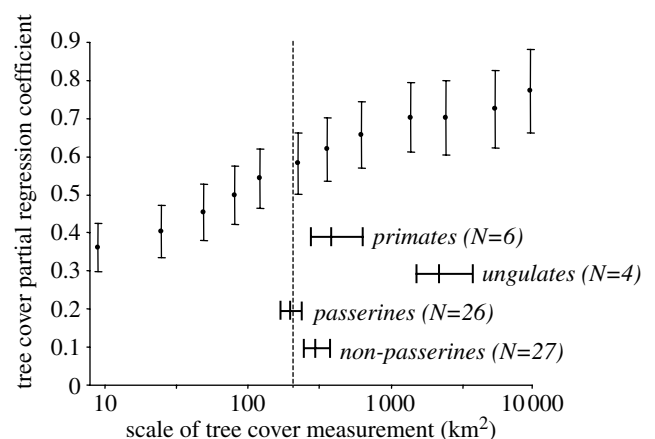

Figure 4. The partial regression coefficient ($\pm$ s.e.) associating tree cover with mean annual rain days measured at 12 different scales centred on the 237 sites that were classed as forested or wooded in 1962, derived from linear models. The vertical dashed line is at 200 km^2, considered to be the minimum area of forest required to support a reasonably intact Atlantic forest vertebrate fauna (Chiarello & de Melo 2001). The horizontal lines show the MASH required to support a population of 7000 individuals of four groups of Atlantic forest vertebrates. The MASH based on the mean population density for species in each group is shown together with estimates obtained using the mean $\pm$ 1 × s.e. population density. The number following the name of each group is the number of species included in the population density estimate.

9 km^2 tree cover were highly significant in the resulting model. We used this fitted model to predict changes in mean annual rain days across the 237 climate stations following four scenarios. First, 9 km^2 tree cover was increased to fully forested (i.e. 80%), with 1369 km^2 tree cover remaining essentially unchanged (although we

Table 2. Partial regression coefficients ($\pm$s.e.) from linear models associating tree cover with mean annual rain days at each of the 12 spatial scales in two subsets of climate stations, those that were classed as forested (not wooded) in 1962 and those falling in the coastal region. See table 1 for formulation of the linear models. All coefficients were significantly positive to at least $p < 0.05$, apart from the coastal only model at 9409 km^2 ($p = 0.0710$). Bold type shows the highest value in each column.

scale of tree cover measurement (km^2)	1962-forest only	coastal only
9	0.23 ± 0.092	0.30 ± 0.096
25	0.23 ± 0.099	0.32 ± 0.103
49	0.26 ± 0.105	0.37 ± 0.110
81	0.29 ± 0.111	0.39 ± 0.117
121	0.33 ± 0.116	0.42 ± 0.121
225	0.34 ± 0.124	0.42 ± 0.129
361	0.36 ± 0.130	0.45 ± 0.133
625	0.38 ± 0.138	0.46 ± 0.140
1369	0.40 ± 0.147	**0.47 ± 0.152**
2401	0.37 ± 0.155	0.42 ± 0.164
5329	0.37 ± 0.166	0.37 ± 0.180
9409	**0.40 ± 0.182**	0.37 ± 0.200

adjusted mean tree cover at the larger scale to take account of changes in tree cover at the smaller scale). The second scenario had maximum forest at 1369 km^2, but retained observed tree cover at 9 km^2. A further two scenarios entailed deforestation (to 10%) at one scale with no change at the other scale. As can be seen in table 3, the effects of changes in large-scale tree cover in the absence of small-scale changes are approximately ten times greater than the effects of small-scale changes in tree cover in the absence of large scale changes. These simple predictions lend support to our general conclusion that local rainfall patterns will be influenced more strongly by the distribution of forest over a large (greater than 1000 km^2) area than by local (less than 10 km^2) forest distribution.

The increase in the accuracy of our models with increasing spatial scale is robust to the measure of effect size taken from the models, which suggests that what we are observing is not simply a methodological artefact resulting from the effects of averaging tree cover values over progressively larger scales. Such averaging may be expected to result in a less noisy relationship between tree cover and rainfall (i.e. higher R^2 at larger scales), but there would be no reason to expect the slope of the relationship (i.e. the partial regression coefficient) to increase, which is precisely what we do observe. Changes in parameters of models formulated at different spatial scales might be predicted as different physical or biological processes become dominant (e.g. Wiens 1989; Holling 1992). However, although we consider a broad range of scales, it seems unlikely that we cross multiple 'domains of scale' *sensu* Wiens (1989), with their associated nonlinear changes in environmental drivers. For instance, even the smallest scale in our study (9 km^2) would be considered large scale in ecological terms (e.g. heterogeneity is at the landscape mosaic level rather than the patch scale and experimental manipulations will be difficult; Wiens 1989) and does not enter the realms of ecophysiology or interspecific interactions; likewise, the largest scales (10^3–10^4 km^2) remain within typical landscape to regional

scales. Our results also hold when subsets of the climate stations are analysed, indicating that they cannot simply be attributed to large scale differences in climate in different bioclimatic zones.

The GAMs showed that, although patterns of covariation in rainfall with latitude, longitude and altitude may be rather complex, the relationship between tree cover and annual rain days does appear to be simple, linear and positive. It remains possible, however, that the relationship varies across space. We tested this by re-running our linear models for the coastal region, with ln(mean annual rain days) as the response variable and tree cover together with latitude, longitude and altitude as explanatory variables; we also considered the two-way interactions between each pair of geographical variables, and between each geographical variable and tree cover. This analysis showed that at the smaller scales (9–225 km^2), the tree cover–rainfall relationship varied with both latitude and longitude, with more strongly positive relationships in more northerly and easterly areas. At larger scales (361–2401 km^2), however, there was no interaction between tree cover and any of the geographical variables, i.e. the significantly positive relationship between tree cover and rainfall was constant over the entire region. At the two largest scales (5329 and 9401 km^2), an interaction between tree cover and longitude reappeared: the relationship between tree cover and rainfall was more strongly positive in more easterly regions (i.e. further inland). This last result probably occurs because for westerly climate stations (those nearest the coast), large-scale tree cover will be estimated over a comparatively smaller area, as cells including only sea were omitted from the tree cover estimates; in other words, high tree cover estimates for these stations at large scales may not accurately reflect the surrounding landscape. This may be one reason why the positive relationship between spatial scale and tree cover coefficient begins to degrade at the largest scales considered (figure 4).

Finally, the subsampling of climate stations widely separated in space suggests that non-independence of forest cover data is not an explanation for our results. We note also that in all of our linear models, the residuals were not correlated with latitude, longitude or altitude, whether singly or in combination. In other words, spatial patterns of rainfall variation unrelated to tree cover appear to have been adequately controlled for in our models. In sum, the doubling over the range of scales considered of the coefficient relating tree cover to annual rain days is robust to a number of potentially confounding factors, and can therefore be considered an important benchmark for studies simulating the impacts of deforestation on mesoclimate.

The situation is somewhat different when total rainfall is considered as the response variable, although the same general pattern of increasing explanatory power of the models with increasing spatial scale of the tree cover estimate holds, at least up to scales of several hundred km^2. There are various ways to interpret these results. The simplest is to consider them simply to be a noisier version of the results obtained with rain days as response variable. This seems reasonable, given that rain days and total rainfall are broadly positively correlated (correlation of 1982–1992 mean values of total rainfall and rain days (both ln-transformed) for the 237 climate stations

Table 3. Predicted changes in the number of annual rain days following changes in forest cover at small (9 km^2) or large (1369 km^2) scales. See text for details.

change in small scale tree cover	change in large scale tree cover	median change in rain days	interquartile range (days)
complete aforestation	no change	+4.4 days	+2.6 to +5.5
no change	complete aforestation	+44.2 days	+29.0 to +52.8
complete deforestation	no change	−1.3 days	−0.2 to −7.1
no change	complete deforestation	−10.8 days	−3.9 to −45.8

analysed here: 0.61, d.f. = 235, $p < 0.0001$). Weaker patterns in total rainfall may simply result from the fact that total rainfall is more variable, and harder to measure exactly, than rain days. However, there are other features of the data, which suggest that the full story may be somewhat more complex. For instance, the linear relationship between tree cover and total rainfall began to break down at large spatial scales (greater than *ca* 10^3 km^2). GAMs confirmed that the relationship at large scales became more complex: at scales up to 625 km^2 tree cover was identified as a linear predictor of total rainfall, but at larger scales the relationship became highly nonlinear. It may be therefore that at smaller scales, patterns of total rainfall reflect those of rain days, but at large scales, regional-scale processes not accounted for in our study determine the total amount of rainfall, whereas the probability of rain on any particular day remains linked to tree cover, perhaps through the effects of forest on the thickness of the convective boundary layer (Fisch *et al.* 2004; Webb *et al.* in press). Under certain circumstances this may lead to fewer, but more intense rain events in deforested compared to forested areas (Machado *et al.* 2004). In addition, there is evidence in this region that total rainfall is strongly influenced by distance to the coast, whereas this effect is not apparent in patterns of rain days (Webb *et al.* in press). Whatever the precise cause, our results are in broad agreement with other studies suggesting that deforestation may have a more marked effect on rain days than on total rainfall (Meher-Homji 1980, 1991; Wilk *et al.* 2001).

Our estimates of the MASH required to hold viable populations (7000 adults; Reed *et al.* 2003) of several Atlantic forest vertebrate taxa were in the range 10^2–10^3 km^2, not dissimilar to the range of scales at which the vegetation–climate relationship was strongest. The primates present a particularly interesting case: 19 of the 24 Atlantic forest species are endemic to the region, with at least nine listed as threatened (Chiarello & de Melo 2001; Macdonald 2001). Conservation strategies aimed at preserving sufficient contiguous forest habitat (270–603 km^2; figure 4) for these species would approach the scales most relevant for the tree cover–rainfall relationship. Thus, effective conservation of these charismatic vertebrates would reduce, but perhaps not eliminate, the probability of adverse climatic effects resulting from deforestation. Of course, the MASH estimates that we produce are dependent on the particular value of MVP chosen, taken here to be 7000 individuals (Reed *et al.* 2003). Although this value may vary between species, and different methods may also produce different estimates, there is an emerging consensus that several thousand breeding individuals are required for the long-term persistence of vertebrate populations (Reed *et al.* 2003). As a lower limit, a species will be listed as vulnerable

under IUCN criteria (IUCN 2001) if it numbers less than 1000 mature individuals, either in total or in any one population; this is likely to correspond to a total population significantly higher. A further factor may have led to underestimates of MASH: we make no distinction in habitat quality between small and large areas of forest, whereas in reality (e.g. due to the increased influence of edge effects) habitat quality is likely to decrease in small forest fragments, with corresponding reductions in population densities particularly of larger, more specialized species (e.g. Laurance *et al.* 2002). In sum, while we would not claim that our MASH estimates are in any way definitive, we feel that they will be broadly correct. Our general conclusion might also be restated independently of considerations of MASH as: the area of forest required to support a population of several thousand individuals of a vertebrate species is likely to be of the same order of magnitude as that required to minimize the risk of adverse climatic effects of deforestation.

It should be emphasized, however, that our estimates of the MASH required for these vertebrates are considerably larger than most existing protected areas in São Paulo state (median size = 11.9 km^2; UNEP-WCMC 2000). Considering both the small size of the existing reserves and the highly fragmented nature of the remaining Atlantic forest, it is not surprising that emphasis has been placed on the conservation value of small forest patches and tiny remnant populations (Ferrari & Diego 1995; Tabanez & Viana 2001). Indeed, conservation practitioners may feel that aiming for a population of 7000 individuals is hopelessly unrealistic, particularly for species such as the golden lion tamarin *Leontopithecus rosalia* with a total population size in the wild of just a few hundred individuals (Macdonald 2001). However, it is becoming increasingly apparent that populations of thousands rather than hundreds really are required for long-term viability (Reed *et al.* 2003), and that consequently we should be thinking in terms of hundreds of square kilometres for forest reserves (Chiarello 1999; Ferraz *et al.* 2003). Our results suggest that if these recommendations for preserving intact vertebrate communities are taken seriously, then the likelihood of climate change feedback resulting from deforestation will also be reduced. Given that people have for centuries blamed perceived detrimental climatic change on forest clearance (Williams 2003), it will be profitable to promote forest conservation programmes by emphasizing possible climatic as well as biodiversity benefits.

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