



# Extinction risk in cloud forest fragments under climate change and habitat loss

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## ABSTRACT

**Aim** To quantify the consequences of major threats to biodiversity, such as climate and land-use change, it is important to use explicit measures of species persistence, such as extinction risk. The extinction risk of metapopulations can be approximated through simple models, providing a regional snapshot of the extinction probability of a species. We evaluated the extinction risk of three species under different climate change scenarios in three different regions of the Mexican cloud forest, a highly fragmented habitat that is particularly vulnerable to climate change.

**Location** Cloud forests in Mexico.

**Methods** Using Maxent, we estimated the potential distribution of cloud forest for three different time horizons (2030, 2050 and 2080) and their overlap with protected areas. Then, we calculated the extinction risk of three contrasting vertebrate species for two scenarios: (1) climate change only (all suitable areas of cloud forest through time) and (2) climate and land-use change (only suitable areas within a currently protected area), using an explicit patch-occupancy approximation model and calculating the joint probability of all populations becoming extinct when the number of remaining patches was less than five.

**Results** Our results show that the extent of environmentally suitable areas for cloud forest in Mexico will sharply decline in the next 70 years. We discovered that if all habitat outside protected areas is transformed, then only species with small area requirements are likely to persist. With habitat loss through climate change only, high dispersal rates are sufficient for persistence, but this requires protection of all remaining cloud forest areas.

**Main conclusions** Even if high dispersal rates mitigate the extinction risk of species due to climate change, the synergistic impacts of changing climate and land use further threaten the persistence of species with higher area requirements. Our approach for assessing the impacts of threats on biodiversity is particularly useful when there is little time or data for detailed population viability analyses.

## Keywords

metapopulations, patch-occupancy model, probability of extinction, species distribution modelling.

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## INTRODUCTION

The main challenge in conservation planning is to ensure the persistence of species through time (Gilpin, 1986; Akçakaya *et al.*, 1999). To try to meet this challenge, researchers have developed methods and tools to identify and select locations for conservation investment such as protected areas.

Generally, protected area systems are designed to maximize the representation of species or ecosystems. However, the dynamic nature of threats, including climate change and land-use change, makes it imperative to include explicit measures of persistence, such as the risk of extinction (Hof & Raphael, 1993; Bevers *et al.*, 1995; Williams & Araujo, 2002; Nicholson & Possingham, 2006), not just implicit measures

such as the percentage of a range secured within protected areas.

Habitat loss and climate change are two of the greatest threats to global biodiversity (Sala *et al.*, 2000; Hansen *et al.*, 2001; Travis, 2003; Duraipappah *et al.*, 2005; Parry, 2007). However, their interactive effects on populations are still not well understood (Duraipappah *et al.*, 2005; Lepers *et al.*, 2005; Parry, 2007; Mantyka-Pringle *et al.*, 2011). Studies of the effects of habitat loss on species (see Bird *et al.*, 2011, for example) are relatively rare compared to the ever-growing number of studies about species' responses to climate change, very few incorporate both (Sala *et al.*, 2000; Bomhard *et al.*, 2005; Jetz *et al.*, 2007). Changes in climate and its synergistic impacts on habitat fragmentation seem likely to exacerbate the extinction risk of many species, and studies linking both are required. Changes in climate and land use are not the only threats to cloud forests species. They could catalyse the impact of other threats, such as chytridiomycosis, the fungal infection that is affecting large numbers of amphibian species in the tropics (Pounds *et al.*, 1999, 2006).

In Mexico, Tropical Montane Cloud Forests (TMCF) are particularly vulnerable to climate change for several reasons: they need very specific environmental conditions (Hamilton, 1995; Bruijnzeel, 2010), they are naturally fragmented (Foster *et al.*, 2003), much of their original extent has already disappeared (Challenger, 1998; Cayuela *et al.*, 2006), and current protected areas are poorly placed with respect to the future distribution of cloud forest under climate change (Ponce-Reyes *et al.*, 2012). It has been estimated that, under conservative climate change scenarios, suitable areas for TMCF in Mexico will decrease by up to 70% by 2080; however, if it is assumed that TMCF outside current protected areas is transformed for other land uses (i.e. agricultural areas, grazing lands, coffee plantations, etc.), less than 1% of TMCF might remain (Ponce-Reyes *et al.*, 2012). In other parts of the world, adjustments in the cloud forest assemblages due changes in the climate are already noticeable (e.g. in Costa Rica (Pounds *et al.*, 1999)).

The fragmented nature of TMCF and its vulnerability to climate change provides strong motivation to explicitly measure the extinction risk of TMCF species. Populations in fragmented landscapes are generally more susceptible to climate change than those in continuous landscapes (Travis, 2003; Opdam & Wascher, 2004). The highly fragmented nature of the TMCF lends itself to applying a metapopulation approach to calculate the extinction risk of species (Nicholson *et al.*, 2006). In a metapopulation model, extinction risk is a function of the ecology of the species, such as dispersal ability and area requirements, and the landscape configuration (Hanski, 1998). Although simple patch-occupancy approximation models that estimate the mean time to extinction do not account for local patch dynamics or individual behaviour (e.g. Frank & Wissel, 2002), these models can be of great use when estimating extinction risk (Day & Possingham, 1995).

The aim of this study was to project forwards the combined impacts of climate change and land use on cloud forest habitat loss and fragmentation, and the subsequent viability of vertebrate species that depend upon TMCF. We used Maxent, a species distribution model, to estimate the potential future distribution of the cloud forest in Mexico, and the potential future locations of cloud forest that are currently in reserves. Next, we estimated the extinction risk through time of three representative vertebrate species with very different life histories, a bird, a frog and a mouse, in cloud forest patches within three regions that have different vulnerabilities to climate change. We estimated extinction risk for two different scenarios: a) considering climate change as the only driver of habitat loss and fragmentation, and b) considering climate and land-use change outside protected areas as the drivers of habitat loss, where we assumed that only the cloud forest-suitable areas that are currently in a protected area would remain.

## METHODS

### Study area and species

Tropical Montane Cloud Forests (TMCF) are found in the tropics, at mid-altitude on the windward slopes, where the clouds intersect with the mountains (Bruijnzeel & Proctor, 1995). The persistent cloud cover over the canopy of the TMCF maintains the high annual precipitation (500–1000 mm) and humidity in these forests. Also, it ameliorates intense sunlight, maintaining a mean temperature of 12–23°C. Due to their high biodiversity and endemism, TMCFs are considered among the most threatened ecosystems of the world (Hamilton, 1995; Leo, 1995; Wege & Long, 1995; Rzedowski, 1996; Still *et al.*, 1999; Aldrich *et al.*, 2000). In Mexico, TMCFs are limited to a narrow strip between 600 and 3000 metres above sea level in the main mountain ranges (Luna-Vega *et al.*, 1988), covering around 0.8% of the region. They are characterized by an archipelagic distribution and high biodiversity: 10% of all Mexican plant species (Rzedowski, 1991, 1996) and 12% of all Mexican terrestrial vertebrates (Flores-Villela & Gerez, 1994) with many endemic taxa. However, very little is known about the population ecology of any of the cloud forest-dependent species.

We sought to estimate the impacts of different climate change and land-use change scenarios on the persistence of groups of species with different life histories by studying three representative vertebrate species. Although we searched the literature for population ecology data on Mexican cloud forest endemic species, little reliable information could be found on species that occur throughout the focal regions. Given the lack of information about TMCF's amphibians and mammals' life history, we parameterized the model with potentially similar vertebrate species found in other forest types. We estimated the impacts of climate change and land-use change on extinction risk of three typical vertebrate species: a bird (resplendent quetzal, *Pharomachrus mocinno*),

a frog (based on the cliff chirping frog, *Eleutherodactylus marnockii*) and a mouse (based on the deer mouse, *Peromyscus maniculatus*; Table 1).

This approach reflects the recommendations for using focal species explored by Nicholson *et al.* (2013). We modelled the species as TCMF endemics occurring in all three focal regions (in reality the distribution of the quetzal in Mexico is restricted to Chiapas, while the frog and mouse are not restricted to cloud forest), with the aim of capturing lesser-known cloud forest endemics with similar ecological characteristics. The parameters that we used in the models are shown in Table 1.

### Modelling the future distribution of Tropical Montane cloud forest

To identify potentially suitable areas for cloud forest in Mexico, we used Maxent (Phillips & Dudík, 2008). Maxent is an algorithm for predicting species distribution models when only the presence data are available (Elith *et al.*, 2006). It has also been shown to be of great utility when projecting models into novel environments (i.e. future scenarios; Hijmans & Graham, 2006; Kearney *et al.*, 2010; Ponce-Reyes *et al.*, 2012). Maxent calculates the observed association between species or habitats and environmental layers with the constraint that the expected value of each environmental variable under the estimated distribution must be similar to its observed average over sample locations (Phillips *et al.*, 2006; Phillips & Dudík, 2008).

To train the models, we selected 30,000 background points. We used a 10-fold cross-validation approach to validate the models before projecting them into the novel climates. Finally, to create a binary map of the presences and absences of the models, we used a threshold value at which training sensitivity equalled specificity, in other words, where positive and negative observations have an equal chance of being correctly predicted (Liu *et al.*, 2005). The standard use of Maxent is to use a series of geographic locations where a

species has been observed or collected. Here, we followed the approach of Carnaval & Moritz (2008) and Ponce-Reyes *et al.* (2012), where TCMF was treated as a species, transforming its occurrence area into locality points. We extracted the square root of the area of occupancy of the TCMF as random points at least 1 km apart to match the scale of the bioclimatic layers.

The present climate datasets used for the analyses were obtained from WorldClim ver.1.3 ([www.worldclim.org](http://www.worldclim.org)), a database containing global climate layers with a resolution of one square kilometre (Table 2, for details about how these layers were created see Hijmans *et al.* (2005)). The bioclimatic layers that we used to develop the models were as follows: annual mean temperature, temperature seasonality, temperature of the coldest and warmest quarter, annual precipitation, precipitation seasonality and precipitation of the driest and wettest quarter. We also included data on soil types as a predictor of environmentally suitable areas for cloud forest. Common cloudiness factors (i.e. cloud frequency, fog presence and wind speed and direction) may influence the formation and maintenance of cloud forests significantly, but as there are no reliable data on their likely trajectories under future climates, we couldn't consider them directly here. We also discarded altitude as a predictor because it is a surrogate for climatic variables rather than a direct driver of habitat suitability.

To assess the importance of uncertainty in future climates, we modelled future distributions using seven different Global Circulation Models (GCMs) from the 4th IPCC initiative downscaled to 1 km<sup>2</sup> resolution by CIAT ([www.ciat.org](http://www.ciat.org)) of the A1b scenario in three time steps: 2030, 2050 and 2080 (Table 2). A1 storylines of the GCMs describe a future world of very rapid economic growth.

In total, we produced 22 models: one for the present distribution and 21 for the future (seven different GCMs in three different times). To deal with the uncertainty of projecting TCMFs current distribution into novel environments, we created a consensus model for the future climates.

**Table 1** Parameter values for the three species. We use  $x = 1$  as a default following Hanski (1998); (Gilpin & Diamond, 1976; Gilpin, 1986)

Species	Home range ( $H$ ) in ha	Mean dispersal distance ( $d$ ) in km	Fecundity rate (number of juveniles) ( $\gamma$ )	Environmental stochasticity ( $x$ )	References
Resplendent Quetzal ( <i>Pharomachrus mocinno</i> )	10	5	0.1	1	Bowes & Allen, 1969; Powell & Bjork, 1995; Powell, 2001; Powell & Steidl, 2002; Solorzano <i>et al.</i> , 2003; Solorzano <i>et al.</i> , 2004; and Dr. Sofia Solorzano pers. comm.
Frog based on chipping frog ( <i>Eleutherodactylus marnockii</i> )	0.06	0.21	0.17	1	Jameson, 1955
Mouse based on Deer mouse ( <i>Peromyscus maniculatus</i> )	1	3.2	0.38	1	Murie & Murie, 1931

**Table 2** Specifications for general circulation models

	Model name	Spatial resolution	Time	Source
Present	WorldClim	30 s	1960–2000	(Hijmans <i>et al.</i> , 2005)
Future	CCCMA	30 s	2030, 2050, 2080	IPCC, 4th assessment
A1b scenario	CSIRO			(downscaled by
	HADCM3			Jarvis <i>et al.</i> , 2008;
	HADGEM			at CIAT)
	IPSL			
	MPI-ECHAM			
	NCAR			

The future consensus model was made by summing the habitat suitabilities of all seven models produced by different future GCMs for each time. For example, CCCMA 2080 + CSIRO 2080 + HADCM3 2080 + HADGEM 2080 + IPSL 2080 + MPI-ECHAM 2080 + NCAR 2080. All pixels with a value of four or more were considered to predict presence in a given grid cell (i.e. four or more models coincide that a determined pixel had suitable conditions for cloud forests). Because we assumed that changes in climate will occur faster than migration and reestablishment of the cloud forest plants elsewhere, we clipped the consensus model at each time to the current distribution of TMCF.

Lastly, we calculated the proportion of cloud forests occurring within protected areas. To do so, we overlapped the current protected areas with the three consensus models (2030, 2050 and 2080).

### Habitat loss, fragmentation and topographic distance

To analyse the projected effects of climate change on the cloud forest, we measured the habitat loss and fragmentation of the cloud forests through time. We followed Fahrig's (2003) suggestion to consider habitat loss separate from fragmentation, considering fragmentation to be the changes in habitat configuration that result from the breaking apart of habitat, independent from habitat loss (Fahrig, 2003). To explore the habitat configuration of the potential distribution of the cloud forests, we used the following four measures: a) reduction in total amount of habitat (total area in ha), b) increase in number of habitat patches (number of patches), c) decrease in average size of habitat patches (mean patch area in ha) and d) increase in isolation of patches (mean Euclidean nearest neighbour distance in metres).

To provide an overview of the potential changes in the future spatial distribution of the Mexican cloud forests, we calculated their total area and number of fragments from the current cloud forest distribution and our species distribution models for each time (2030, 2050 and 2080). In addition, we measured the four fragmentation metrics described above for three focal regions: Chiapas North, Chiapas South and Oaxaca. For these three regions, we overlaid the protected areas to assess how much of the

cloud forest would be protected and how fragmentation would affect the reserve network.

We quantified the spatial characteristics of the cloud forest patches using Fragstats 3.3 (McGarigal *et al.*, 2002). Patches were delineated with the 8-neighbour rule. This means that the four orthogonal neighbours of a focal cell and the four diagonals were used to delimit a patch. For each of the three regions at present (2010) and for each consensus model at the different future time frames (2030, 2050 and 2080), we estimated mean patch area, total area, number of patches, patch density and the Euclidean nearest neighbour distance through time. We also used a threshold patch size: patches less than 2 km<sup>2</sup> and separated by more than 1 km from other patches were not considered in further analyses. This threshold value was based on the area required for a minimum population size, as suggested by Frankel & Soule (1981), in this case, 45 pairs of quetzals in each patch. We based the minimum patch on quetzals as they had the biggest home range of the species that we considered in this study (Table 1).

Cloud forests occur within a narrow altitudinal range (1500–2500 metres above sea level) such that they resemble an archipelagic system: 'islands' of cloud forests separated from each other by valleys. This spatial configuration may hinder the dispersal of individuals between populations (Epps *et al.*, 2004). To calculate the topographic distance between patches in each of the three regions, we found the centroid of each cloud forest patch. Then, with Landscape Genetics 1.2.3 toolbox (Etherington, 2011) for ArcGis 9.3, we created a layer of straight lines that connected all the possible combination of patches' centroids. Finally, with the surface length tool from ArcGis 3D Analyst and a 90 m DEM produced by NASA and downscaled by CIAT (Jarvis *et al.*, 2008), we measured the topographic distance between all cloud forest patches.

### Estimating extinction risk

Extinction risk is the probability that a species will become extinct or quasi-extinct during a time frame (Burgman *et al.*, 1993). In this study, we use a moving window to estimate the relative extinction risk value of local populations. We calculated the probability of extinction over 100 years using

an approximation for the mean time to extinction of a metapopulation (equation 1) developed by Frank & Wissel (2002):

$$T_x(x) = \frac{1}{v_{agg}} \frac{(M-1)!}{M(M-1)^{M-1}} e^{M/z} z^{M-1}, \quad (1)$$

where  $T_k(x)$  is the mean time to extinction of species  $k$  in region  $x$ ;  $M$  is the number of habitat patches;  $v_x$  is the effective local extinction rate.

The mean time to extinction of a metapopulation (equation 1) is estimated using the effective colonization abilities of subpopulations ( $z$ , equation 2),

$$z = \prod_{i=1}^M \max \left( \sqrt{2}, \sqrt{\frac{1}{2} \left[ \left( \frac{\sum_{j(\neq i)} c_{ij}}{v_i} \right)^{-2} + \left( \frac{\sum_{j(\neq i)} c_{ji}}{v_i} \right)^{-2} \right]^{-1}} \right)^{1/M}, \quad (2)$$

$$c_{ij} = \gamma_k \frac{A_i}{H_k} b e^{-d_{ij}/d_k},$$

where

$$b = \frac{1}{\pi} \arctan \left( \frac{\sqrt{A_j/\pi}}{d_{ij}} \right) \text{ for } d_{ij} \geq \sqrt{A_j/\pi}, \quad (3)$$

and where  $c_{ij}$  is the colonization rate of species  $k$  from patch  $i$  to patch  $j$  based on colonization rates between individual patches  $c_{ij}$  (equation 2–3),  $d_{ij}$  is the distance between patches  $i$  and  $j$  in km (here, we used the topographic distance between patches), and  $A_j$  is the area of patch  $j$ . This model requires relatively few parameters to estimate local extinction rates and colonization rates: the home range of a species  $k$  ( $H_k$ ), mean dispersal distance of species  $k$  in km ( $d_k$ ), emigration rate of young females per unit area ( $\gamma_k$ ) and environmental stochasticity ( $x_k$ ) – see Table 1. The effective local extinction rate ( $v_x$ , equation 4) is based on the local extinction rates of each patch  $v_i$  (equation 5)

$$v_{agg} = \left( \prod_{i=1}^M v_i \right)^{1/M}, \quad (4)$$

$$v_i = \frac{-\ln(0.01)}{100} \left( \frac{A_i}{H_k} \right)^{-x_k}, \quad (5)$$

Grimm & Wissel (2004) show how mean time to extinction can be used to approximate the annual probability of extinction

$$p_k(x) = 1 - e^{-100/T_k(x)}, \quad (6)$$

The model we used to assess metapopulation extinction risk is limited to cases where there are five or more patches (Frank & Wissel, 2002). In some of the scenarios in our study, Chiapas South 2080 and protected areas Chiapas North and Oaxaca in 2050–80, the number of fragments  $M$

decreased to less than five. Therefore when the number of patches fell to below five, the extinction risk of the metapopulation was modelled as the probability that all subpopulations became extinct, assuming they were independent and with no dispersal between them (Nicholson & Possingham, 2006), given by:

$$p_k(x) = \prod_{i=1}^M p_i(x), \quad (7)$$

We estimated the probability of extinction of a subpopulation in a patch  $i$ , using the local extinction rate  $v_i$ , a function of the number of home ranges for the species in a patch (equation 5), and the time frame under consideration (in this case 100 years):

$$p_i = 1 - \exp(-100v_i). \quad (8)$$

## Sensitivity analyses

### Extinction risk

Given all the sources of parameter uncertainty in the metapopulation model, we varied the parameters for the frog model in the Oaxaca region to assess the sensitivity of the estimate of extinction risk to parameter uncertainty. We varied the estimates for the home range, dispersal distance and the fecundity values from half to two times the best estimate values for each parameter.

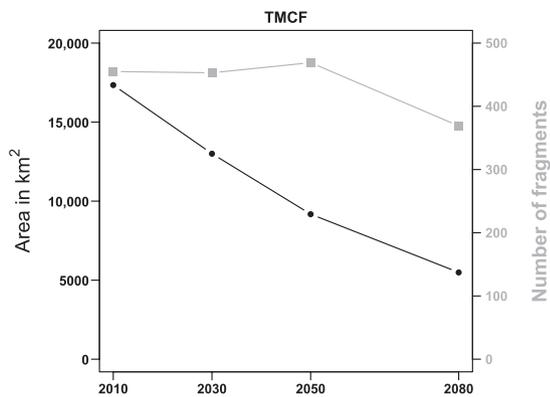
### Consensus model

We also explored the sensitivity of the results to uncertainty regarding whether a cell should be considered climatically suitable for cloud forest in 2080, by altering the number of distribution models required to agree with the condition. Here, we tested for the influence of alternative threshold values for the number of models required to produce a consensus model by calculating the nestedness ‘temperature’ of presence–absence matrices (Rodríguez-Gironés & Santamaría, 2006). We used the package bipartite (Dormann *et al.*, 2008) in R (R Development Core Team, 2007) to perform the calculations.

## RESULTS

### Fragmentation process of the Mexican cloud forests through time

Currently, cloud forests in Mexico cover around 1% of the country (c. 1,734,577 ha) in 455 separated patches. However, the distribution modelling predicted a major and continuous reduction in their extent through time (Fig. 1). For 2030, we estimated that the number of patches would be reduced slightly to 453, and the total area would diminish to 1,300,362 ha. In 2050, our models predicted that



**Figure 1** Predictions of the total area of Mexican cloud forest through time (left axis and black line) and number of fragments (right axis and grey line) with climate change.

917,629 ha might remain suitable for cloud forest in a slightly higher number of fragments (469). Finally, we found that for 2080, less than 30% of current cloud forest areas were likely to remain suitable for this vegetation type in 368 patches.

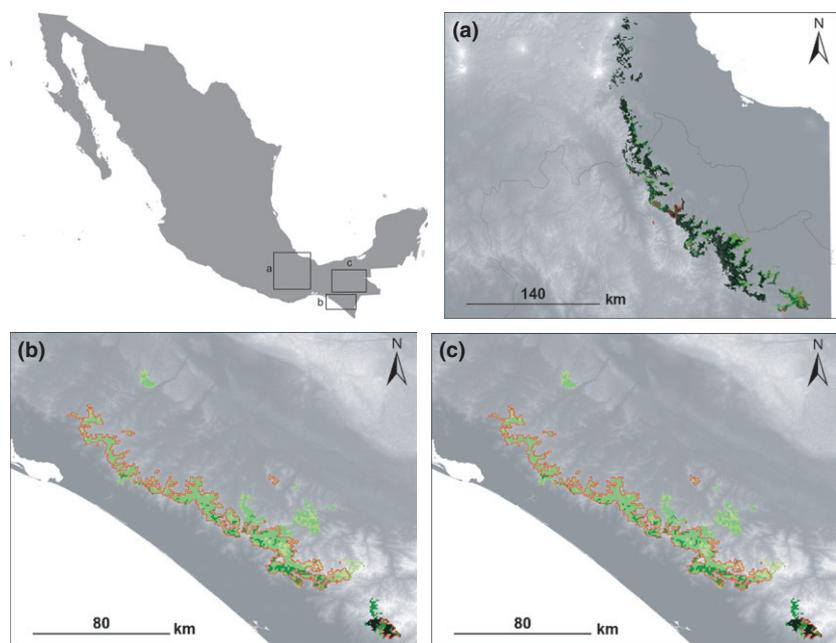
### Fragmentation statistics by region

When we examined the three selected regions (Oaxaca, Chiapas South and Chiapas North), we found a similar pattern to the overall changes in distribution under climate change: the number of fragments increased slightly as the total area decreased, until the reduction in the total area saw patches disappear and the number of patches drop rapidly.

Cloud forests in the Oaxaca region seemed to be the more stable in terms of total area relative to the other regions (Fig. 2a; Table 3a). Currently, Oaxaca has the largest extent, and the least fragmented cloud forest of all three regions.

Although in the future projections the number of fragments increased constantly as climate changed (from 12 to 21), the distance between them did not vary much (2.4–2.6 km; Table 3a). Our models suggested that the more drastic reduction in cloud forest-suitable areas in this region would occur in 2080, with about 40% of the current total cloud forest area becoming climatically unsuitable for cloud forest when assuming only changes in climate are the only threat. Although the mean patch area decreased in the Oaxacan cloud forest in response to climate change, the Euclidean mean distance remains very similar in 2010 and 2080. Unfortunately, this region has the smallest proportion of their cloud forest under protection (around 4% of cloud forest at present). The more pessimistic scenario, which assumes that all the cloud forests outside of protected areas could disappear due to land-use change, produced even more dramatic results, predicting that slightly more than 2% of Oaxacan current cloud forest might remain in only one patch (Fig. 2a red polygons overlapping black areas).

The total area of the cloud forest in Chiapas South (Fig. 2b; Table 3b) is the smallest of the three regions. Currently, this region is not very fragmented, with only 14 patches separated by a mean distance of 6.5 km. The main habitat loss in this region due to climate change is expected to be around 2050, where about 85% of the current-suitable areas for cloud forest are predicted to become unsuitable, and the mean distance between the 18 patches will increase to more than 7.6 km. We predicted that in 2080 the suitable areas for cloud forest will contract dramatically to only two patches covering around 3% of the forest's current extent. Our models predicted that these two patches might remain relatively close together (around 3 km from centroid to centroid). In Chiapas South, about 72% of current cloud forests are in a reserve. However, when we assumed that only the cloud forest within a protected area might remain in 2080



**Figure 2** Close ups of the predicted potential distribution of the cloud forests in three regions in Mexico (inset) are as follows: (a) Oaxaca, (b) Chiapas North and (c) Chiapas South. Current distribution (2010) is shown in light green, darkening through time until 2080 which is shown in black. Currently, protected areas are outlined in red.

Year	Total area (ha)	Number of patches	Mean patch area (ha)	Euclidean mean distance (km)
(a) Oaxaca				
2010	403,180 (16,887)	12 (5)	12,442 (3377)	2.648 (17,223)
2030	362,560 (14,970)	17 (5)	10,256 (2994)	2.400 (17,223)
2050	314,000 (12,779)	17 (4)	7,142 (2994)	2.402 (6,941)
2080	231,575 (5385)	21 (1)	3,644 (5385)	2.646 (-)
(b) Chiapas south				
2010	206,747 (148,876)	13 (13)	14,768 (11,452)	6.548 (496)
2030	161,016 (122,679)	18 (18)	7,667 (4662)	5.449 (6203)
2050	30,305 (20,994)	14 (14)	1,684 (1235)	7.608 (5495)
2080	7,112 (3560)	2 (1)	3,560 (3560)	3.445 (-)
(c) Chiapas north				
2010	385,654 (26,836)	32 (5)	9641 (5367)	3.047 (14,683)
2030	306,607 (22,911)	38 (5)	6968 (4582)	3.273 (1578)
2050	194,698 (9493)	38 (3)	3674 (3164)	3.345 (24,379)
2080	63,074 (274)	28 (1)	1911 (274)	4.481 (-)

**Table 3** Fragmentation statistics for the three regions, numbers in brackets showing the data for forests within the protected area system

(Fig. 2b red polygons overlapping black areas), our models predicted that in this area, only one patch might remain suitable for cloud forest with about 3% of the original cloud forest extent.

Chiapas North (Fig. 2c) is the most fragmented region, currently comprising 40 patches of cloud forest separated by mean Euclidean distance of 3 km (Table 3c). In this region, about 7% of cloud forest is currently protected. By 2050, the extent of suitable areas for cloud forests is expected to halve, while the proportion of cloud forest in reserves is expected to decrease by 60%. The distance between the nearest patches predicted to remain in 2050 that are currently in a protected area will greatly increase (from 15 to 24 km). Finally in 2080, only 16% of current cloud forest might remain in climatically suitable areas and of those, less than 0.5% will be within a reserve in only one patch (Fig. 2c red polygons overlapping black areas).

### Estimated extinction risk

Forest patches in each region had different vulnerabilities to climate change; therefore, the representative species that we used to parameterize the model there had different risks of extinction. Here, we present the extinction risk of the three representative species using the metapopulation model (Fig. 3), but using the joint probability of all populations becoming extinct when there are fewer than 5 patches, as is the case in Fig. 3(b) Chiapas South 2080 and Figs. 3(d–f) Chiapas North and Oaxaca 2050 and 2080.

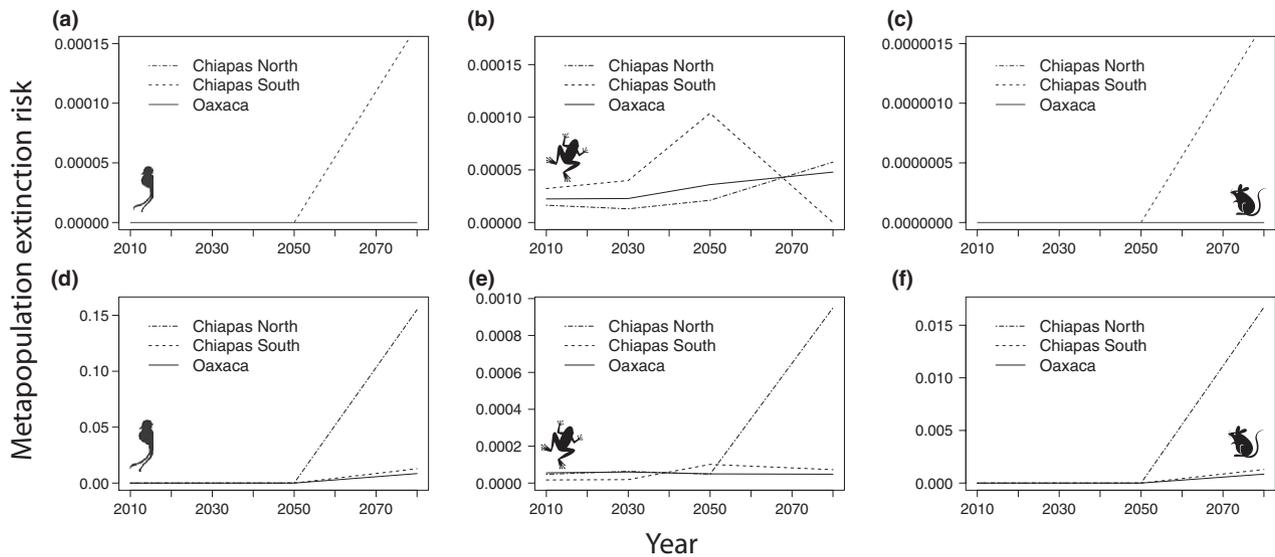
The probability of extinction using the metapopulation model is very small, because the model accounts for recolonization after local extinctions, and all populations would need to disappear to lose the metapopulation as a whole. However, the curve representing the probability of extinction increases through time.

When we analysed the extinction risk of the three representative species using the metapopulation model by region assuming climate change was the only threat to cloud forests,

we found that the populations in Chiapas South were the most threatened (dashed line in Fig. 3a–c). The frog had the highest probability of extinction (Fig. 3b) until 2050 because it had the most limited dispersal ability (Table 1). As the metapopulation model takes into account the recolonizations between patches, the distance between patches and the dispersal distance of the species are very important. The mean Euclidean distance in the Chiapas South region varies between 5.4 and 7.6 km (Table 3c), while the dispersal distance of the frog is about 0.2 km (Table 1). Thus, the distance between patches has a great impact. However, in 2080, the frog's extinction risk in this region drops. This is because in 2080 in Chiapas South the number of predicted fragments is only two, and as the metapopulation model requires at least five subpopulations we estimated the probability of extinction as the joint probability of all populations becoming extinct (equation 7). The joint probability of all populations becoming extinct is almost certainly optimistic, as it assumes all populations are independent. It is based on the local extinction rate, which only takes into account the home range of the species and the extent of the habitat. The predicted remaining fragments have an area of more than 3000 ha each, while the frog's home range is 0.06 ha.

It is also interesting to note that the probability of extinction of populations of quetzal and mice in Chiapas South is effectively zero until 2050 (Figs. 3a and c). In the other two regions, Chiapas North and Oaxaca (dotted line and continuous line in Fig. 3a–c, respectively), the probability of extinction for the quetzal (Fig. 3a) and mouse (Fig. 3c) is always zero. Again, in these two regions only the frog (Fig. 3b) is at increased risk of extinction across time, but the probability is not as high as in Chiapas South.

When we analysed the patterns within protected areas, Chiapas North always had the highest probability of extinction for the three species (Fig. 3d–f). Although we predict that only one patch of cloud forest will remain protected for each of the regions, Chiapas North is predicted to lose more of its suitable habitat (compared to the other two regions).



**Figure 3** Annual probabilities of extinction of the metapopulations of the quetzal, frog and mouse in three regions of the Mexican cloud forests (a–c) and in the protected areas (d–f).

In this case, the most endangered species was the quetzal (Fig. 3e), because this species requires the largest home range. Although the quetzal had the greatest dispersal ability of the three species, it also had the biggest home range, which may make it more susceptible to habitat loss caused by climate change, or in other words in the remaining fragments that are currently in a reserve. This was especially true for those cases in which fewer than five patches remained, entailing a different model for extinction probability (equation 8). The frog (Fig. 3e) appears less threatened than the other two species when only considering protected areas because of their small home range requirements, but the extinction risk here was higher than when considering all remaining cloud forests. The mouse (Fig. 3f) has higher extinction risks in the reserves of Chiapas North than in the reserves of the other two regions, because this region had the highest decrease in suitable areas for cloud forest.

### Sensitivity analyses

#### Extinction risk

Sensitivity analyses for the frog model (Figs. 4a–c) represent how the extinction risk changes according to the values of the different parameters. Home range (Fig. 4a) is the most important parameter, suggesting that a modest error in estimating the home range size of the frog could result in a substantial error in our estimate of extinction risk. The results were less sensitive to error in estimating dispersal distance (Fig. 4b) and quite insensitive to fecundity rate (Fig. 4c).

#### Consensus model

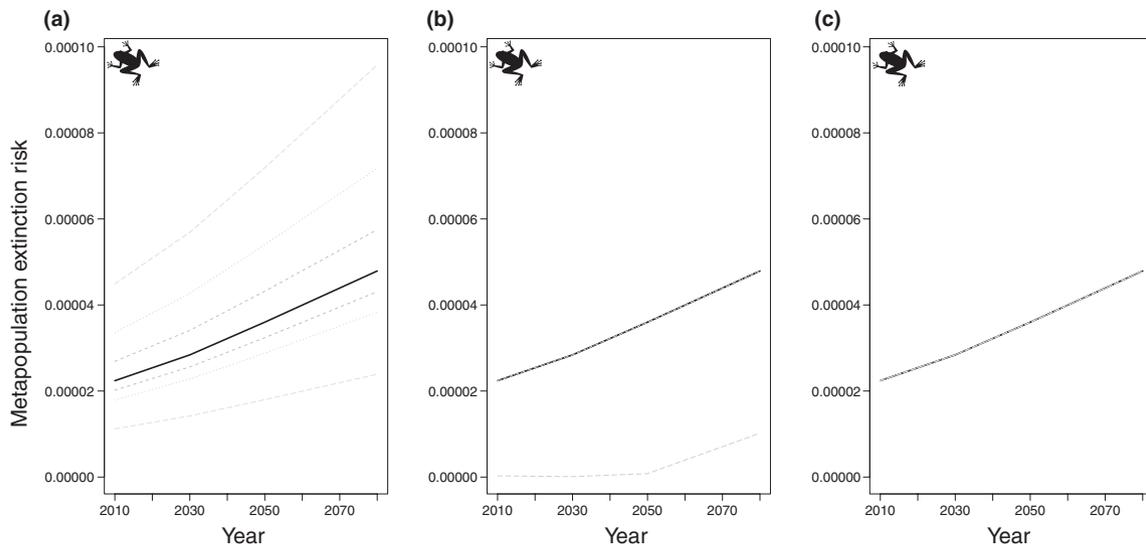
The extent of predicted presence decreased when more models were considered (Table 4). However, the extent of pre-

dicted presence at any given number of models was strongly spatially nested within the area predicted by the next lowest number of models (temperature) (Rodríguez-Gironés & Santamaría, 2006) = 1.272645, indicating substantial agreement about the locations that will remain climatically suitable for cloud forest in 2080.

### DISCUSSION

Measures of species viability such as the models for extinction risk used in this study provide a quantitative and process-based link between patterns of ecosystem change and species persistence and form a sound basis for conservation decision-making. Such models have a strong mathematical basis (Frank & Wissel, 2002) and are relatively easy to apply. Our results suggest that Mexican cloud forest does not have a promising future. The reduction in its area in the next 70 years under climate change is projected to be considerable, and the loss and fragmentation of habitat will result in increasing extinction risk for cloud forest species.

We recognize that there are multiple uncertainties affecting such model predictions; one of the few certainties is that the estimated probabilities are inaccurate. Nonetheless, the relative changes in extinction risk under different landscape scenarios are informative (McCarthy *et al.*, 2003). The relative risks demonstrate the combined impacts of climate change and land clearance and have the potential to allow us to identify which regions and patches are more vulnerable to the threats and potentially rank management strategies. For example, although Chiapas South is relatively prone to climate change impacts, losing over 96% of its cloud forest extent by 2080 (Table 3b), the interactive effects of land-use change and climate change are most pronounced in Chiapas North, suggesting an even more pressing need for land protection in this region. Chiapas North will also experience the smallest and most dispersed



**Figure 4** Sensitivity analysis for the representative frog species in the Oaxacan area. Values for each parameter range from 0.5 to 2 times the parameter value found in the literature.  $H$  = home range (a);  $d$  = dispersal distance (b) and  $y$  = fecundity rate (c).

**Table 4** Extent of cloud forest in 2080 predicted by consensus among different numbers of models

	Number of models agreeing				
	≥ 3	≥ 4	≥ 5	≥ 6	7
Extent of cloud forest predicted in 2080 (km <sup>2</sup> )	6987	5589	4679	3266	1464

Temperature is used as an index of nestedness (Rodríguez-Gironés & Santamaría, 2006). Here, the area of predicted presence at any given threshold was strongly spatially nested within the area predicted by the next lowest threshold (temperature = 1.272645). Temperature values range from zero (highly nested) to 100 (no significant nestedness).

patches by 2080 (Table 3c), placing area-demanding (quetzal) or low-mobility species (frog) particularly at risk in this region.

Models are most often limited by the amount and quality of available data (Burgman *et al.*, 1993). When data are unavailable, using existing data on related species under the assumption that they have similar ecological characteristics to species in the area of interest may be the only option. However, it is necessary to be cautious when interpreting the results. One way of assessing the impacts of parameter uncertainty is by performing sensitivity analyses such as those shown in Figure 4. We found that although the absolute estimates of extinction risk varied, the patterns of increasing extinction risk with time did not. Parameter sensitivity can inform management decisions, for example the relative sensitivity of frog extinction risk to home range estimates compared to dispersal distance or fecundity (Fig. 4) suggests that risk-averse managers may consider reserving extra buffer area rather than intervening directly in the population through

translocation or captive breeding (depending also on the relative costs of each option). Heard *et al.* (2013) provide a similar example in which population and spatial models can be used to support decision-making under uncertainty. Sensitivity analyses can also identify which life history traits have more influence on the extinction risk of a species, and they can also be placed within a decision-making framework to allow decisions to be made that account for uncertainty (Drechsler, 2004; Nicholson & Possingham, 2007).

Other uncertainties included in our analyses are those inherent to climate change modelling and those produced by using a species distribution model. Although no one can predict exactly how the climate will change, there are alternatives to try to reduce the uncertainty. One way is using a consensus model based on a range of available GCMs and to select a threshold of models to create a presence–absence map (Ponce-Reyes *et al.*, 2012). The uncertainties arising from the species distribution models also result from the coarse resolution of the climate layers used to create the models and with errors in presence localities that are used to build the model.

In this paper, we showed that is possible to quickly estimate the extinction risk of species in a threatened ecosystem on a large scale without embarking on a full-blown and expensive population viability analysis (Burgman & Possingham, 2000). Similar methods could be used to assess the effectiveness of alternative management strategies, such as identifying areas that are less prone to extinction for protection, or comparing climate change adaptation strategies. Although for this analysis we considered habitat loss due to changes in climate and land use, other threats could also be incorporated, such as more explicit land-use change models. Instead of assuming future deforestation, for example, it could be empirically predicted by modelling future deforestation based on environmental and socio-economic parameters

(Soares-Filho *et al.*, 2006; Pereira *et al.*, 2010). Other alternatives that could be interesting to test are combining models for decision support (Jankowski & Richard, 1994; Malczewski, 1996; Joerin *et al.*, 2001; Geneletti, 2004) or models of coupled dynamic bioclimatic models with stochastic population models (Keith *et al.*, 2008). The downside of such approaches is that more complex models usually require data that in most cases have not yet been collected (see Leung & Steele, 2013). In the absence of more detailed information, approaches like this study that allow a quick snapshot analysis can be of great value.

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## SUPPORTING INFORMATION

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

**Figure S1** Sensitivity analyses—Examples of testing the parameters of the frog in Chiapas South.

**Figure S2** Sensitivity analyses—Examples of testing the parameters of the frog in Chiapas North.

## BIOSKETCH

This study is part of **Rocio Ponce-Reyes**'s PhD project at the Environmental Decisions Group. Her project is focused on the integration of evolutionary processes in conservation planning. Rocio's main research interest is improving conservation planning strategies in a dynamic environment through the inclusion of ecological end evolutionary processes.

The Environmental Decisions Group is a network of conservation researchers working on the science of effective decision-making to better conserve biodiversity ([www.edg.org.au](http://www.edg.org.au)).

Author Contributions: All authors designed the study. RPR collected the data; RPR and EN analysed the data. All authors contributed to the writing of the manuscript.

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