¿Qué factores incrementan la vulnerabilidad de un ecosistema? Evaluación del grado de amenaza de los ecosistemas de El Salvador

Tesis

entregada a la Universidad de Chile

en el cumplimiento parcial de los requisitos para optar al grado de

Magister en Ciencias Biológicas

Facultad de Ciencias

Silvio J. Crespín

Director de Tesis:

Javier A. Simonetti

Santiago, Octubre 2013

Universidad de Chile, Facultad de Ciencias, Escuela de Postgrado

INFORME DE APROBACIÓN DE TESIS DE MAGISTER

Silvio J. Crespín

Ha sido aprobado por la comisión de evaluación de tesis como requisito para optar al grado de Magister en Ciencias Biológicas, en el examen de Defensa Privada de Tesis rendido el lunes 02 de Septiembre 2013.

Director de tesis:

Javier A. Simonetti ....

Comisión de evaluación:

Dra. Mary T. K. Arroyo ....
(Presidente de Comisión)

Dr. Pablo Marquet ....
(Evaluador de Comisión)

> "We abuse land because we see it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect."
>
> — Aldo Leopold

Biografía

Nací en El Salvador (1985). Soy biólogo y me enorgullece tener a la Universidad de El Salvador como mi *alma mater* (2009). Desde el 2011 he formado parte del Laboratorio de Conservación Biológica en la Universidad de Chile, donde mis intereses se centran en biodiversidad y conservación, y discerniendo como comunicar de manera efectiva hallazgos a tomadores de decisiones. En general, planeo investigar cómo diferentes actividades humanas afectan el estado de las interacciones biológicas. Durante mi estancia, específicamente evalué el estado de conservación de los ecosistemas terrestres de El Salvador, usando distintos factores para predecir riesgo de colapso, y finalmente determine como el cambio del uso de tierra ha alterado la el valor de la provisión de servicios ecosistémicos y su importancia relativa al ingreso nacional. Actualmente estoy interesado en averiguar cómo países sin paisaje natural aun pueden proteger su biodiversidad restante, a través de estrategias de conservación innovadoras. Mi meta a largo plazo es salvar la tierra, comenzando con El Salvador.

AGRADECIMIENTOS

A mi familia, quienes hicieron posible mis estudios, y creyeron en mí y en mi visión para un mejor El Salvador.

A Javier A. Simonetti, por enseñarme lo que es hacer ciencia y compartir mi pasión por hacer conservación que impacte. Agradezco su confianza y paciencia.

A Laura, por acompañarme en esta aventura que se llama vida.

A mis amigos, por formar parte de mi familia en Chile, compartieron su casa cuando lo necesite y me dieron ánimo durante momentos difíciles.

A José Linares, Vladlen Henríquez y Néstor Herrera, por su apoyo en la obtención de los mapas y ayuda en SIG. Al Ministerio de Medio Ambiente y Recursos Naturales de El Salvador por permitirme el uso de los shapefiles necesarios para ambos manuscritos.

A la Facultad de Ciencias de la Universidad de Chile, por apoyarme durante mi primer año de estudios con una Beca de Arancel.

A la Agencia de Cooperación Internacional de Chile, por su Beca para realizar mis estudios.

ÍNDICE

Agradecimientos i
Indice ii
Resumen 1
Abstract 2
General Introduction 3
References 5

Chapter I: Predicting ecosystem risk of collapse, an example from El Salvador

Abstract 7
Introduction 7
Methods 10
Results 13
Discussion 17
Acknowledgements 19
Literature Cited 20

Chapter II: Loss of ecosystem services calls for a change in land use policy in El Salvador

Abstract 24
Introduction 25
Methods 26
Results 29
Discussion 33
Acknowledgements 37
Literature cited 37

General Conclusions 41

RESUMEN

Cambios en el uso de suelo durante el último siglo han provocado la transformación de los biomas, y nos ha desafiado con una dualidad aparente de abastecer demanda humana y conservar la biodiversidad de la cual extraemos los bienes y servicios que nos sustentan. En este marco, surge la necesidad de evaluar el estado de conservación a nivel de ecosistema, identificar los factores que predicen el riesgo de colapso de ecosistemas y determinar las repercusiones que afectan la sociedad humana. En el primer capítulo, evaluamos el estado de conservación de los ecosistemas de El Salvador utilizando los criterios de la Lista Roja de la UICN, y utilizamos la consiguiente pérdida de superficie como proxy de vulnerabilidad para predecir el riesgo de colapso de ecosistemas, a la vez que construimos un modelo mínimo adecuado factores que predigan riesgo a colapso. En el segundo capítulo, estimamos como pérdida de superficie de ecosistemas ha impactado la provisión de servicios ambientales en El Salvador, un país con necesidad de regulación de los daños causados por desastres naturales al sufrir descapitalización sus biomas. Los principales hallazgos son los siguientes: (1) la pérdida de superficie de ecosistemas no es aleatoria, por lo que factores deberían predecir el riesgo de colapso, tales como (2) la densidad humana y la capacidad de los suelos, ambos significativamente asociados con el riesgo de colapso. (3) Durante el período de 13 años evaluado, el valor de los servicios ambientales en El Salvador se redujo en un 2,6% ó $ 258,5 millones desde $ 9764,4 millones por año hasta $ 9505,9 millones por año, lo que actualmente equivale al 44% de su PIB. Concluimos que el cambio de uso de la tierra, impulsado por una mayor demanda por espacio y producción de alimento, a menos que se desarrolle estratégicamente, seguirá afectando negativamente a la sociedad humana, como se evidencia en un país donde cada desastre natural representa el 3,6% del PIB al año, una pérdida que podría ser mitigada con la provisión perdida de servicios ecosistémicos.

ABSTRACT

Land use change in the last century has caused the transformation of biomes, challenging us with the seemingly opposing duality of supplying human demand and conserving the biodiversity from which we extract the goods and services that sustain us. From this framework, the need arises to assess conservation status at the ecosystem level, identify factors that predict ecosystem risk of collapse and determine the repercussions felt by human society. In the first chapter, we assessed the conservation status of the ecosystems of El Salvador using IUCN Red List criteria, and used the resulting loss of surface area as proxy for predicting risk of collapse while we built a minimum adequate model with possible predictor factors. In the second chapter, we estimated how loss of ecosystem surface area has impacted ecosystem service value in El Salvador, a country with need of services to regulate natural disaster damages and avoid decapitalization. Main findings include the following: (1) loss of ecosystem surface area is non-random, allowing factors to act as predictors of risk of collapse, (2) such as human density and soil capability, which are significantly associated with ecosystem risk of collapse. (3) During the assessed 13 year period, ecosystem service value in El Salvador declined by 2.6% or $258.5 million from $9764.4 million per year to $9505.9 million per year, and currently equates to 44% of its GDP. We conclude that land use change, driven by increased demand for living space and food production, unless strategically developed, will continue to negatively affect human society, as evidenced in a country where each natural disaster represents 3.6% of a year's GDP, a loss that could be mitigated with the lost provision of ecosystem services.

GENERAL INTRODUCTION

Biodiversity is threatened by habitat loss and fragmentation associated with extensive forestry and agricultural industry and human settlement, factors affecting the quantity and quality of remaining habitat (Matson et al. 1997). Changes threaten biodiversity at all levels, and impinges upon human well-being. Assessing both the conservation status along with the factors that affect the vulnerability of species to extinction allows the development of conservation strategies and recovery programs (Hayward 2011). However, in nearly five decades, the status of only 65,521 species have been assessed (IUCN 2013), which amount to just 0.8% of the 8.7 million species estimated to exist (Mora et al. 2011). Furthermore, the assessment contains a taxonomic bias toward higher vertebrates (Stuart et al. 2010). Therefore, a comprehensive assessment of biodiversity at the species level would involve a significant amount of time and effort, which instead could be used to implement conservation actions (Cowling et al. 2004). A complement to using species to assess the status of biodiversity is to assess it at the ecosystem level. This approach could result in shorter times for analysis due to fewer units to evaluate, as whole ecosystems comprise the units to be assessed instead of individual species (Rodriguez et al. 2011). Even if a complete assessment of the status of all species were available, assessing biodiversity at different levels of organization is a need that has long been recognized, especially at the ecosystem level. Ecosystem conservation is potentially proactive, protecting habitats before single species die out, and the processes that give rise to the services that human society requires emerge from the interaction of a multitude of component species (Noss 1996). Ecosystem conservation is a pressing matter that cannot be ignored, hence evaluating their status is a pressing need.

At the species level, intrinsic attributes such as body size, geographic range, habitat breadth and extrinsic factors such as habitat loss, overexploitation or persecution, often explain risk of extinction faced by mammals and birds (Pocock 2011, Collen et al. 2011). In the same way, factors could explain vulnerability to human disturbance at the ecosystem level. To date, only Venezuela (Rodriguez et al. 2010) and New Zealand (Holdaway et al. 2012) have assessed the conservation status of their ecosystems, but not the factors that affect their vulnerability. In fact, among the 500 most recent publications that consider the terms "ecosystem* AND vulnerabili*" in the ISI Web of Knowledge, none have yet approached factors that could explain ecosystem risk of collapse.

Changes in the status of ecosystems affect goods and services they provide to human society (Millennium Ecosystem Assessment 2005). Since landscape transformation effectively changes the provision of ecosystem services (e.g.: Kreuter et al., 2001, Zhao et al., 2004, Yoshida et al. 2010), it also represents a reduction of natural capital (Diaz et al. 2006). However, we have yet to evaluate the significance of changes in the state of ecosystems and loss of ecosystem services with respect to the material welfare of human society.

Within this framework, in the first chapter I determine the conservation status of the terrestrial ecosystems of El Salvador, and identify factors that account for risk of collapse. In the second chapter, I insert the ecosystem conservation status into a socio-economic context, by determining the loss of ecosystem services expressed in monetary losses to the subsidies felt by the Salvadoran people.

Conservation strategies require that we effectively know the status of biodiversity, and decision makers within policy need to be informed of the consequences regarding loss of biodiversity. Ecologists should endeavor to pursue such a framework, predicting which ecosystems are most vulnerable to collapse and the socioeconomic consequences of ignoring this. We anticipate these findings to help achieve this goal.

REFERENCES

Collen, B., L. McRae, S. Deinet, A. De Palma, T. Carranza, N. Cooper, J. Loh and J.E.M. Baillie. 2011. Predicting how populations decline to extinction. Philosophical Transactions of the Royal Society B-Biological Sciences 366:2577-2586.

Cowling, R.M., A.T. Knight, D.P. Faith, S. Ferrier, A.T. Lombard, A. Driver, M. Rouget, K. Maze, and P.G. Desmet. 2004. Nature conservation requires more than a passion for species. Conservation Biology 18:1674–1676.

Díaz, S., J. Fargione, F.S. Chapin, and D. Tillman. 2006. Biodiversity loss threatens human well-being. PLoS Biol 4:e277.Hayward, M.W. 2011. Using the IUCN Red List to determine effective conservation strategies. Biodiversity and Conservation 20:2563-2573.

Holdaway, R.J., S.K. Wiser, and P.A. Williams. 2012. Status assessment of New Zealand's naturally uncommon ecosystems. Conservation biology 26:619-629.

IUCN (International Union for Conservation of Nature). 2013. IUCN Red List of threatened species. Version 2012.2. IUCN, Species Survival Commission, Gland. Available from http://www.iucnredlist.org (accessed March 2013).

Kreuter, U.P., H.G. Harris, M.D. Matlock, and R.E. Lacey. 2001. Change in ecosystem service values in the San Antonio area. Ecological Economics 39:333-346.

Matson, P.A., W.J. Parton, A.G. Power, and M.J. Swift. 1997. Agricultural intensification and ecosystem properties. Science 277:504-509.

Millennium Ecosystem Assessment. 2005. Ecosystems and human wellbeing: synthesis. Island Press, Washington D.C, USA.

Mora, C., D.P. Tittensor, S. Adl, A.S.B. Simpson, and B. Worm. 2011. How many species are there on Earth and in the ocean? PLoS Biology 9:e1001127.

Noss, R. F. 1996. Ecosystems as conservation targets. Trends in Ecology and Evolution 11: 351.

Pocock, M.J.O. 2011. Can traits predict species' vulnerability? A test with farmland passerines in two continents. Proceedings of the Royal Society B 278:1532-1538.

Rodríguez, J.P., F. Rojas-Suárez, and D. Giraldo Hernández. (eds.) 2010. Libro Rojo de los ecosistemas terrestres de Venezuela. Provita, Shell Venezuela and Lenovo Venezuela. Caracas, Venezuela.

Rodríguez, J.P., K.M. Rodríguez-Clark, J.E.M. Baillie, N. Ash, J. Benson, T. Boucher, C. Brown, N.D. Burgess, B. Collen, M. Jennings, D.A. Keith, E. Nicholson, C. Revenga, B. Reyers, M. Rouget, T. Smith, M. Spalding, A. Taber, M. Walpole, I. Zager, and T. Zamin. 2011. Establishing IUCN Red List criteria for threatened ecosystems. Conservation Biology 25:21-29.

Stuart, S.N., E.O. Wilson, J.A. McNeely, R.A. Mittermeier, and J.P. Rodríguez. 2010. The barometer of life. Science 328:177.

Yoshida, A., H. Chanhda, Y. M. Ye, and Y. R. Liang. 2010. Ecosystem service values and land use change in the opium poppy cultivation region in Northern Part of Lao PDR. Acta Ecologica Sinica 30:56-61.

Zhao, B., E. Kreuter, B. Li, Z. J. Ma, J. K. Chen, and N. Nakagoshi. 2004. An ecosystem service value assessment of land-use change on Chongming Island, China. Land Use Policy 21:139-148.

Chapter I

PREDICTING ECOSYSTEM RISK OF COLLAPSE, AN EXAMPLE FROM EL SALVADOR

ABSTRACT

Can we predict which ecosystems collapse? Biological traits at the species level explain extinction, but none are yet known at the ecosystem level. Using ecosystem Red List criteria from the IUCN, we calculated risk of collapse in El Salvador's ecosystems and determined that it is non-random. Also, 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 world-wide database at the ecosystem level once a single classification system is agreed upon.

Keywords: Ecosystem vulnerability; ecosystem collapse; endangered ecosystems; IUCN categories and criteria; Ecosystem Red List

INTRODUCTION

Factors leading to extinction in a non-random pattern at the species level have been supported in past studies (Raup 1994, Russell et al. 1998, Purvis et al. 2000), yet none have been posited at the ecosystem level. Analogue of species extinction is the operational definition of ecosystem collapse as an endpoint for ecosystems, considered to occur when an ecosystem ceases to exist, including the transformation of characteristic features or replacement by a novel ecosystem (Keith et al. 2013).

When the functional processes supplied by ecosystems decrease below a certain threshold, the life support system that sustains human society ceases to function (Costanza et al. 1997), making the conservation of whole ecosystems a priority over single species. In the same way that red lists now classify species by extinction risk, guiding policy and interventions at all levels (see IUCN 2013), a red list of ecosystems has already begun (Rodriguez et al. 2011), and its criteria applied, such as in Venezuela (Rodriguez et al. 2010) and New Zealand (Holdaway et al. 2012). Loss of biodiversity is affected by many factors, including the uncontested 'evil quartet', processes of habitat loss, over-exploitation, introduced species and secondary extinctions (Diamond 1984), with species extinctions seldom being random. Many studies have explored statistical differences in extinction vulnerability looking to make predictions about extinctions with species attributes, with such correlates having been assessed in mammals (Purvis et al. 2000, Davidson et al. 2009, Collen et al. 2011), birds (Owens & Bennet 2000, Pocock 2011), and frogs (Bielby et al. 2008). With collapse having been defined as analogue to extinction, loss of biodiversity should also be approached at the ecosystem level in the same manner as nonrandom patterns describe species vulnerability to extinction.

The transformation of ecosystems ultimately involves loss of surface area, which varies among ecosystems, and causes some ecosystems to be closer to collapse. Therefore, if loss of surface area increases the risk of collapse, then ecosystems will approach the point of collapse in nonrandom patterns depending on the various factors that define loss of habitat and that underlie ecosystem vulnerability. We base our predictions on the most well-known factors, and focus on tropical systems, which are the most diverse (Pimm & Raven 2000, Bradshaw et al. 2008, Gibson et al. 2011). Beginning with location, the place where humans have settled could present a threat to ecosystems, due to the loss of habitat that is positively correlated to population growth in 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 greatly affects deforestation (Wilson et al. 2005, Echeverria et al. 2008); fertile soils are sought out 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. Moreover, taking into account that the majority of the global population is distributed at low altitudes (Cohen & Small 1998), ecosystems at lower elevations are likely to correlate with higher risk of collapse. In addition, anthropogenic activities such as wood extraction and fruit gathering could increase vulnerability in forest ecosystems (Geist & Lambin 2002). Finally, a reduced spatial extent should increase accessibility to ecosystems, enabling intervention to take place across an entire surface in a shorter amount of time: small ecosystems should be more vulnerable than larger ones.

We chose to assess the Republic of El Salvador (Fig. 1) because it has a history of ecological non-deference (Dull 2008, Kernan & Serrano 2010). Moreover, because of its size (21,000 km^2), El Salvador is small and well known enough to count with data on the pre-established predicting factors of vulnerability to allow a country-level assessment along with a diverse array of ecosystems, threats, and impacts. The precariousness of El Salvador's ecological state is expressed in that less than 2% of total land area remains as primary forests (Hampshire 2001) which has led to assertions such as "Nature has already been extinguished in El Salvador" (Terborgh 1999). Despite these facts and its small extension, El Salvador still hosts numerous types of vegetation cover ranging from distinct tropical and mangrove forests to grasslands (Vreugdenhil et al. 2012), making it imperative that we objectively define their conservation status and establish to what extent a recovery is feasible.

Our aim was to construct a model to predict ecosystem collapse, by first assessing the conservation status of El Salvador's natural ecosystems, determining whether ecosystem collapse is nonrandom, and finally using the observed loss of ecosystem distribution as proxy of risk of collapse to identify factors that predict ecosystem risk of collapse.

Fig 1. Location of study area, El Salvador.

METHODS

Conservation status assessment

To determine conservation status of the 19 terrestrial ecosystems of El Salvador and assess the risk of collapse throughout their current distribution, we used the IUCN Red List criteria for threatened ecosystems (Rodriguez et al. 2011), based on surface area and rates of decline (Table 1). We used the difference between current ecosystem distributions and a preterit state to estimate rate of change and project an estimated short term decline in distribution over the last 50 years (criteria A1), within the next 50 years (criteria A2) and over a period of 50 years including both past and present (criteria A3). We used the difference between potential and current distributions to calculate historical decline in the last 500 years (criteria B1). We used the current distribution map to calculate the extent of occurrence (criteria C1) and area of occupancy (criteria C2) for each ecosystem between 100-20,000 km^2, as well as to determine which ecosystems qualified for very small distribution thresholds, 10-100 km^2 (criteria D).

Table 1. Categories and criteria (*sensu* Rodriguez et al. 2011) used for the El Salvador ecosystem conservation status assessment.

Criterion	Subcriterion	Status
A: Short-term decline (in distribution or ecological function) on the basis of any subcriterion	1. observed, estimated, inferred or suspected decline in distribution of	
	≥80%,	CR
	≥50%, or	EN
	≥30%	VU
	over the last 50 years	
	2. projected or suspected decline in distribution of	
	≥80%,	CR
	≥50%, or	EN
	≥30%	VU
	within the next 50 years	
	3. observed, estimated, inferred, projected, or suspected decline in distribution of	
	≥80%,	CR
	≥50%, or	EN
	≥30%	VU
	over any 50-year period, where the period must include both the past and the future	
	4. relative to a reference state appropriate to the ecosystem, a reduction or likely reduction of ecological function that is	
	(a) very severe, in at least one major ecological process, throughout ≥80% of its extant distribution within the last or next 50 years;	CR
	(b1) very severe, throughout ≥50% of its distribution within the last or next 50 years;	EN
	(b2) severe, in at least one major ecological process, throughout ≥80% of its distribution within the last or next 50 years;	EN
	(c1) very severe, in at least one major ecological process, throughout ≥30% of its distribution within the last or next 50 years;	VU
	(c2) severe, in at least one major ecological process, throughout ≥50% of its distribution within the last or next 50 years.	VU
	(c3) moderately severe, in at least one major ecological process, throughout ≥80% of its distribution within the last or next 50 years	VU

B: Historical decline (in distribution or ecological function) on the basis of either subcriterion 1 or 2	1. estimated, inferred, or suspected decline in distribution of ≥90%, ≥70%, or ≥50% in the last 500 years	CR EN VU
	2. relative to a reference state appropriate to the ecosystem, a very severe reduction in at least one major ecological function over ≥90%, ≥70%, or ≥50% of its distribution in the last 500 years	CR EN VU
C: Small current distribution and decline (in distribution or ecological function) or very few locations on the basis of either subcriterion 1 or 2	1. extent of occurrencec estimated to be ≤100 km2, ≤5,000 km2, or ≤20,000 km2	CR EN VU
	and at least one of the following: (a) observed, estimated, inferred, or suspected continuing decline in distribution, (b) observed, estimated, inferred, or suspected severe reduction in at least one major ecological process, (c) ecosystem exists at only one location, 5 or fewer locations, or 10 or fewer locations. or	CR EN VU
	2. area of occupancyc estimated to be ≤10 km2, ≤500 km2, or ≤2000 km2 and at least one of the following:	CR EN VU
	(a) observed, estimated, inferred, or suspected continuing decline in distribution, (b) observed, estimated, inferred, or suspected severe reduction in at least one major ecological process, (c) ecosystem exists at only one location, 5 or fewer locations, or 10 or fewer locations	CR EN VU
D: Very small current distribution, estimated to be	≤5 km2, ≤50 km2, or ≤100 km2, and serious plausible threats, but not necessarily evidence of past or current decline in area or function.	CR EN VU

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 which heavily relies on vegetation structure and physiognomy, elevation, and hydric regime. 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.

Predictors of ecosystem collapse

To analyze whether some ecosystems are more prone to risk of collapse, we first determined if the trend in surface area change is non-random by testing for departures from randomness. We compared observed current surface area proportions with the expected proportions had they not changed from the potential distribution through a G-test. If changes in surface area are non-random, 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 that did not have potential distributions for being of anthropic origin (Vreugdenhil et al. 2012), and grouped some ecosystems in order to meet the requirements of the G-test. We grouped high montane tropical evergreen seasonal broad-leaved forests with the paramo based on elevation, and both tropical evergreen seasonal needle-leaved forests based on leaf physiognomy likeness.

We define ecosystem vulnerability as the risk of collapse throughout assessed distribution, following the IUCN Red List of Ecosystems categories (Keith et al. 2013), and use the percentage of surface area change in a given ecosystem as a response variable. The previous hypotheses were used to select variables to act as predictors for surface area loss. We collated data on original surface area, soil suited for cultivation, human population density, elevation and tree species with anthropogenic use. We estimated the original ecosystem surface area (km^2) of each ecosystem using the "ecosystem maps from El Salvador, 2012 update" (Vreugdenhil et al. 2012). We defined soil suited for cultivation for each ecosystem as the percentage of total area covered by soil types suited for cultivation (types 1-4) according to the U.S. Natural Resources Conservation Service's National Soil Survey Handbook (NRCS 2012) and estimated it using the official agrological map of El Salvador (MARN 2010). We obtained human population density and elevation data (resolution of 1 km$^{2)}$ from the Center for International Earth Science Information Network (2000) and Jarvis et al. (2008), respectively. To determine the values of these factors (human density and elevation) for each ecosystem, we used an intersect of the shapefiles of each factor with the original ecosystem surface area shapefile. Since each polygon differentially contributed to an ecosystem's total area, we used the weighted mean from all polygons in a given ecosystem as the predictor value for that ecosystem. We estimated richness of useful tree species for each ecosystem from a list of species presence/absence data in each ecosystem (J. Linares, unpublished data) and cross referenced with the list of Mesoamerican tree species sourcebook for farm planting and ecological restoration (Cordero & Boshier 2003), and standardized per 10,000 km^2.

Analyses

The change in surface area as response variable was logarithmically transformed prior to analysis to normalize distribution. We began with a preliminary analysis using a spearman rank order correlation matrix 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. 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. (2000) 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.

RESULTS

Conservation status

We applied the IUCN red list guidelines to assess the conservation status of the 19 terrestrial ecosystems of El Salvador (Table 2). All ecosystems qualify as threatened: 10 (53%) are critically endangered, 7 (37%) are endangered and 2 (11%) are vulnerable. Currently, natural terrestrial ecosystems cover 13% (2,846 km^2) of El Salvador's land area. Tropical forests, whose surface area range from 3 to 1229 km^2 comprise most (80%) of the remaining natural surface area in El Salvador, are made up of 6 ecosystems considered critically endangered and 4 endangered. The mangrove forest of 384 km^2 is endangered. Among grasslands, the smaller (6 km^2) short-grass savanna with evergreen shrubs is endangered, while the larger savannah with semi deciduous shrubs (30 km^2) and the paramo (3 km^2) are critically endangered. Desert type systems such as transitional coastal vegetation (2 km^2) and tropical dunes (23 km^2) classify as critically endangered and endangered, respectively. Both scarcely vegetated lava flows (63 km^2) and reed swamp formations (55 km^2) are classified as vulnerable. Some ecosystems met multiple criteria for classification. More ecosystems meet criteria thresholds for small distributions than for rate of decline, indicating that stochastic events should now be considered comparable threats next to anthropogenic impacts.

Table 2. 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 (C2c;D)
Tropical evergreen seasonal needle-leaved upper-montane forest	EN (C2ac;D)
Tropical evergreen seasonal needle-leaved lowland forest	CR (C2c;D)
Tropical evergreen seasonal broad-leaved altimontane forest	CR (C2a)
Tropical evergreen seasonal broad-leaved alluvial forest, occasionally inundated	CR (A2+3)
Tropical semi-deciduous broad-leaved well-drained lowland forest	CR (B)
Tropical semi-deciduous broad-leaved submontane forest	CR (B)
Tropical semi-deciduous mixed submontane forest	EN (B;C2a)
Tropical semi-deciduous broad-leaved lower montane forest	CR (B)
Tropical semi-deciduous mixed lower montane forest	EN (C2a)
Pacific mangrove forest on clay	EN (C2a)
Tropical deciduous broad-leaved lowland forest, well-drained	CR (A2+3;B1)
Short-grass savanna lowland with evergreen broad-leaved shrubs, well-drained, *Curatella americana* variant	EN (D)
Short-grass savanna with semi-deciduous broad-leaved shrubs, well-drained, *Crescentia alata* variant	CR (A2+3)
Tropical altimontane meadow or paramo	CR (C2c;D)
Scarcely vegetated lava flow	VU (C2c;D)
Scarcely vegetated tropical dune and beaches	EN (D)
Tropical coastal vegetation in succesional transition on very recent sediments, moderately drained	CR (D)
Tropical freshwater reed-swamp formation	VU (D)

Predictors of risk of collapse

We analyzed risk of collapse in the 13 natural ecosystems found in the potential distribution map. Risk of collapse is non-random (G-test; $p<<0.0001$; Table 3). Current observed proportions of ecosystem surface area differ from what would be expected by chance, allowing for the possibility of factors to act as predictors of risk of collapse. Ecosystems with less area than expected if surface loss was random proportional to original surface, are the tropical deciduous and semi-deciduous broad-leaved forests, which tended to show high soil capability, large original surface area, high human density, low elevation and few useful tree species.

Table 3. Present area of ecosystems in El Salvador. Figures are the observed and expected km^2 per ecosystem. Some ecosystems were grouped in order to attain the requirements of the G-test proof that does not permit expected numbers smaller than 1 ($p << 0.0001$).

Biomes	Observed (expected) km^2
Tropical evergreen seasonal needle-leaved forests	33(12)
Tropical evergreen seasonal broad-leaved montane forests, altimontane meadow or paramo	36(7)
Tropical evergreen seasonal broad-leaved alluvial forest, occasionally inundated	94(85)
Tropical semi-deciduous broad-leaved well-drained lowland forest	367(600)
Tropical semi-deciduous broad-leaved submontane forest	90(288)
Tropical semi-deciduous mixed submontane forest	281(137)
Tropical semi-deciduous broad-leaved lower montane forest	19(40)
Tropical semi-deciduous mixed lower montane forest	134(44)
Pacific mangrove forest on clay	384(70)
Tropical deciduous broad-leaved lowland forest, well-drained	1229(1384)

Preliminary results indicate that strong correlates for surface area change exist with soil capability and original surface (Table 4). 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, while original surface area loses significance (Table 5). Although soil capability explains 26% of the model's variation, it is human density that emerges as the most important predictor (53%).

Table 4. Detailed rank order correlation matrix of single predictors and % 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	-0.73*	1.00	0.83**	0.34	-0.66	-0.02
original surface area	-0.75*	0.83**	1.00	0.36	-0.71*	-0.11
human density	-0.57	0.34	0.36	1.00	-0.21	-0.29
elevation	0.41	-0.66	-0.71*	-0.21	1.00	-0.10
useful tree species	-0.10	-0.02	-0.11	-0.29	-0.10	1.00

*P<0.05, **p<0.01 (all tests one-tailed).

Table 5. 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

The correlation pattern holds when we simplified factors with the MAM, accounting for 68% of the variance (Table 6). Higher risk of collapse correlates with higher human densities (t=-3.65) and soil capabilities (t=-2.15). Note that original surface area is eliminated from the model, even when it emerged as significant and presented strong multicollinearity with soil capability in the previous correlation matrix (Table 4). 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.

Table 6. Minimum adequate multiple regression model across ecosystems for predicting risk of collapse in declining ecosystems (all tests one-tailed).

Predictor	beta coefficient	*t*	P
soil capability	-0.389	-2.15	<0.05
original surface area	—	—	—
human density	-0.662	-3.65	<0.01
elevation	—	—	—
useful tree species	—	—	—

Sample size: 13 ecosystems. The minimum adequate model accounts for 68.1% of the total variance ($p < 0.002$, one-tailed). Dashes indicate absent predictors from the model.

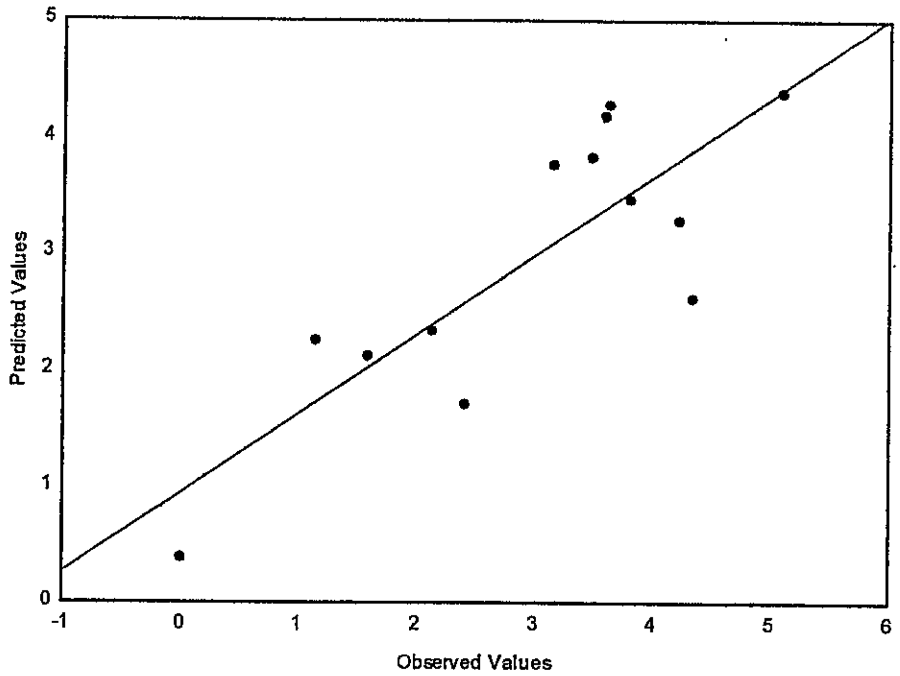

Fig 2. Prediction of surface area change (logarithmically transformed %) from the minimum adequate multiple regression model for declining ecosystems plotted against the observed values. Fit of predicted to observed values contemplates 68% of the variance explained by human density and soil capability.

DISCUSSION

Ecosystem risk of collapse

Determining ecosystem risk of collapse can potentially increase the speed at which the state of biodiversity is assessed, allowing more time for planning conservation strategies. Moreover, effectively predicting which ecosystems are more prone to having a higher risk of collapse allows for preventive conservation action to take place. 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. These factors are the major drivers behind land use change and re-stress the fact that land use is the most important driver of biodiversity loss (Sala et al. 2000).

Ecosystem surface area does not affect risk of 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 minimum adequate model. Although small ecosystems may have a higher risk of succumbing to stochastic events, within this 13 year 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 1980-1992, mostly from rural families. Remittances from family members working in the United States became an important source of income and caused a concomitant retraction of the agricultural frontier (Hecht & Saatchi, 2007), which has reduced the need for rural households and farmers to obtain fruit, firewood and other raw materials from the remaining natural woodland. This suggests that a global answer may lie in using human wellbeing as an explanatory variable instead of the immediate resources, as higher quality of life brought on by the remittances in El Salvador enable people to cover living expenses (Hecht & Saatchi, 2007). Moreover, such a hypothesis could explain increased extraction of fruit, firewood or other raw materials with low quality of life. 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 & Smalls 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, interestingly 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, empirical evidence available shows a significant loss of component species past a loss of 60% of native forest cover in fragmented landscapes (Hanski et al. 2013). This suggests that explicitly taking into account threats such as fragmentation in future revisions of the ecosystem Red List may be warranted.

Future endeavors

Purvis et al (2000) 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 in ecosystems. 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 endeavors need not only increase sample size, but also accrue a more balanced sampling across geographic regions and ecosystem types. Other variables that could act as factors and should be included in future model predictions include extrinsic factors such as climate variables, 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.

Our assessment of ecosystem risk of collapse assumes 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). Although the IUCN definition of collapse describes the event in which an ecosystem ceases to exist, it is not necessary for an ecosystem to linearly reach zero surface area to collapse, since after crossing a given threshold, systems might shift states (Scheffer et al. 2001). For simplicity's sake supposing a linear loss should suffice for assessing 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.

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 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; IUCN 2013) to fine-grained (e.g. EUNIS; EEA 2013) descriptions, making scale the most pressing matter. With a Linnean-like universally accepted system, the issue would be resolved, and more widely applicable predictions could commence.

ACKNOWLEDGMENTS

S.J.C. is a fellow of the Chilean International Cooperation Agency (AGCI), as well as fellow of the Faculty of Science, University of Chile. Their support is appreciated. We especially thank V. Henríquez, for providing the three shapefiles of El Salvador's ecosystems, and J. Linares for a complete list of presences and absences of tree species for each ecosystem. We thank the Ministerio de Medio Ambiente y Recursos Naturales of El Salvador for its support and permission to use the ecosystem shapefiles.

LITERATURE CITED

Bielby J., N. Cooper, A. A. Cunningham, T. W. J. Garner, and A. Purvis. 2008. Predicting susceptibility to future declines in the world's frogs. Conservation Letters **1**:82-90. doi: 10.1111/j.1755-263X.2008.00015.x

Bradshaw C. J. A., N. S. Sodhi, and B. W. Brook. 2009. Tropical turmoil: a biodiversity tragedy in progress. Frontiers in Ecology and the Environment **7**: 79-87. doi: 10.1890/070193

Center for International Earth Science Information Network (CIESIN) and Centro Internacional de Agricultura Tropical (CIAT). 2005. Gridded population of the world Version 3. CIESIN and Columbia University, Palisades, USA. Available from http://sedac.ciesin.columbia.edu/gpw/index.jsp (accessed January 2013).

Cohen E. J., and C. Small. 1998. Hypsographic demography: the distribution of human population by altitude. Proceedings of the National Academy of Sciences of the United States of America **95**:14009-14014. doi: 10.1073/pnas.95.24.14009

Collen B., L. McRae, S. Deinet, A. De Palma, T. Carranza, N. Cooper, J. Loh, and J. E. M. Baillie. 2011. Predicting how populations decline to extinction. Philosophical Transactions of the Royal Society B **366**:2577-2586. doi: 10.1098/rstb.1011.0015

Cordero, J., and D. Boshier. 2003. Arboles de Centroamerica: un manual para extensionistas. OFI/CATIE, Oxford, UK.

Costanza R., et al. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253 - 260, doi: 10.1038/387253a0

Davidson, A. D., M. J. Hamilton, A. G. Boyer, J. H. Brown, and G. Ceballos. 2009. Multiple pathways to extinction in mammals. Proceedings of the National Academy of Sciences of the United States of America **106**:10702-10705. doi: 10.1073/pnas.0901956106

DeFries, R. S., T. Rudel, M. Uriarte, and M. Hansen. 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. Nature Geoscience **3**:178-181. doi: 10.1038/ngeo756

Diamond, J. M. 1984. `Normal' extinctions of isolated populations. Pages 191-246 in M. H. Niteck, editor. Extinctions. Chicago University Press, Chicago, USA.

Dull, R.A. 2008. Unpacking El Salvador's ecological predicament: theoretical templates and "long-view" ecologies. Global Environment Change **18**:319-329. doi: 10.1016/j.gloenvcha.2008.03.002

Echeverria, C., A. D. Coomes, M. Hall, and A. C. Newton. 2008. Spatially explicit models to analyze forest loss and fragmentation between 1976 and 2020 in southern Chile. Ecological Modelling **212**:439-449. doi: 10.1016/j.ecolmodel.2007.10.045

EEA (European Environment Agency). 2013. EUNIS web application. Available from http://eunis.eea.europa.eu (accessed March 2013)

Geist, H. J., and E. F. Lambin. 2002. Proximate causes and underlying driving forces of tropical deforestation. Bioscience **52**:143-150. doi: 10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2

Gibson L., et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature **478**:378-381. doi: 10.1038/nature10425

Hampshire, R. J. 1989. El Salvador. Pages 295-298 in D. G. Campbell and H. D. Hammond, editors. Floristic Inventory of Tropical Countries: The Status of Plant Systematics, Collections and Vegetation, plus Recommendations for the Future. New York Botanical Garden, New York, USA.

Hanski, I., G. A. Zurita, M. I. Bellocq, and J. Rybicki. 2013. Species-fragmented area relationship. Proceedings of the National Academy of Sciences of the United States of America **110**:12715-12720, doi:10.1073/pnas.1311491110.

Hecht, S., and S. Saatchi. 2007. Globalization and forest resurgence: changes in forest cover in El Salvador. Bioscience **57**:663-672, doi: 10.1641/B570806.

Holdaway, R. J., S. K. Wiser, and P. A. Williams. 2012. Status assessment of New Zealand's naturally uncommon ecosystems. Conservation Biology **26**:619-629. doi: 10.1111/j.1523-1739.2012.01868.x

Hugget, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biological Conservation **124**:301-310. doi: 10.1016/j.biocon.2005.01.037

IUCN (International Union for Conservation of Nature). 2010. IUCN Red List of threatened species. Version 2010.1. IUCN, Species Survival Commission, Gland, Switzerland. Available from http://www.iucnredlist.org (accessed March 2013).

IUCN (International Union for Conservation of Nature). 2013. Habitats Classification Scheme Version 3.0. Available from http://www.iucnredlist.org

IUCN, UNEP-WCMC. 2013. The World Database on Protected Areas: January 2013. UNEP-WCMC, Cambridge. http://www.wdpa.org (accessed 23.09.13).

Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. Hole-filled seamless SRTM for the globe Version 4. International Centre for Tropical Agriculture (CIAT), Cali, Colombia. Available from http://srtm.csi.cgiar.org (accessed December 2012).

Keith D.A. et al. 2013. Scientific foundations for an IUCN red list of ecosystems. PLoS ONE **8**:e62111. doi:10.1371/journal.pone.0062111

Kernan, B.S., F. Serrano. 2010. Report on biodiversity and tropical forests in El Salvador. USAID, San Salvador.

MARN (Ministerio de Medio Ambiente y Recursos Naturales). 2010. Mapa agrologico de El Salvador. MARN, San Salvador, El Salvador. Available from http://www.marn.gob.sv (accessed December 2012).

NRCS (Natural Resources Conservation Service). 2012. National soil survey handbook, title 430-VI. U.S. Department of Agriculture, Washington D.C., USA. Available online at http://soils.usda.gov/technical/handbook/ (accessed January 2013).

Owens I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America **97**:12144-12148. doi: 10.1073/pnas.200223397

Pimm S. L., and P. Raven. 2000. Biodiversity: extinction by numbers. Nature **403**:843-845. doi: 10.1038/35002708

Pocock, M. J. O. 2011. Can traits predict species' vulnerability? A test with farmland passerines in two continents. Proceedings of the Royal Society B **278**:1532- 1538. doi: 10.1098/rspb.2010.1971

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declinging species. Proceedings of the Royal Society of London. Series B **267**:1947-1952. doi: 10.1098/rspb.2000.1234

Purvis, A., P.-M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. Science **288:**328-330.

Raup, D. M. 1994. The role of extinction in evolution. Proceedings of the National Academy of Sciences of the United States of America **91:**6758-6763.

Rodríguez, J. P., et al. 2011. Establishing IUCN Red List criteria for threatened ecosystems. Conservation Biology **25**:21-29. doi: 10.1111/j.1523-1739.2010.01598.x

Rodríguez, J. P., F. Rojas-Suárez and D. Giraldo Hernández, editors. 2010. Libro Rojo de los ecosistemas terrestres de Venezuela. Provita, Shell Venezuela, Lenovo Venezuela, Caracas, Venezuela.

Russell, G. J., T. M. Brooks, M. M. McKinney, and C. G. Anderson. 1998. Present and future taxonomic selectivity in bird and mammal extinctions. Conservation Biology **12**:1365-1376.

Sala O. E. et al. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770–1774. doi: 10.1126/science.287.5459.1770

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596. doi: 10.1038/35098000

Terborgh, J. 1999. Requiem for Nature. Island Press, Washington, DC, USA.

UNESCO. 1973. International classification and mapping of vegetation. Imprimeries Populaires de Genève, Paris.

Vreugdenhil, D., J. Linares, O. Komar, V. E. Henríquez, J. E. Barraza and M. Machado. 2012. Mapa de los ecosistemas de El Salvador, actualización 2012 con detección de cambios 1999 – 2011. World Institute for Conservation and Environment, Shepherdstown, USA.

Wilson, K., A. Newton, C. Echeverria, C. Weston, and M. Burgman. 2005. A vulnerability analysis of the temperate forests of south central Chile. Biological Conservation **122**:9-21. doi: 10.1016/j.biocon.2004.06.015

Chapter II

LOSS OF ECOSYSTEM SERVICES CALLS FOR A CHANGE IN LAND USE POLICY IN EL SALVADOR

ABSTRACT

Land use change is the leading threat to biodiversity, the biotic component of natural capital. Ecosystem services can be valued, and bear even greater importance in countries home to frequent natural disasters with need of regulating services. The Republic of El Salvador, still-recovering after its civil war and with the smallest protected area system and largest human density in Central America, is one such country. We estimated how land use change has impacted ecosystem service value in a country with need of services to regulate natural disaster damages and avoid decapitalization. We used polygonal maps of El Salvador's ecosystems between 1998 and 2011 to estimate changes in surface area and employ published value coefficients to estimate changes in the value of each and overall ecosystem services. During this 13 year period ecosystem service value in El Salvador declined by 2.6% or $258.5 million from $9764.4 million per year to $9505.9 million per year, and currently equates to 44% of GDP, when each disaster represents 3.6% of a year's GDP. The greatest changes in magnitude occur in provisioning services (-11.27%), followed by cultural (-8.79%), regulating (-1.64%) and lastly habitat services (-0.98%). Of the 77% of ecosystem services that declined, the highest changes occurred in pollination, air quality regulation (both 16.2%), and climate regulation (15.8%). Changes in surface area of tropical forests are largely responsible for the loss of ecosystem service value, accounting for 90% of total value loss, followed by coastal wetlands which account for 9%. Although our sensitivity analysis indicates the estimates to be robust, sensitivity coefficients for coastal wetlands were much higher (0.789) than tropical forests (0.126), emphasizing the severity of impacts that further losses in coastal wetlands may incur. We suggest focusing government funds in conservation towards tropical forests and coastal wetlands and conclude that although cultivated lands currently represent the greatest threat to El Salvador's ecosystems, ecosystem services will need to be generated outside protected areas, through conservation strategies employing the agricultural matrix.

Key words: El Salvador, ecosystem services, land use, natural capital, agricultural matrix

INTRODUCTION

Loss and modification of natural habitats brought about by land use activities are one of the leading threats to biodiversity (Foley et al., 2005). These changes reduce the provision of ecosystem services towards human society. Because the loss of goods and services is rarely given weight in driving policy decisions, neglecting society's dependence on these provisions and ignoring their importance effectively means ignoring society's life support system. However, the value of this life support system can be economically assessed, which allows a direct comparison to other components normally included in decision making (i.e. economic services, manufactured goods), and enables appropriate assignment of priorities.

Policy decisions generally rely on human and manufactured capital. The stock of materials at a given point in time and the manpower capable of functioning as cogs in national policy systems have historically taken precedence over natural capital. Ecosystem services are the ecological processes resulting from the interactions among the components of natural capital stocks that combine with manufactured and human capital to produce human welfare (Costanza et al., 1997). Ignoring the services of ecological systems undermines the importance of natural capital and reduces the sustainability of the human species in the biosphere. Therefore, changes in the flow of ecosystem services should be accounted for in national incomes.

The Republic of El Salvador is the smallest nation (21,000 km^2) in Central America, yet holds its highest population density (294 p/km^2) (UNSD, 2013). Like the rest of the region, El Salvador has a history of ecological disturbance of over 4000 years by pre-Colombian farming leading into modern agricultural practices (Dull, 2008). Today, less than 1% of the land surface remains as primary forest (Kernan and Serrano, 2010), although forest resurgence during the civil war that the country suffered from 1980 to 1992 continued to increase total forest cover to 14% until 2001 (UNSD, 2013) due to a retraction of the agricultural frontier stemming from international migration (Hecht and Saatchi, 2007). Change in land use has brought about changes in the flow of ecosystem services through habitat loss; moreover, assigning this change an economic value allows us to ascertain if the increase of other kinds of capital in national incomes compensates for the loss in ecosystem services. Our aim was to determine how changes in land use have altered natural capital in El Salvador, and identify the importance that ecosystem services hold in a nation's income.

METHODS

The provision of ecosystem services can be inferred from changes in the surface area of ecosystems as assessed in Kreuter et al. (2001), Zhao et al. (2004), and Liu et al. (2012). A loss in the surface area of ecosystems can translate into monetary losses through the use of ecosystem service estimates of production per unit of area. This requires land cover data spanning at least two time periods to determine land use change, ecosystem service values per unit of area for each biome type, and a test of elasticity to determine the robustness of the estimated values.

Data collection

To estimate changes in the surface area of ecosystems in El Salvador, we used data from the Ministry of Environment and Natural Resources (MARN) (Vreugdenhil et al., 2012). The data consist of two polygonal maps of El Salvador's ecosystems in 1998 and 2011. We considered changes in the 25 land categories identified in the shapefiles, which consist of 23 terrestrial ecosystems that El Salvador hosts as well as the two major land use categories recognized: agro-productive systems and urban areas (Vreugdenhil et al., 2012).

Ecosystem classification and biome assignment

The ecosystem shapefiles (Vreugdenhill et al. 2012) use the UNESCO (1973) classification system which heavily relies on vegetation structure and physiognomy, elevation, and hydric regime. We used de Groot et al.'s (2012) ecosystem service valuation that classifies land cover according to biomes, a higher level of organization than ecosystems, and assigns a corresponding ecosystem service value per ha per year ($/ha/year) to each biome. In order to estimate ecosystem service values in El Salvador, we first assigned each of El Salvador's ecosystems to one of de Groot et al.'s 8 recognized terrestrial biomes with the corresponding ecosystem service value ($/ha/year, 2007 price levels). We also included cultivated land, urban areas, desert, and ice/rock/polar biomes which do not receive any value in de Groot et al.'s valuation, as these have anthropogenic origins or insufficient data for meaningful analysis. While ecosystem service values have previously been assigned to cultivated lands and urban areas (Costanza et al, 1997), following de Groot et al. (2012), we are interested only in services provided by natural ecosystems, therefore we assigned these biomes a value of zero (Table 1).

Table 1. Land use categories and ecosystem service coefficient

Equivalent biome*	Land use category**	Ecosystem service coefficient ($/ha/year, 2007 price levels)*
Tropical forest	Tropical evergreen seasonal needle-leaved lowland forest	5263
	Tropical deciduous broad-leaved lowland forest, well-drained	
	Tropical semi-deciduous broad-leaved submontane forest	
	Tropical semi-deciduous mixed submontane forest	
	Tropical semi-deciduous broad-leaved well-drained lowland forest	
	Tropical semi-deciduous broad-leaved lower montane forest	
	Tropical semi-deciduous mixed lower montane forest	
	Tropical evergreen seasonal needle-leaved upper-montane forest	
	Tropical evergreen seasonal broad-leaved altimontane forest	
	Tropical evergreen seasonal broad-leaved alluvial forest, occasionally inundated	
	Tropical evergreen seasonal broad-leaved upper-montane forest	
Grasslands	Tropical altimontane meadow or paramo	2872
	Short-grass savanna lowland with evergreen broad-leaved shrubs, well-drained, *Curatella americana* variant	
	Short-grass savanna with semi-deciduous broad-leaved shrubs, well-drained, *Crescentia alata* variant	
Coastal wetlands	Pacific mangrove forest on clay	193843
Inland wetlands	Tropical freshwater reed-swamp formation	25681
Rivers and lakes	Predominantly brackish lake or canal of the Caribbean littoral plain	4267
	Predominantly freshwater lake of the Pacific littoral plain	
	River segment of the Pacific littoral	
Coastal systems	Open estuary of the Pacific	28916
Desert	Scarcely vegetated tropical dune and beaches	0
	Tropical coastal vegetation in succesional transition on very recent sediments, moderately drained	
Ice/rock/polar	Scarcely vegetated lava flow	0
Cultivated land	Agro-productive system	0
Urban areas	Urban area	0

*Cited from de Groot et al 2012.

**Cited from Vreugdenhil et al 2012.

ESV calculation

The total ecosystem service value provided by each biome was estimated using Kreuter et al.'s (2001) method, which consists of using biome type as a proxy for ecosystem services, multiplying the area of each biome by the service value of one unit of area for each land use category, which we obtained from the de Groot et al. (2012) supplementary material, as:

$$ESV_y=\sum(A_k \times VC_k), \qquad (1)$$

where ESV_y is the total estimated ecosystem service value for a single year in the sum of biome surface, A_k the area (ha) and VC_k the value coefficient ($/ha/year) for "*k*" biome. The change in ESV was estimated as the difference between the estimated values for each biome in 1998 and 2011. Although most studies upon which de Groot et al. (2012) base their values do not originate from Latin America, they represent a global average that grants them applicability to in different biomes.

Due to any uncertainty regarding the precision of de Groot et al.'s biomes as representations of El Salvador's grouped ecosystems, we determined how dependent our estimates are if the value coefficients change, and tested the robustness of the analysis by calculating elasticity; that is the percentage change in the output for a given percentage change in an input (Mansfield, 1985). Elasticity was assessed as:

$$CS= \frac{\frac{ESVj - ESVi}{ESVi}}{\frac{VCjk - VCik}{VCik}}, \qquad (2)$$

where CS is the coefficient of sensitivity, ESV is the estimated ecosystem service value, VC is the value coefficient ($/ha/year), '*i*' and '*j*' are the initial and adjusted values, respectively, and '*k*' represents the land use category.

To be robust, we would expect the estimated ESVs to remain invariant when other variables change. If CS is greater than one, then the estimated ecosystem value is elastic with respect to the changed coefficient, changing when other variables change. But if the ratio is less than one, then the estimated ecosystem value is considered to be inelastic. After Kreuter et al. (2001), we adjusted a change in magnitude of 50% for each coefficient, in case large enough shifts up to that magnitude occur that could affect the global average values for ecosystem services that de Groot et al. provide. Hence, if our ESVs are inelastic with respect to a variation of 50% we conclude the analysis to be robust.

Comparison to national income

Changes in land use in El Salvador have altered natural capital, here valued as economic changes in the provision of ecosystem services at the national level. This in turn allows for a comparison between the value of services provided by natural capital and national economic indicators of production from manufactured and human capital, such as GDP. To compare the change in ESV to El Salvador's GDP, we converted all GDP data in U.S. dollars from their original source to a constant 2007 price value using the Oregon State University inflation convertor (Sahr, 2012).

RESULTS

Land use change

Seven out of ten biomes exhibited changes in land use. Tropical forests, grasslands and coastal wetlands decreased (accounting for 93.5%, 6.2% and 0.3%, respectively, of biome reduction), while cultivated land, urban areas, inland wetlands and rivers and lakes increased (accounting for 74.4%, 25.0%, 0.5% and 0.1%, respectively, of biome increase). Ice/rock/polar, desert and coastal systems did not present detectable changes.

Cultivated land is the most common landscape category (82% of El Salvador's total area), whose 2% increase alone from 1998 to 2011 is nine times the remaining extent of natural grasslands and is nearly equal to the current extent of the coastal wetlands (Table 2). In total, 12% of terrestrial biome surface has been substituted by cultivated land and urban areas since 1998. Grasslands lost 42.7% of total area, decreasing from 6882 ha in 1998 to 3942 ha in 2011. Tropical forest suffered a 16.2% loss of area, and lastly coastal wetlands had a small decrease in area of 0.3%. In contrast, urban areas grew from 28751 ha to 40531 ha, increasing by 40.9%, while inland wetlands, cultivated land as well as rivers and lakes increased 4.06%, 2.07% and 0.16%, respectively.

Table 2. Estimated areas and land use change in El Salvador from 1998 to 2011.

	1998		2011		1998-2011	
Biome	ha	%	ha	%	ha	%
Urban areas	28751.54	1.36	40531.62	1.92	11780.07	40.97
Cultivated land	1694643.22	80.24	1729742.41	81.91	35099.19	2.07
Tropical forest	272049.00	12.88	227955.06	10.79	-44093.94	-16.21
Grasslands	6882.06	0.33	3942.58	0.19	-2939.48	-42.71
Inland wetlands	5326.82	0.25	5542.88	0.26	216.06	4.06
Coastal wetlands	38565.69	1.83	38443.00	1.82	-122.69	-0.32
Rivers and lakes	38302.38	1.81	38363.17	1.82	60.79	0.16
Ice/rock/polar	6323.08	0.30	6323.08	0.30	0.00	0.00
Desert	2432.21	0.12	2432.20	0.12	0.00	0.00
Coastal systems	18568.90	0.88	18568.90	0.88	0.00	0.00
Total	2111844.89	100.00	2111844.89	100.00		

Ecosystem service sensitivity analysis

Adjusting coefficients used to estimate ESV by 50% did not produce CS values above 1, suggesting robustness (Table 3). Changing the coefficient for coastal wetlands by 50% caused the highest change in value, followed by tropical forests, accounting for 38.3% and 7.3% of the applied 50% change (CS of 0.15 and 0.77, respectively) in 1998, and 39.2% and 6.3% (CS of 0.13 and 0.78, respectively) of the applied 50% change in 2011. Tropical forests comprise the largest extension of natural landscapes (66.7%), while coastal wetlands, formed mainly from mangrove forests, represent a much smaller extension (11.3%). However, coastal wetlands hold the largest ecosystem service coefficient, and therefore any change in coastal wetlands will impact with greater magnitude than other biomes.

Table 3. Percentage change in the total ESV in El Salvador following an adjustment of 50% in ecosystem valuation coefficients (VC) and resulting coefficient of sensitivity (CS).

	1998		2011	
Biome	± %	CS	± %	CS
Urban areas VC ± 50%	0.00	0.000	0.00	0.000
Cultivated land VC ± 50%	0.00	0.000	0.00	0.000
Tropical forest VC ± 50%	7.33	0.147	6.31	0.126
Grass/rangeland VC ± 50%	0.10	0.002	0.06	0.001
Inland wetlands VC ± 50%	0.70	0.014	0.75	0.015
Coastal wetlands VC ± 50%	38.28	0.766	39.20	0.784
Rivers and lakes VC ± 50%	0.84	0.017	0.86	0.017
Ice/rock/polar VC ± 50%	0.00	0.000	0.00	0.000
Desert VC ± 50%	0.00	0.000	0.00	0.000
Coastal systems VC ± 50%	2.75	0.055	2.82	0.056
Total	50	1.000	50	1.000

Changes in ecosystem service value

During the 13 year period elapsed between 1998 and 2011, ESV in El Salvador decreased by 2.6% or $258.5 million from $9764.4 million per year to $9505.9 million per year (Table 4). Supposing a linear loss, this extends to an accumulative net loss of $1,809.35 million in ecosystem services between 1998 and 2011.

Most individual ecosystem services tend to decline: 77% of the 22 service types present negative changes (Table 5). The three highest drops in value occurred in pollination and air quality regulation, both decreasing by 16.2%, and in climate regulation, declining 15.8%. As a whole, the greatest changes in magnitude occur in provisioning services (-11.27%), followed by cultural (-8.79%), regulating (-1.64%) and lastly habitat services (-0.98%). Changes in tropical forests are largely responsible for the loss of ecosystem service value, accounting for 90% of total ESV loss.

Table 4. Total ecosystem service value (ESV in US$ x 10^6/yr, 2007 price levels) estimated for each biome in El Salvador using de Groot *et al.* coefficients, and the overall change and rate of change between 1998 and 2011.

		1998		2011		1998-2011		
Biome	ESV ($/ha/year)	$/year	%	$/year	%	$/year	%	%/year
Urban areas	0	0	0.00	0	0.00	0	0.00	0.00
Cultivated land	0	0	0.00	0	0.00	0	0.00	0.00
Tropical forest	5263	1431793881	14.66	1199727460	12.62	-232066421	-16.21	-1.25
Grasslands	2872	19765273	0.20	11323096	0.12	-8442178	-42.71	-3.29
Inland wetlands	25681	136798130	1.40	142346676	1.50	5548546	4.06	0.31
Coastal wetlands	193843	7475688863	76.56	7451906837	78.39	-23782026	-0.32	-0.02
Rivers and lakes	4267	163436252	1.67	163695634	1.72	259382	0.16	0.01
Ice/rock/polar	0	0	0.00	0	0.00	0	0.00	0.00
Desert	0	0	0.00	0	0.00	0	0.00	0.00
Coastal systems	28916	536938190	5.50	536938168	5.65	-22	0.00	0.00
Total		9764420588	100.00	9505937869	100.00	-258482719	-2.65	-0.20

Table 5. Total ecosystem service value in El Salvador (ESV in US$ x 10^6/yr, 2007 price levels) estimated for each service, overall change between 1998 and 2011, and tendency to increase or decrease.

Service type	1998 $/year	2011 $/year	1998-2011 $/year	%
Provisioning services	748519262	664183885	-84335377.45	-11.27
Food provisioning	157058663	144738813	-12319850	-7.84
Water supply	126116735	124798575	-1318160	-1.05
Raw materials	39510108	35698327	-3811781	-9.65
Genetic resources	3922294	3347846	-574448	-14.65
Medicinal resources	421304204	354968435	-66335769	-15.75
Ornamental resources	607258	631888	24630	4.06
Regulating services	7883302736	7754041845	-129260892	-1.64
Air quality regulation	3264588	2735461	-529127	-16.21
Climate regulation	570344196	480196059	-90148138	-15.81
Disturbance moderation	240226128	237304574	-2921554	-1.22
Regulation of water flows	122902925	109034009	-13868916	-11.28
Waste treatment/water purification	6277833700	6258120816	-19712885	-0.31
Erosion prevention	640850912	640141368	-709544	-0.11
Nutrient cycling/soil fertility	11676450	11908752	232302	1.99
Pollination	8161470	6838652	-1322818	-16.21
Biological control	8042367	7762155	-280212	-3.48
Habitat services	699925626	693065245	-6860381	-0.98
Lifecyle maintenance	425458227	423724417	-1733810	-0.41
Genetic diversity	274467398	269340828	-5126571	-1.87
Cultural services	432672964	394646895	-38026068	-8.79
Esthetic information	8031559	7819811	-211748	-2.64
Recreation	420114167	382148606	-37965560	-9.04
Inspiration	3728776	3880015	151240	4.06
Spiritual experience	389947	389947	0	0.00
Cognitive development	408516	408516	0	0.00
Total	9764420588	9505937869	-258482719	-2.65

National economic importance of ecosystem services

The value of ecosystem services in 1998 (9,764 x106 $) is equivalent to 63% of the GDP (15,277 x106 $), decreasing to 44% (9,505 x106 $) of the GDP (21,606 x106 $) in 2011. Note that during this period, ESV declined by 2.6% and GDP increased 41% (Table 6).

Table 6. Total GDP (US$, at constant prices for 2007) for El Salvador and estimated ESV for 1998 and 2011 in El Salvador

	1998	2011
GDP	15277989822	21606373008
ESV	9764420588	9505937869
Δ GDP-ESV	5513569234	12100435140
Δ GDP-ESV %	63.9%	44.0%

DISCUSSION

Worldwide, avoiding depletion of natural capital is a priority (Millennium Ecosystem Assessment, 2005), and globally, land use change is the major driver of changes in biodiversity (Sala et al., 2000). In El Salvador, the current trend in land use change is associated with a decrease in natural landscapes, accompanied with an increasing emphasis on urban area expansion (Fig 1). In the span of 13 years, the decrease in ecosystem service value in El Salvador has translated to a loss of 2.6% in the yearly provision of services during a process of replacing 12% of natural landscapes with agro-productive systems and urban areas. This difference in value is not a trivial amount. It represents 1.7% of El Salvador's GDP in 1998. Despite that the decline in ESV per year for El Salvador is not relatively high when compared to ecosystem service valuations in the US, Laos and China (Table 7), for El Salvador this means a total net loss from 1998 to 2011 that is enough to pay nearly 14% of the country's public debt of $12,951 million (BCR, 2012). This is a conservative estimate, since if we employed maximum values for the ecosystem service coefficients then the yearly loss of ESV would ascend to 11% of the 1998's GDP while the ESV ascends to more than four times its normal value and accounts for more than twice the GDP.

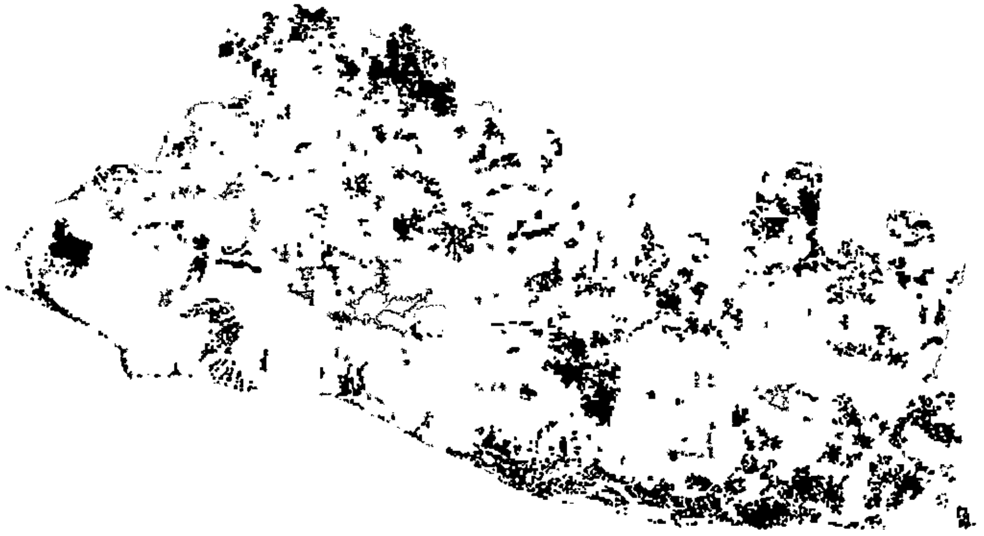

Fig 1. Natural landscapes remaining in El Salvador c. 2011. Black represents remaining natural landscape, hollowed out sections represent water, light grey and dark grey represent cultivated land and urban areas, respectively.

Among all values for the estimated ecosystem services, pollination is the most affected, critical when 11.6% of El Salvador's GDP comes from the agricultural sector (BCR, 2012), and 20.9% of El Salvador's employed population depends on agriculture as a way of life (World Bank, 2012). Although globally frequent pollinators consist of introduced species, in the tropics visits from stingless native bees produce significant increases in crop yield (Heard, 1999). If pollination services continue to drop, eventually the agro-productive sector will need to compensate to pollinate crops, and prices may start to drive up in order to maintain revenue. Air quality regulation follows, worse still as it directly affects human health conditions, since annual particulate matter with diameter of 10 µm (PM10) in El Salvador is 52 µg/m^3, over the guideline limit of 20 µg/m^3 suggested by the World Health Organization (WHO, 2011). This exemplifies that loss of natural capital is not only tied to the economy, but as it wanes, so does the life support system that we depend upon.

Table 7. Previous ecosystem service valuations of land use change and percentage of decline reported in ESV.

Location	Study period	Δ ESV %	Δ ESV %/yr	References
Zoige Plateu, China	1975-2005	-4.6	-0.15	Li et al., 2010
NW Guangxi, China	1985-2005	-3.1	-0.15	Zhang et al., 2011
Taiyuan City, China	1990-2005	-2.7	-0.18	Liu et al., 2012
El Salvador	1998-2011	-2.6	-0.20	This study
San Antonio, Texas, USA	1976-1991	-3.6	-0.24	Kreuter et al., 2001
Northern Part of Lao PDR	1992-2002	-16.2	-1.62	Yoshida et al., 2010
Sanjiang Plain, Heilongjiang Province, China	1980-2000	-41.5	-2.08	Wang et al., 2006
HaDaQi Industrial corridor, Heilongjiang Province, China	1990-2005	-29.0	-2.26	Zang et al., 2011
Chongming Island, China	1990-2000	-62.0	-6.20	Zhao et al., 2004

The consequences of other declining services such as climate regulation and water flow regulation have already been felt: causing expenditures of up to 2,715x10^6 $ (EM-DAT, 2012) or ~1.1% of the GDP in damage costs from floods and hurricanes with a substantial amount of casualties during this same period. Considering costs per event, each disaster represents 3.6% of a year's GDP, while the agricultural sector, which has eliminated native forests (Vreugdenhil et al., 2012), amounts to an average of 10% of a year's GDP during the same period. This illustrates that by losing ecosystem services we do not only cease to receive previously unfelt benefits, but begin to feel the adverse effects as compensations begin to add up for the aforementioned loss. Preventing further loss of ecosystem service provision then becomes a priority.

This loss of ecosystem service value is mostly attributable to a decreasing area of tropical forest, where a loss of 16% of its area is responsible for 90% of the total observed loss in ESV. Coastal wetlands account for 9% of the loss, even when only having decreased 0.3% in size. This result emphasizes the severity of impacts that further losses in coastal wetlands may incur. El Salvador's coastal wetlands, represented by mangrove forests, are the first barrier against flooding and tsunamis, preventing erosion and natural disasters, and maintaining lifecycles and nursery of stock upon which much of El Salvador's local and commercial fisheries sustain themselves. Had the mangrove forests lost the same percentage of area as tropical forests, the total loss of ecosystem services in El Salvador would have risen to 4.7 times its current amount. Therefore we suggest focusing funds in conservation towards tropical forests and coastal wetlands.

While woodland resurgence occurred from 1992 to 2001 due to processes such as the Salvadoran Civil War, the resulting international migration, the associated remittances and a concomitant retraction of agricultural frontier (Hecht and Saatchi, 2007), the last decade (1998-2011) has reversed the trend. Because tropical forests and coastal wetlands are the prime contributors towards ESV in El Salvador, protection of these biomes should now be a conservation priority, as they are essential in slowing down the rate of decline in the provision of ecosystem services. However, public spending on protected areas in El Salvador in 2008 added to $395,404 (Bovarnick et al., 2012), equal to 0.004% of the ESV for 2011. In the 13 years since El Salvador first established its environmental law in 1998 (Diario Oficial, 1998), it has increased its protected area system from 0.4 to 0.8% of its land area, leaving 94% of natural land biomes susceptible to threats (IUCN & UNEP-WCMC, 2013). If natural biomes are limited as in El Salvador, where they represent 16% of land area, it should be an imperative that all natural area be protected.

Averting further loss of natural capital now becomes a question of not only how to prevent further shifts from natural to anthropic landscapes, but also of how to gain back lost ground. It is agro-productive systems, whose increase of 2.1% is thrice the expansion of urban areas in absolute terms, which represent the greatest threat to the biodiversity and natural landscapes of El Salvador, as they threaten 44.2% of El Salvador's threatened species (IUCN, 2012). However, cultivated land is not barren, since native species are known to use it (Vandermeer and Perfecto, 2007). Although it may not be the most suitable habitat, agro-productive systems can still be of use for biodiversity. In this context, a strategy that minimizes the contrast between the agricultural matrix and tropical forests should have the highest probability of succeeding in minimizing loss of service provision.

To avoid further depletion of natural capital, proactive strategies must be implemented. Protection of all natural biomes is certainly necessary yet would not be enough, requiring the use of the dominant land use in El Salvador, the agro-productive systems. Payments for environmental services (PES), such as environmental certifications, can be extended as subsidies for maintaining current extensions, maintaining current agricultural frontiers or incentivizing crops that form an agricultural matrix that offers the least amount of contrast with native forests. Implementation of PES will need identification and quantification of services present (Herrador and Dimas, 2000). Ready-to-use mechanisms include the World Bank's BioCarbon Fund (http://wbcarbonfinance.org/BioCF; McDowell, 2002) and the newly designed REDD+ (http://www.un-redd.org; Groom and Palmer, 2012; Kettle, 2012) to stop deforestation, addressing the need regulation of water flows felt during floods and hurricanes. The creation of markets for other environmental services such as globally affecting regulations for air and water quality may increase the viability of ecological restoration efforts. To achieve this, it is imperative for policy to not only consider effectively slowing down the rate of loss of natural landscapes, but to consider generating ecosystem services outside protected areas, through conservation strategies employing the agricultural matrix. Doing so will enable El Salvador to prevent further loss of natural capital and incorporate it in its development.

ACKNOWLEDGMENTS

S. J. C. is a fellow of the Chilean International Cooperation Agency (AGCI), as well as fellow of the Faculty of Science, University of Chile. Their support is appreciated.

LITERATURE CITED

Banco Central de Reserva de El Salvador, 2012. Base de datos económica-financiera. http://www.bcr.gob.sv/ (accessed 4.10.12).

Bovarnick, A., Fernandez Baca, J., Galindo, J., Negret, H., 2010. Financial sustainability of protected areas in Latin America and the Caribbean: investment policy guidance. United Nations Development Programme (UNDP) and The Nature Conservancy (TNC), New York.

Constanza, R., d'Arge, R., de Groot, D., Farber, S., Grasso, M., Hannon, B., Limburg, K, Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M.,1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

De Groot, R., Brander, L., van der Ploeg, S., Costanza, R., Bernard, F., Braat, L., Christie, M., Crossman, N., Ghhermandi, A., Hein, L., Hussain, S., Kumar, P., McVittie, A., Portela, R., Rodriguez, L.C., ten Brink, P., van Beukering, P., 2012. Global estimates of the value of ecosystems and their services in monetary units. Ecosystem Services 1, 50-61, doi: 10.1016/j.ecoser.2012.07.005.

Diario Oficial, 1998. Ley del Medio Ambiente. Decreto legislativo No.233. El Salvador, San Salvador.

Dull, R.A., 2008. Unpacking El Salvador's ecological predicament: Theoretical templates and "long-view" ecologies. Global Environment Change 18, 319-329, doi: 10.1016/j.gloenvcha.2008.03.002.

EM-DAT, 2012. The OFDA/CRED International Disaster Database. Université Catholique de Louvain, Brussels. http://www.emdat.be/ (accessed 11.07.12).

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 390, 570-574 doi: 10.1126/science.1111772.

Groom, B., Palmer, C., 2012. REDD+ and rural livelihoods. Biological Conservation 154, 42-52, doi: 10.1016/j.biocon.2012.03.002.

Heard, T.A.,1999. The Role of stingless bees in crop pollination. Annual Review of Entomology 44, 183-206, doi: 10.1146/annurev.ento.44.1.183

Hecht, S., Saatchi, S., 2007. Globalization and forest resurgence: changes in forest cover in El Salvador. Bioscience 57, 663-672, doi: 10.1641/B570806.

Herrador, D., Dimas, L., 2000. Payment for environmental services in El Salvador. Mountain Research and Development 20, 306-309, doi: 10.1659/0276-4741(2000)020[0306:PFESIE]2.0.CO;2

IUCN, UNEP-WCMC. 2013. The World Database on Protected Areas: January 2013. UNEP-WCMC, Cambridge. http://www.wdpa.org (accessed 23.09.13).

Kernan, B.S., Serrano, F., 2010. Report on biodiversity and tropical forests in El Salvador. USAID, San Salvador.

Kettle, C.J., 2012. Seeding ecological restoration of tropical forests: priority setting under REDD+. Biological Conservation 154, 34-41, doi: 10.1016/j.biocon.2012.03.016.

Kreuter, U.P., Harris, H.G., Matlock, M.D., Lacey, R.E., 2001. Change in ecosystem service values in the San Antonio area, Texas. Ecological Economics 39, 333-346, doi: 10.1016/S0921-8009(01)00250-6

Li, J., Wang W., Hu, G., Wei, Z., 2010. Changes in ecosystem service values in Zoige Plateau, China. Agriculture, Ecosystems and Environment 139, 766-770, doi: 10.1016/j.agee.2010.10.019

Liu, Y., Li, J., Zhang, H., 2012. An ecosystem service valuation of land use change in Taiyuan City, China. Ecological Modelling 225,127-132, doi: 10.1016/j.ecolmodel.2011.11.017

Mansfield, E., 1985. Microeconomics: theory and applications, fifth ed. W.W. Norton and Company, New York.

McDowell, N., 2002. Developing countries to gain from carbon-trading fund. Nature 420, 4, doi: 10.1038/420004a.

Millennium Ecosystem Assessment, 2005. Ecosystems and human wellbeing: synthesis. Island Press, Washington D.C.

Sahr, R., 2012. 2012 Inflation conversion factor revision. Oregon State University. Corvallis OR. http://oregonstate.edu/cla/polisci/sahr/sahr (accessed 12.10.12).

UNESCO, 1973. International classification and mapping of vegetation. Imprimeries Populaires de Genève, Paris.

UNSD, 2013. UNdata. New York. http://data.un.org (accessed 14.01.13).

Vandermeer, J., Perfecto, J., 2007. The agricultural matrix and a future paradigm for conservation. Conservation Biology 21, 274-277, doi: 10.1111/j.1523-1739.2006.00582.x.

Vreugdenhil, D., Linares, J., Komar, O., Henríquez C., V. E., Barraza, J. E., & Machado, M., 2012. Mapa de los ecosistemas de El Salvador, actualización 2012 con detección de cambios 1999 – 2011. World Institute for Conservation and Environment, Shepherdstown.

Wang, Z., Zhang, B., Zhang, S., Li, X., Liu, D., Song, K., Li, J., Li, F., Duan, H., 2006. Changes of Land Use and of Ecosystem Service Values in Sanjiang Plain, Northeast China. Environmental Monitoring and Assessment 112, 69-91, doi: 10.1007/s10661-006-0312-5

World Bank, 2012. World Development Indicators. ESDS International, University of Manchester, doi: 10.5257/wb/wdi/2012-04.

World Health Organization, 2011. Urban outdoor air pollution database. http://www.who.int/phe (accessed 7.11.12).

Yoshida, A., Chanhda, H., Yan-Mei Ye, Yue-Rong Liang, 2010. Ecosystem service values and land use change in the opium poppy cultivation region in Northern Part of Lao PDR. Acta Ecologica Sinica 30, 56-61, doi: 10.1016/j.chnaes.2010.03.002

Zang S., Wu, C., Liu, H., Na, X., 2011. Impact of urbanization on natural ecosystem service values: a comparative study. Environmental Monitoring and Assessment 179, 575-588, doi: 10.1007/s10661-010-1764-1

Zhang, M., Zhang, C., Wang, K., Yue, Y., Qi, X., Fan, F., 2011. Spatiotemporal Variation of Karst Ecosystem Service Values and Its Correlation with Environmental Factors in Northwest Guangxi, China. Environmental Management 48, 933-944, doi: 10.1007/s00267-011-9735-z

Zhao, B., Kreuter, U., Li, B., Ma, Z.J., Chen, J.K., Nakagoshi, N., 2004. An ecosystem service value assessment of land-use change on Chongming Island, China. Land Use Policy 21, 139-148, doi: 10.1016/j.landusepol.2003.10.003.

GENERAL CONCLUSIONS

Land use change is the major driver behind ecosystem collapse. Reductions in ecosystem surface area in El Salvador are non-random, with some ecosystems losing more area than what would be expected by chance. This led to finding that ecosystems in the presence of large human settlements and on top of soils with high production value are likely to have a high risk of collapse.

Ecosystems with high risk of collapse carry consequences felt by human society. During the same 13 year period that we assessed ecosystem conservation status, ecosystem service value declined by 2.6%, and is currently equal to 44% of El Salvador's GDP. A country such as El Salvador, which loses 3.6% of its GDP with each natural disaster, cannot wantonly allow such a loss of ecosystem services, especially those associated with climate and water regulation.

Ecosystems are endangered. To effectively manage biodiversity at the ecosystem level, we suggest the building of simple models to predict risk of collapse with which to establish priority ecosystems, and encourage the founding of a world-wide ecosystem database with a universally accepted classification system. As for El Salvador, avoiding further depletion of natural capital should be a state priority, and proactive strategies could be the key. Alternatives such as generating ecosystem services outside protected areas by decreasing agricultural matrix contrast with native forest could satisfy the deficit of ecosystem service loss, aiding environmentally impoverished nations.