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Predicting ecosystem collapse: Spatial factors that influence risks to tropical ecosystems

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Abstract Biological traits explain extinction at the species level, but what factors explain collapse at the ecosystem level? Using ecosystem Red List criteria from the International Union for Conservation of Nature, we calculated risk of collapse in El Salvador's ecosystems and determined that it is nonrandom, indicating the existence of explaining factors. We present the first model to predict risk of ecosystem collapse, showing that human density and soil capability are significantly associated with risk of collapse and explain 68% of the total variation. To attain an effective management strategy for global ecosystems, we suggest not only determining risk of collapse, but also the building of simple prediction models to establish priorities, and the founding of a worldwide database at the ecosystem level once a single classification system is agreed upon.

Key words: ecosystem collapse, ecosystem vulnerability, endangered ecosystem, IUCN categories and criteria, Red List of ecosystems.

INTRODUCTION

The risk of extinction is nonrandom across species (Purvis *et al.* 2000a), but ecosystems are also threatened and we are yet unaware of the pattern at the ecosystem level. Since 1700, more than half of the terrestrial biosphere has been transformed, leaving less than a quarter in their natural state by the year 2000 (Ellis *et al.* 2010). The operational definition of ecosystem collapse is an analogue to species extinction, considered to occur when an ecosystem ceases to exist and includes the transformation of characteristic features or replacement by a novel ecosystem (Keith *et al.* 2013).

Risk of ecosystem collapse has not only biological but also societal consequences. When the services supplied by ecosystems decrease below a certain threshold, the life support system that sustains human society ceases to function (Díaz *et al.* 2006), making the conservation of whole ecosystems a priority. Attending the need for present human well-being and the future permanence of the human species, we have employed Red Listing to ascertain the conservation status of ecosystems. In the same way that Red Listing classifies species according to their extinction risk in order to guide policy and interventions at local and regional scales (see International Union for Conservation of Nature (IUCN) 2013a), an assessment of the status of biodiversity at the ecosystem level is already being performed in an independent fashion (Rodríguez *et al.* 2011), and its criteria applied, such as in Venezuela and New Zealand (Rodríguez *et al.* 2010; Holdaway *et al.* 2012).

At the species level, loss of biodiversity is affected by many factors, including the uncontested 'evil quartet', processes of habitat loss, overexploitation, introduced species and secondary extinctions (Diamond 1984), with species extinctions being nonrandom. Intrinsic and extrinsic species attributes increase vulnerability, and allow predictions about extinctions, with such correlates having been assessed in mammals (Collen *et al.* 2011), birds (Pocock 2011) and frogs (Bielby *et al.* 2008). At the ecosystem level, land use change is identified as the major driver for change in terrestrial ecosystems (Sala *et al.* 2000). Therefore the transformation of ecosystems ultimately involves varying loss of surface area (Hannah *et al.* 1995), which could cause some ecosystems to be closer to collapse. Risks posed by such processes might be assessed using the IUCN Red List criteria for ecosystems (Keith *et al.* 2013), specifically criteria A and B, which define ordinal categories of risk based on rates of decline in distribution and the degree to which the distribution is restricted, respectively. Following the logic behind correlates of extinction risks at the species level, factors that place ecosystems at risk of collapse due to land use change can also be identified. In this sense, location, the place where humans have settled, could present a threat to ecosystems considering that loss of habitat is positively correlated to population growth in

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urban areas (DeFries *et al.* 2010). This in turn, is associated with an increased demand of resources that translates into increased land use change towards farmland and infrastructure (Geist & Lambin 2002). Soil type also affects habitat loss (Echeverria *et al.* 2008); fertile soils are sought after for their greater capability in agricultural use, likely to be subject to utilization for crop production. Therefore, the most threatened ecosystems should be those situated on soils with greater production capability. Furthermore, as the majority of the global population is distributed at low altitudes (Cohen & Small 1998), ecosystems at lower elevations are likely to be at higher risk. In addition, anthropogenic activities such as wood extraction and fruit gathering could increase vulnerability of forest ecosystems (Geist & Lambin 2002), whereby ecosystems with more exploitable species may be more vulnerable. Finally, an originally reduced spatial extent should enable intervention to take place across an entire surface in a shorter amount of time: small ecosystems should be more vulnerable than larger ones. Therefore, ecosystems should approach the point of collapse in nonrandom patterns depending on the various factors that define loss of habitat and underlie ecosystem vulnerability in the same manner as nonrandom patterns describe species vulnerability to extinction.

We chose to assess the Republic of El Salvador because it has a history of ecological nondeference (Dull 2008; Kernan & Serrano 2010). The precariousness of El Salvador's ecological state is expressed in that less than 2% of total land area remains as primary forests (Hampshire 1989), which has led to assertions such as 'Nature has already been extinguished in El Salvador' (Terborgh 1999). Since the establishment of the Environmental Law in 1998 (Diario Oficial 1998), the protected area system in El Salvador has managed to include a 0.9% of terrestrial biomes, far from achieving the Convention on Biological Diversity's target of 17% of each terrestrial biome (IUCN & UNEP-WCMC 2013). While it is true that El Salvador maintains the highest population density in Central America (294 p km^{-2}; UNSD 2013) and is the smallest country in continental America (21 000 km^2), El Salvador still hosts numerous ecosystems, ranging from tropical and mangrove forests to grasslands (Vreugdenhil *et al.* 2012), making it an imperative to objectively define their conservation status, and allowing for feasible testing of hypotheses on nonrandom risk of ecosystem collapse. Our aim was to identify factors that explain risk of ecosystem collapse, assessing (i) the relative importance of intrinsic (original surface area, exploitable species and soil capability) and extrinsic factors (human density and elevation) in predicting risk through a multiple regression model, and (ii) the status of ecosystems as classified by the IUCN Red List of Ecosystems criteria.

METHODS

Ecosystem data collection

We collated spatially explicit data on the surface area of ecosystems in El Salvador from the Ministry of Environment and Natural Resources. Specifically, we relied on three polygonal maps of El Salvador's ecosystems: historic distribution and current distributions circa 1998 and 2011 (Vreugdenhil *et al.* 2012). Ecosystems were defined after the United Nations Educational, Scientific and Cultural Organization classification system (UNESCO 1973) which relies on vegetation structure and physiognomy, elevation and hydric regime (see Appendix S1). Ecosystem distribution data for 1998 were generated by bands 4, 5 and 3 from Landsat 7 scenes at a 30×30 m resolution by a combination of paths 18 and 19 with rows 50 and 51. Data for 2011 were generated at a 15×15 m resolution from multiple ASTER tiles. Ground verification during 2011 allowed for independent corroboration of distinct vegetation groups. Historic distribution for ecosystems refers to their potential distributions, based on a combination of criteria for current physiognomy at different elevations obtained from a digital elevation model (DEM) generated from a mosaic of the 2011 ASTER tiles.

Predictors of ecosystem collapse

We define ecosystem vulnerability as the risk of collapse throughout assessed distribution, and use the percentage of surface area change in a given ecosystem as a response variable. To analyse whether some ecosystems are more prone to collapse, we determined if the trend in surface area change is nonrandom. We tested for departures from randomness through a G-test by comparing observed current surface area proportions with the expected proportions according to their potential distribution. Had proportions remained the same, then the rate of decline among ecosystems is considered to be random. If changes in surface area are nonrandom, then factors could be causing some ecosystems to change more than expected by chance, and thus drive loss of surface area. We excluded all ecosystems with anthropogenic origin (Vreugdenhil *et al.* 2012), and grouped some ecosystems in order to meet the requirements of having expected frequencies higher than 1 for the G-test. Tropical evergreen seasonal needle-leaved lowland and broad-leaved altimontane forests along with the tropical altimontane paramo did not present expected frequencies of at least 1 km^2. We therefore grouped tropical evergreen seasonal broad-leaved upper montane and altimontane forests with the paramo based on elevation, and both tropical evergreen seasonal needle-leaved forests based on leaf physiognomy likeness.

The selected variables act as predictors for surface area loss (Appendix S2). We collated data on original surface area, soil suited for cultivation, human population density, elevation and tree species with anthropogenic use. We used ecosystem potential distributions as proxy of the original ecosystem surface area (km^2) (Vreugdenhil *et al.* 2012). Soil crop production values have been expressed in eight soil types (Natural Resources Conservation Service (NRCS)

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2012), describing decreasing soil capability at each type increment, with the first four types being the most suitable for establishing cropland. We defined soil suited for cultivation for each ecosystem as the percentage of total area covered by soil types 1–4 (Natural Resources Conservation Service (NRCS) 2012) and estimated it using the official shapefiles of the agrological map of El Salvador (Ministerio de Medio Ambiente y Recursos Naturales (MARN) 2010). We obtained human population density (1 km grid cells, circa 2000) and elevation data (1 km grid cells, 90 m DEM) from the Center for International Earth Science Information Network (CIESIN) & Centro Internacional de Agricultura Tropical (CIAT) (2005) and Jarvis *et al.* (2008), respectively, and transformed them to vectors. To determine the value of predictor variables for each ecosystem, we used an intersection of the shapefiles of each variable with the historic distribution shapefile. Since each polygon differentially contributed to an ecosystem's total area, we used the weighted mean from all polygons in the resulting intersect for a given ecosystem as the predictor value for that ecosystem. The extraction of highly valuable tree species might lead to land clearance (e.g. the impacts of selective logging, Asner *et al.* 2005). Therefore, a higher number of useful tree species may increase the likelihood of forest loss. We estimated richness of useful tree species for each ecosystem from a list of species in each ecosystem (J. Linares (2011), unpubl. data) and cross-referenced with the list of Mesoamerican tree species sourcebook for farm planting and ecological restoration (Cordero & Boshier 2003), and standardized per 10^4 km^2.

Analyses and model structure

The change in surface area as response variable was logarithmically transformed prior to analysis to normalize distribution. In order to identify correlates with surface area loss and possible multicollinearity, as well as to discern directionality of the relationships in the collated data, we began with a preliminary analysis using a Spearman rank order correlation matrix. No significant multicollinearity was detected and no variables were removed from the following tests (see Appendix S2 for multicollinearity tolerance levels). To account for the increase in type I error due to multiple comparisons, we adjusted *P*-values with the Holm–Bonferroni method.

We then tested the significance of each predictor through simple least square regression analysis. Finally, to build a multivariate model explaining change in surface area using these predictors, we used multiple regression analysis following the model simplification procedure described by Purvis *et al.* (2000b) and generated a minimum adequate model (MAM). We iterated the analysis beginning with all factors included as predictors, and subsequently eliminated the predictor with the lowest marginal reduction in variance at each step, until only significant predictors remained. Following Pocock (2011), since each regression tested an *a priori* hypothesis, corrections for multiple tests were not needed. All tests were one tailed.

Conservation status assessment

To determine conservation status of the 19 terrestrial ecosystems of El Salvador (see Appendix S3), we used the IUCN Red List criteria for ecosystems version 2.0 (Keith *et al.* 2013). The current model for Red List criteria recognizes four symptoms of ecosystem risk based on distribution and function, assessing each one as separate criteria: (A) reduction in geographic distribution; (B) restricted geographic distribution; (C) environmental (abiotic) degradation; and (D) disruption of biotic processes. Criterion (E), quantitative analysis that estimates the probability of ecosystem collapse, allows modelling of ecosystem dynamics and integrates the four symptoms in simulations of ecosystem collapse.

Following our approach on land use change, we focused on rates of decline in distribution and the degree of geographic restriction (criteria A and B). We based our assessment on reduction in geographic distribution (criteria A) by using the difference between current distributions (2011) and a preterit state (1998) to estimate rate of change and project its decline over the last 50 years (1961–2011; criteria A1), within the next 50 years (2011–2061; criteria A2a) and over a period of 50 years including both past and present (1998–2048; criteria A2b) assuming a constant rate of decline in the observed time lapse for a linear loss of surface area. We used the difference between historic and current distributions to estimate historical decline since 1750 (criteria A3). Given a dearth of maps ranging from 1750s, the potential distribution of vegetation is the best approximation we have. We also assessed ecosystems threatened by restricted geographic distribution (criteria B) by using current distribution to calculate the extent of occurrence (extent of minimum convex polygon enclosing all occurrences, criteria B1) and area of occupancy (number of 10×10 km grid cells occupied by at least 1 km^2, criteria B2) for each ecosystem (Fig. 1), specifically by observed or inferred continuing decline (criteria B1a + 2a), threatening processes likely to produce continuing decline (criteria B1b + 2b) and low number of locations (criteria B1c + 2c) (see Keith *et al.* 2013). For qualitative criteria such as ongoing threatening processes, we consulted each ecosystem definition in Vreugdenhil *et al.* (2012), which provided a description of anthropogenic activities likely to cause surface area change.

We estimated percentage of surface area change for each ecosystem by comparing current distribution and historical distribution, with data from the 'ecosystem maps from El Salvador, 2012 update' (Vreugdenhil *et al.* 2012) which uses the UNESCO (1973) classification system. Data consist of three polygonal maps of El Salvador's ecosystems corresponding to each time frame needed to meet the criteria requirements: potential (as proxy of historical distributions) and current distributions *ca.* 1998 and 2011.

Caveats and limitations

It is important to note that the variables that serve as predictors are from the current era, yet the assessment pertains to changes in ecosystems over hundreds of years. Evidently, data for these ecosystems exist only as they are now, which includes original surface area for each ecosystem: no data exist for ecosystems which may no longer exist. There may also be many more explanatory variables other than the ones assessed here that function as possible drivers of ecosystem risk of collapse. Some ecosystems may be more prone to

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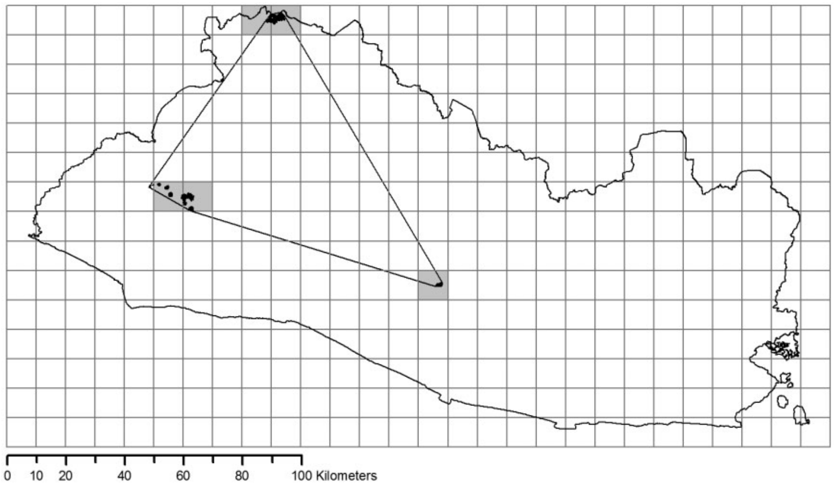

Fig. 1. Distribution of the tropical evergreen seasonal broad-leaved upper montane forests with all occurrences enclosed in a minimum convex polygon (extent of occurrence) and occupied 10 × 10 km grid cells (area of occupancy) by more than 1 km^2.

Table 1. Current ecosystem surface area in El Salvador and deviation from expectation given a random spatial pattern of habitat loss

Ecosystem	Observed (deviation) km^2
Tropical evergreen seasonal needle-leaved forests†	33 (+21)
Tropical evergreen seasonal broad-leaved montane forests, altimontane meadow or paramo†	36 (+29)
Tropical evergreen seasonal broad-leaved alluvial forest, occasionally inundated	94 (+9)
Tropical semi-deciduous broad-leaved well-drained lowland forest	367 (–233)
Tropical semi-deciduous broad-leaved submontane forest	90 (–198)
Tropical semi-deciduous mixed submontane forest	281 (+144)
Tropical semi-deciduous broad-leaved lower montane forest	19 (–21)
Tropical semi-deciduous mixed lower montane forest	134 (+90)
Pacific mangrove forest on clay	384 (+314)
Tropical deciduous broad-leaved lowland forest, well-drained	1229 (–155)

†Contains grouped ecosystems in order to attain the requirements of the G-test proof that does not permit expected numbers smaller than 1 ($P << 0.0001$). See text for ecosystems. Figures are the observed squared kilometers and deviation difference expected per ecosystem.

climate change, and others to anthropogenic variables linked to resource consumption (economic, demographic and agroforestry production variables). Our model is not intended as a be-all and end-all for predicting risk of ecosystem collapse, and our choice reflects the most general and likeliest predictors available to the region.

RESULTS

Predictors of risk of collapse

Risk of collapse is nonrandom (G-test; $P << 0.0001$; Table 1). Current observed proportions of ecosystem surface area differ from what would be expected by chance alone. Ecosystems with smaller remnant area than expected are the tropical deciduous and semi-deciduous broad-leaved forests, which tend to show high soil capability, large original surface area, high human density, low elevation and fewer useful tree species (Table 2).

Although no predictor pair presented multicollinearity (Appendix S2), preliminary results from the correlation matrix indicate that strong correlates for surface area change exist with soil capability and original surface (Table 3). Among predictors, we found strong correlations between soil capability and original surface area, as well as original surface area and elevation. However this pattern changes with single predictor regressions, which show that only soil capability ($t = -1.95$) and now human density ($t = -3.55$) constitute significant correlates (Fig. 2), while original surface area loses significance (Table 4). Soil capability explains 26% of the

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Table 2. Data used for hypothesis tests of predictors for risk of ecosystem collapse

Ecosystem	Surface area change (%)	Soil capability (%)	Original surface area (km^2)	Human density (people per km^2)	Elevation (meters)	Useful tree species (spp per 10^2 km^2)
Tropical semi-deciduous broad-leaved submontane forest	–95.97	28.50	2 230.48	631.64	874.56	1.84
Tropical semi-deciduous broad-leaved lower montane forest	–93.85	15.22	306.09	353.40	1421.58	2.61
Tropical semi-deciduous broad-leaved well-drained lowland forest	–92.11	48.40	4 646.48	241.53	240.95	1.46
Tropical deciduous broad-leaved lowland forest, well-drained	–88.54	29.95	10 725.34	277.36	379.30	0.62
Tropical evergreen seasonal broad-leaved alluvial forest, occasionally inundated	–85.80	83.95	660.51	166.47	12.08	3.18
Tropical semi-deciduous mixed submontane forest	–73.53	8.47	1 062.01	112.50	899.51	2.82
Tropical evergreen seasonal needle-leaved upper-montane forest	–64.48	23.22	84.00	39.81	1996.15	7.14
Tropical semi-deciduous mixed lower montane forest	–60.29	5.34	338.53	51.63	1420.76	2.66
Tropical evergreen seasonal needle-leaved lowland forest	–59.38	0	7.02	55.57	708.41	113.89
Tropical evergreen seasonal broad-leaved upper-montane forest	–51.78	1.52	48.34	194.77	1972.56	10.34
Pacific mangrove forest on clay	–29.22	17.32	543.14	161.21	9.18	1.66
Tropical altimontane meadow or paramo	–20.07	0	3.20	351.81	2185.04	0.00
Tropical evergreen seasonal broad-leaved altimontane forest	65.45	0	6.10	36.38	2441.59	0.00

Labels for factors include units of measure in parenthesis. Values for human density and elevation are weighted averages.

Table 3. Detailed rank order correlation matrix of single predictors and percent of ecosystem surface change, with significance values adjusted on each bivariate comparison by the Holm–Bonferroni method

	Surface area change	Soil capability	Original surface area	Human density	Elevation	Useful tree species
Surface area change	1.00	–0.73*	–0.75*	–0.57	0.41	–0.10
Soil capability		1.00	0.83**	0.34	–0.66	–0.02
Original surface area			1.00	0.36	–0.71*	–0.11
Human density				1.00	–0.21	–0.29
Elevation					1.00	–0.10
Useful tree species						1.00

Probabilities: *$P < 0.05$, **$P < 0.01$ (all tests one-tailed).

observed variation, but it is human density that emerges as the most important predictor (53%) (Table 4).

The correlation pattern holds when we simplified factors with the MAM, accounting for 68.1% of the variance ($P < 0.002$, one tailed) when predicting risk of collapse for declining ecosystems (Fig. 3). Higher risk of collapse correlates with higher human densities ($t = -3.65$; $\beta = -0.662$; $P < 0.01$) and soil capabilities ($t = -2.15$; $\beta = -0389$; $P < 0.05$). Factors eliminated from the model include elevation, useful tree species and original surface area, even when it had previously emerged as significant and presented strong multicollinearity with soil capability in the previous correlation matrix. The most important predictor is again human density, whose effect (beta coefficient) over risk of collapse is almost double as that exerted by soil capability.

Conservation status

Two ecosystems met both criteria for rate of decline in distribution (A) and restricted distribution (B) for

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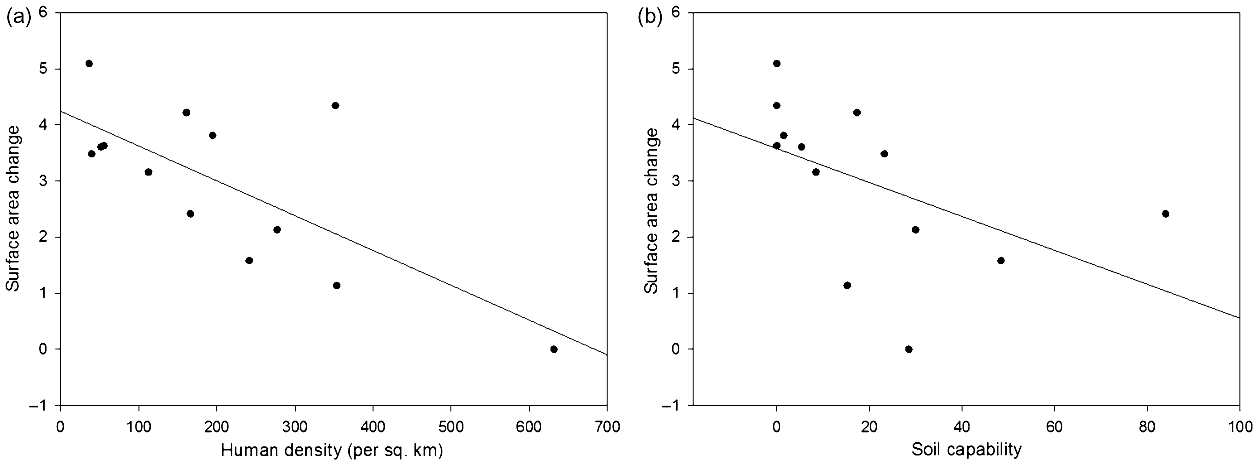

Fig. 2. Bivariate plots of human density (a) and soil capability (b) as predictors of ecosystem surface area change (logarithmically transformed %).

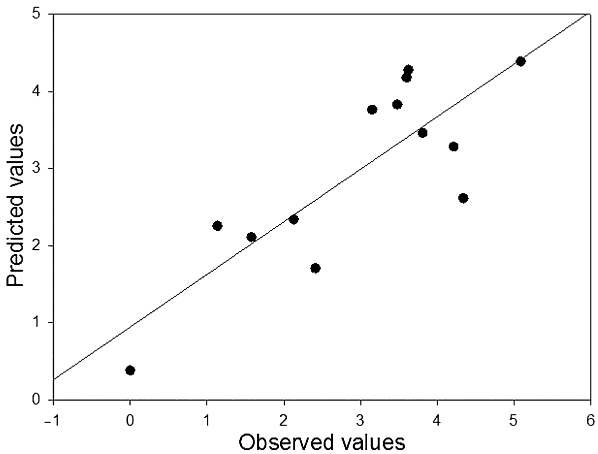

Fig. 3. Prediction of surface area change (logarithmically transformed %) from the minimum adequate multiple regression model for declining ecosystems plotted against the observed values. Fit of predicted to observed values contemplates 68% of the variance explained by human density and soil capability.

classification, 5 only for rate of decline and 11 only for restricted distribution (for data see Appendix S1). Currently, natural terrestrial ecosystems cover 13% (2846 km^2) of El Salvador's land area. All but one of the 19 terrestrial ecosystems qualify as threatened: 1 (5%) has collapsed, 11 (58%) are critically endangered and 6 (32%) are endangered (Table 5). Tropical forests, ranging from 3 to 1229 km^2, comprise up to eight critically endangered and three endangered ecosystems, yet constitute most (80%) of the remaining natural surface area in El Salvador. The mangrove forest of 384 km^2 is endangered. Among grasslands, the smaller (6 km^2) short-grass savanna with evergreen shrubs, the larger savannah with semi-deciduous shrubs (30 km^2) and the paramo (3 km^2) are all critically endangered. Desert type systems such as tropical dunes (23 km^2) classify as endangered, while transitional coastal vegetation (2 km^2) is considered to have collapsed, failing to meet the minimum threshold for extent of occurrence and area of occupancy because this ecosystem stretches along the coast and fails to cover the recommended minimum of at least 1 km^2 of any cell area. Reed swamp formations (55 km^2) are classified as endangered. Scarcely vegetated lava flow (63 km^2) is the only ecosystem to be considered of least concern. More ecosystems meet criteria thresholds for small distributions rather than for rate of decline, indicating that stochastic events should now be considered comparable threats next to anthropogenic impacts.

Table 4. Single predictor least squares regressions for predicting risk of collapse in declining ecosystems (all tests one-tailed)

Predictor	r^2	t	P
Human density	0.53	−3.55	<0.01
Soil capability	0.26	−1.95	<0.05
Elevation	0.20	1.66	0.06
Original surface area	0.17	−1.51	0.08
Useful tree species	0.02	0.48	0.32

DISCUSSION

Ecosystem risk of collapse

Determining ecosystem risk of collapse is a prerequisite for engaging in priority setting and allows strategic resource allocation. Moreover, effectively predicting which ecosystems are more prone to

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Table 5. Conservation status of the 19 terrestrial ecosystems in El Salvador with accompanying criteria justifying threats

Ecosystem	Conservation status (criteria)
Tropical evergreen seasonal broad-leaved upper-montane forest	EN (B1b + 2b)
Tropical evergreen seasonal needle-leaved upper-montane forest	CR (B1a(i)bc + 2b)
Tropical evergreen seasonal needle-leaved lowland forest	CR (B1bc + 2bc)
Tropical evergreen seasonal broad-leaved altimontane forest	CR (B1a(i)bc + 2a(i)bc)
Tropical evergreen seasonal broad-leaved alluvial forest, occasionally inundated	CR (A2ab)
Tropical semi-deciduous broad-leaved well-drained lowland forest	CR (A3)
Tropical semi-deciduous broad-leaved submontane forest	CR (A3)
Tropical semi-deciduous mixed submontane forest	EN (A3;B1a(i)b)
Tropical semi-deciduous broad-leaved lower montane forest	CR (A3)
Tropical semi-deciduous mixed lower montane forest	EN (B1a(i)b + 2a(i)b)
Pacific mangrove forest on clay	EN (B1a(i)b)
Tropical deciduous broad-leaved lowland forest, well-drained	CR (A2ab)
Short-grass savanna lowland with evergreen broad-leaved shrubs, well-drained, *Curatella americana* variant	CR (B1c + 2c)
Short-grass savanna with semi-deciduous broad-leaved shrubs, well-drained, *Crescentia alata* variant	CR (A1 + 2ab;B1a(i) + 1c)
Tropical altimontane meadow or paramo	CR (B1c + 2c)
Scarcely vegetated lava flow	LC
Scarcely vegetated tropical dune and beaches	EN (B1b + 2b)
Tropical coastal vegetation in successional transition on very recent sediments, moderately drained	CO (B2)
Tropical freshwater reed-swamp formation	EN (B1b + 2b)

Red List categories include least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR) and collapsed (CO).

having a higher risk of collapse allows for preventive actions to take place in order to avoid an anthropogenically driven collapse. Our results indicate that ecosystems tend to have higher risk of collapse if they are in the presence of human settlements and hold soils with high production value, driving land use change through agricultural transformation and re-stressing the fact that land use is the most important driver of biodiversity loss (Sala *et al.* 2000). True enough, the system with less soil input and of little production value, vegetated lava flow, is the only nonendangered ecosystem. Coastal vegetation, which we considered collapsed by not meeting a minimum of one occupied cell (criteria B2), is prone to conversion as development for tourism and port infrastructure along the shores increase pressure (Vreugdenhil *et al.* 2012).

Original surface area does not affect risk of ecosystem collapse. This is interesting as it was highly correlated with soil capability, which does ultimately explain 25% of the observed variation and is included in the MAM. Although small ecosystems may have a higher probability of succumbing to stochastic events, within the 13-year study period, we did not detect any difference in the rate of decline due to surface area. Number of exploited tree species also does not affect risk of collapse, perhaps due to the massive international migration resulting from the civil war that engulfed El Salvador from 1980 to 1992, mostly from rural families. Remittances from family members working in the United States became an important source of income, granting higher quality of life by enabling people to cover living expenses and reducing the need for rural households and farmers to obtain fruit, firewood and other raw materials from the remaining natural woodland, resulting in a concomitant retraction of the agricultural frontier (Hecht & Saatchi 2007). This suggests that an alternative explanatory factor to ecosystem risk of collapse may lie in human well-being. Such a hypothesis could predict increased extraction of fruit, firewood or other raw materials in areas with low quality of life where salaries cannot cover living expenses. That elevation does not have a significant effect on risk of collapse was unexpected according to theory, as globally most people reside at low altitudes (Cohen & Small 1998). However, this lack of relation was succinctly corroborated as we did not find any correlation between human density and elevation.

Although we did not assess ecosystem fragmentation, a process different from habitat loss, we did register a very strong positive correlation between ecosystem surface area and the number of fragments ($r = 0.92$, $P << 0.01$), again supporting the fact that smaller ecosystems are at a higher risk of collapse due to stochastic events. Indeed, available empirical evidence shows a significant loss of component species past a loss of 60% of native forest cover in

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fragmented landscapes (Hanski *et al.* 2013). This suggests that explicitly taking into account threats such as fragmentation through thresholds of spatial metrics (number, size, shape of patches and connectivity) as separate criteria in future revisions of the IUCN Red List for ecosystems may be warranted.

Regional context

El Salvador is part of the Mesoamerican Biological Corridor (MBC) and could considerably stand to gain from international cooperation when developing conservation strategies for ecosystems at a regional scale. At the species level, due to its small extent, El Salvador requires integrating neighbouring nations to effectively provide enough habitat for far-roaming species, and the MBC could be part of the solution (Crespin & García-Villalta 2014). A similar desired outcome can be envisioned at the ecosystem level, where contiguous vegetation cover is shared among nations and regional networking could allow assessments to identify critical ecosystems in a regional setting.

Future endeavours

Purvis *et al.* (2000b) demonstrated how traits alone can explain vulnerability to extinction on a species level, while our analysis has shown how basic factors can explain risk of collapse at the ecosystem level. Our model explains up to 68% of the total variance observed on a country level, but predictor variables could be different from the limited amount of factors that we could incorporate into the model. Latitudinal shifts between tropical and temperate systems and the nature of distinct types of ecosystems could change the importance of predictor variables, suggesting that further endeavours need not only increase sample size, but also accrue a more balanced sampling across geographic regions and ecosystem types. Specific variables that could act as factors and should be included in future model predictions include extrinsic factors such as climate change, anthropogenic N deposition, CO^2 emissions and biological invasions, as well as intrinsic factors to ecosystems themselves, such as species identity, community complexity and ecological functioning. The risk these factors pose can be directly assessed under the current Red List criteria C, D and E, although the next step required to model risk of collapse could lay in ecosystem co-collapse. Much like co-extinctions, ecosystem co-collapse can be thought of occurring when loss of species with complementary habitat in each or material flow shared between ecosystems causes a collapse in one system followed by a collapse in a second one. Risk analysis including the threat of co-collapses might give us a clearer picture of the problem and how to deal with it.

Our assessment of ecosystem risk of collapse assumes an annual rate as a basis for cautious extrapolation of a linear loss of surface area, yet one would be hard-pressed to find linear dynamics in ecological systems, especially considering ecological thresholds that could convey a change in state (Hugget 2005). Moreover, the IUCN criteria define ordinal thresholds that identify increasing levels of threat, and do not specify the shape of the trajectory. Although the IUCN definition of collapse describes the event in which an ecosystem ceases to exist, it is not necessary for an ecosystem to reach zero surface area in order to collapse, since after crossing a given threshold, systems might shift states (Scheffer *et al.* 2001). For simplicity's sake, we assumed a linear loss to assess risk of collapse, but precise long-term predictions may require several data points to identify the existence of critical thresholds that could inform managerial decisions. Future research should endeavor to answer the question: do decline of biotic and abiotic processes share the same shape as the trajectory of decline in distribution?

CONCLUDING REMARKS

Despite the precarious state of El Salvador's natural systems, we should be able to recuperate and lower the risk of most ecosystems. That all ecosystems but one in a country as small as El Salvador are threatened should not be disheartening, but instead inspire swift action to take place by conjuring responses from policy and management and widespread global efforts to assess the conservation status of all systems in the biosphere. Moreover, to effectively manage ecosystems, we need not only know which ones are threatened, but also what factors act as drivers of ecosystem collapse, along with simple models to predict which ecosystems are most vulnerable. A world ecosystem database would enable researchers to test the previous hypotheses, but first and foremost a single classification system would need to be agreed upon, yet so far existing schemes range from coarse-grained (e.g. IUCN habitats classification scheme; International Union for Conservation of Nature (IUCN) 2013b) to fine-grained (e.g. European Nature Information System EUNIS; European Environment Agency (EEA) 2013) descriptions, making scale the most pressing matter (Keith *et al.* 2013). Despite the fact that no universal classification for ecosystems exists, our analysis suggests that it is possible to analyse drivers

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of risk for ecosystem collapse at the country level. By approaching the identity of threats, policy is better informed to respond, prescribe ways of preventing collapse and achieve long-term viability of natural systems in order to salvage a nation's natural capital.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Ecosystem raw data and definition.
Appendix S2. Predictor variables.
Appendix S3. Mapped distribution of El Salvador ecosystems.

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