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ESTIMATIVA DA VULNERABILIDADE DOS CORAIS BRASILEIROS

Orientador: Prof. Dr. Paulo De Marco Júnior

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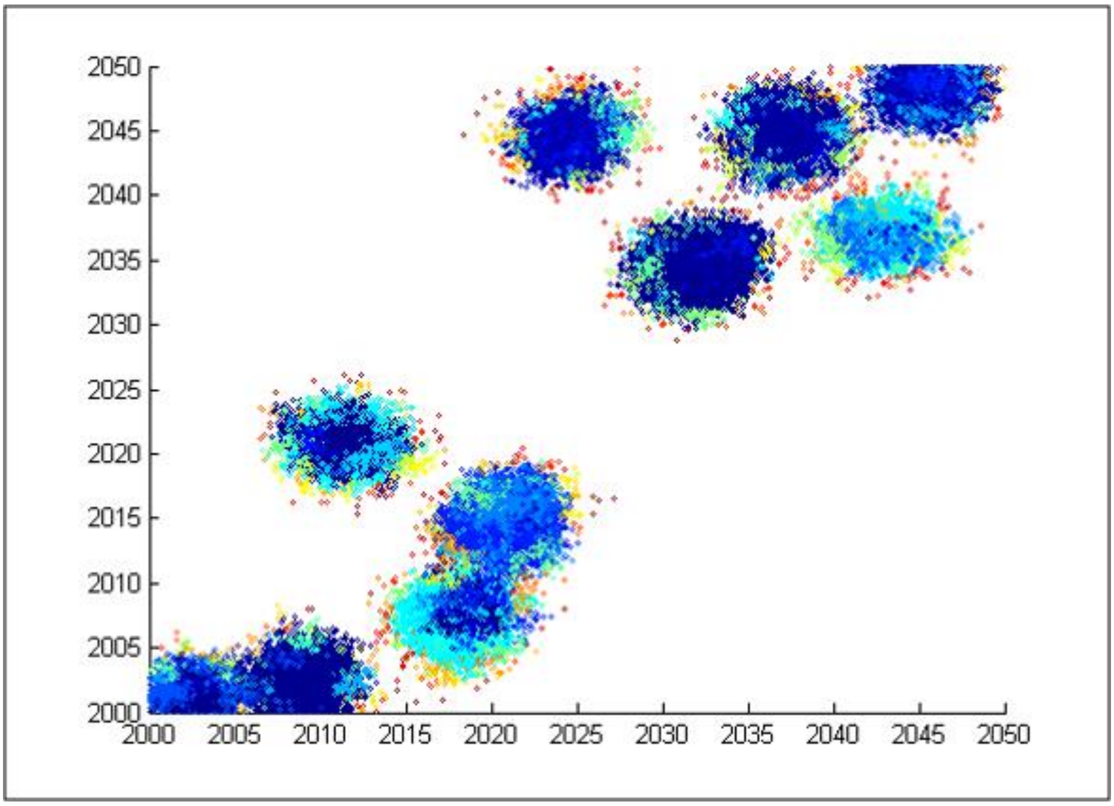

Colônias de *Tubastraea coccinea* (coral sol) geradas por um Modelo Baseado em Indivíduo

“*Wyrd Bið Ful Aræd (*O destino é inexorável) ” **Uhtred of Bebbanburg**

(As Crônicas Saxônicas

Bernard Cornwell, 2004)

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Montar uma dissertação é como montar um quebra cabeça de 5000 peças. Tudo começa com uma única peça e a ela se somam mais tantas outras. No entanto, do instante em que se inicia a montagem até a colocação da última peça existe toda uma gama de pessoas envolvidas, não somente aquele que se dispôs a montar o quebra cabeça inicialmente. No final todo o processo de montagem se transforma em uma atividade coletiva, de forma que graças ao conjunto o quebra cabeça é completado e de uma maneira muito mais eficiente e divertida do que se este fosse executado por uma única pessoa. Portanto, esse espaço dedico a todas as pessoas que foram essenciais para que esse quebra cabeça chamado dissertação fosse concluído. Muito obrigado a todos, jamais teria conseguido sem vocês!

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Sumário

Introdução Geral

A capacidade humana de alterar rapidamente o ambiente é uma força a ser reconhecida. Tais alterações do ambiente se refletem nas taxas de extinção, 100 vezes mais elevadas se comparadas ao período anterior à existência humana (Pimm et al. 2014). É possível categorizar impactos relacionados a atividades humanas em duas escalas: i) impactos de larga escala, como por exemplo mudanças climáticas e aumento do nível do mar, e ii) impactos em escala local, como empreendimentos e desenvolvimento, espécies invasoras e mudanças no estado de comunidades. Impactos de larga escala, principalmente relacionados a mudanças climáticas, têm recebido maior atenção devido ao fato de seus efeitos não permanecerem restritos a uma área ou grupo de espécies. Estudos que avaliam espécies dos grupos taxonômicos mais representativos e que levam em conta um cenário conservador, com alterações medianas de temperatura (aumento de 1.8-2.0ºC até 2050), concluíram que 15-37% da biodiversidade atual corre risco de ser extinta devido apenas às mudanças climáticas (Thomas et al. 2004). Apesar da menor abrangência, impactos locais representam uma ameaça tão grande quanto alterações globais. De acordo com a Lista Vermelha da IUCN (*International Union for Conservation of Nature*) (IUCN 2015), das 22781 espécies classificadas como “Vulnerável (VU), Em perigo (EN) ou Criticamente em perigo (CR)”, 88% se encontram nas respectivas classes devido a impactos locais, sendo que uma considerável parcela dessas espécies (37%) sofre com impactos causados pela agricultura ou aquacultura.

Apesar do grande peso de atividades humanas sobre a biodiversidade, tais efeitos não são homogêneos, já que variam espacialmente e afetam de forma distinta os elementos da biodiversidade (Jetz et al. 2007, Hof et al. 2011). Tal comportamento idiossincrático causa problemas em modelos que buscam um padrão geral para o efeito desses impactos sobre espécies, já que a existência de tal padrão é improvável, fato que é especialmente problemático para espécies ou ambientes pouco conhecidos. Ecossistemas marinhos são um dos sistemas que mais sofrem com tais idiossincrasias. Em comparação com sistemas terrestres, ambientes marinhos possuem um número consideravelmente menor de estudos a longo prazo (Rosenzweig et al. 2008) e um percentual duas vezes maior de espécies com dados insuficientes na Lista Vermelha da IUCN (IUCN 2015). Apesar de avanços recentes no entendimento de impactos climáticos e antropogênicos em espécies marinhas (e.g. Halpern et al. 2008, 2015, Hoegh-Guldberg and Bruno 2010, Foden et al. 2013), há ainda uma grande defasagem, em especial sobre a interação desses fatores, e a necessidade de estudos em nível de espécie, que levem em conta a heterogeneidade dos impactos sobre as mesmas.

Recifes de corais são um dos mais estudados ecossistemas marinhos, em parte devido a sua importância ecológica e social, já que corais são responsáveis por seis diferentes funções e 19 serviços ecossistêmicos (Moberg and Folke 1999). A estrutura recifal criada por corais é fundamental para manutenção de uma grande diversidade de espécies, pois promove a diversificação de nicho e permite a coexistência de um elevado número de espécies em uma área relativamente pequena (Reaka-Kudla 1994, Birkeland 1997). Além disso, corais, mangues e bancos de gramas marinhas criam uma dinâmica recíproca, na qual cada sistema está envolvido em processos essenciais para os outros, além da existência de tal dinâmica ser necessária para o ciclo de vida e manutenção de diversas espécies (Ogden 1988, Moberg and Folke 1999, Nagelkerken et al. 2000).

Além de sua importância ecológica, corais também possuem grande contribuição social e econômica e são a principal fonte de renda de diversas comunidades. Um dos recifes de coral mais famosos do mundo, a Grande Barreira de Corais na Austrália, teve seu valor estimado em aproximadamente U$ 500 milhões/ano em 1994 (Drimil 1994). Tal valor é devido à grande quantidade de serviços relacionadas a um recife de corais, como suporte pesqueiro (McAllister 1988), prevenção de erosão da costa (Spurgeon 1992), turismo (Pendleton 1995) e diversos outros serviços culturais, religiosos e espirituais (Moberg and Folke 1999, Cesar 2002). Um segundo fator que justifica os esforços de estudo e proteção de corais é a sua sensibilidade a alterações no ambiente. Aproximadamente um terço das espécies de corais estão sob ameaça de extinção devido a mudanças climáticas, sendo que os principais fenômenos relacionados a alterações no clima que ameaçam os corais são o branqueamento e a acidificação dos oceanos. Tanto o branqueamento quanto a acidificação ocorrem atualmente, no entanto, devido ao aumento dos níveis de CO_2 e temperatura, espera-se que haja um aumento em sua frequência e intensidade nos próximos anos (Carpenter et al. 2008, Foden et al. 2013). O branqueamento dos corais está relacionado com o aumento na temperatura e com a maior recorrência de temperaturas extremas que fazem com que os corais expulsem suas simbiontes zooxantelas, responsáveis pela fotossíntese, fonte de alimentação do coral. Em situações nas quais os corais ficam sem as simbiontes por períodos prolongado ou estes episódios ocorram de maneira recorrente, há a possibilidade que o branqueamento cause danos a esses corais, o que pode leva-los à morte (Hughes et al. 2003). A acidificação dos oceanos, por outro lado, está relacionada diretamente ao aumento dos níveis de CO_2, que interfere na capacidade de acreção e crescimento dos corais. O CO_2 atmosférico se dissolve naturalmente na água e combina com íons de carbonato necessários para o processo de acreção dos corais. Tal processo ocorre atualmente, no entanto atingirá níveis críticos para os corais caso os níveis de dióxido de carbono atmosférico atinjam 580ppm, 1.5 vezes os níveis atuais, já que o aumento de CO_2 dissolvido causará o sequestro de uma maior quantidade de ións de carbonato (Hoegh-Guldberg et al. 2007).

Em relação a atividades humanas, a situação dos corais também é crítica já que sua ocorrência é limitada à zona costeira, região com alta densidade populacional e, consequentemente, com elevados índice de impactos. As atividades mais danosas aos corais são: pesca artesanal, principalmente combinada com métodos destrutivos como envenenamento e uso de explosivos, exploração excessiva de recursos pesqueiros, especialmente de peixes necessários para a sobrevivência dos corais, sedimentação e poluição, provenientes dos centros urbanos costeiros (Cesar 2002, Halpern et al. 2008, 2015). Apesar do estado altamente colonizado e saturado das regiões costeiras, os impactos a ambientes costeiros não alcançaram um patamar estável e ainda estão em crescimento. Em estudo recente, Halpern *et al.* (2015) demonstrou que todas as fontes de impactos consideradas sofreram um aumento ao comparar os dados de 2013 com dados de 2008. Tal aumento é ainda mais crítico ao considerar que mesmo em 2008 a vasta maioria dos recifes de coral já experimentava elevadas pressões(Halpern et al. 2008).

A situação é ainda mais preocupante para os corais brasileiros, que além de sofrerem com ameaças climáticas e humanas, ainda possuem déficits Wallaceanos (falta de conhecimento sobre a distribuição geográfica das espécies) e Darwinianos (falta de conhecimento sobre a história evolutiva das espécies), o que dificulta esforços de conservação de uma fauna única no mundo (Moura 2000, Castro and Pires 2001). Os corais brasileiros foram descritos por Laborel (1970) como não formadores de extensas estruturas recifais, com uma relativa baixa diversidade, porém com altas taxas de endemismo. As espécies endêmicas do Brasil podem ser categorizadas em dois grupos, classificados pela origem de seu endemismo: espécies relacionadas à fauna coralínea do Caribe e espécies remanescentes do Terciário (Leão et al. 2003). O primeiro grupo, de espécies com alguma relação com corais do Caribe, teve sua ligação com a região cortada durante o soerguimento dos Andes e a inversão do curso do Rio Amazonas para o Oceano Atlântico, que agora atuaria como um filtro para a dispersão de larvas dos corais, devido à sua baixa salinidade (Frost 1977, Neves et al. 2010, Cordeiro et al. 2015). Corais do segundo grupo, relacionados a espécies do Terciário, persistiram durante a recessão do nível do mar no Pleistoceno devido a refúgios criados pelas montanhas marinhas de Abrolhos e a cadeia de montanhas Vitória-Trindade (Leão 1983). Esses dois fenômenos são os responsáveis pela fauna brasileira possuir altos índices de endemismo e, consequentemente, importância mundial, mesmo com baixa diversidade se comparada a outras áreas como o Caribe e os arquipélagos do sudeste Asiático (Moura 2000).

Tendo em vista a falta de informações a respeito da diversidade, distribuição, ecologia e conservação dos corais brasileiros e sua importância, tanto para a biodiversidade mundial de corais quanto para a economia brasileira, esse trabalho visa contribuir para a melhor compreensão da vulnerabilidade dos corais frente a ameaças climáticas a antropogênicas, além de fazer uma análise comparativa e definir qual fator mais crítico para os corais brasileiros e propor locais prioritários para a conservação frente a tais ameaças. Para isso nós recorremos a Modelos de Nicho Ambiental (*Ecological Niche Models* - ENMs), uma técnica baseada na teoria do nicho e comumente utilizada para estabelecer relações entre a ocorrência de espécies e as condições ambientais. A presente dissertação é dividida em dois capítulos: (i) desenvolvimento de um novo e confiável método de avaliação de ENMs, tendo em vista que os métodos atuais superestimam a performance dos modelos e podem levar a conclusões equivocadas (Capítulo submetido para *Ecography*); (ii) avaliação da vulnerabilidade dos corais brasileiros a mudanças climáticas e atividades humanas e definição de áreas prioritárias para conservação que visam mitigar tais impactos e preservar ao máximo a biodiversidade desses corais (A ser submetido para *Marine Ecology Progress Series*) (Fig 1).

Literatura Citada

Birkeland, C. 1997. Life and Death of Coral reefs.

Carpenter, K. E. et al. 2008. One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. - Science (80-.). 321: 560–563.

Castro, C. C. B. and Pires, D. O. DO 2001. Brazilian coral reefs: what we already know and what is still missing. - Bull. Mar. Sci. 69: 357–371.

Cesar, H. S. J. 2002. Coral Reefs : Their Functions, Threats and Economic Value. - In: Collected essays on the economics of coral reefs. pp. 14–39.

Cordeiro, R. T. S. et al. 2015. Mesophotic coral ecosystems occur offshore and north of the Amazon River. - Bull. Mar. Sci. 91: 491–510.

Drimil, S. 1994. Protection for profit: Economic and financial values of the Great Barrier Reef World Heritage Area and other protected areas.

Foden, W. B. et al. 2013. Identifying the World’s Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals (S Lavergne, Ed.). - PLoS One 8: e65427.

Frost, S. H. 1977. Cenozoic reef system of the Caribbean. Prospects for Paleoecologic Synthesis. - In: Reef and Related Carbonates, Ecology and Sedimentology Studies in Geology No. 4. pp. 93–110.

Halpern, B. S. et al. 2008. A global map of human impact on marine ecosystems. - Science 319: 948–52.

Halpern, B. S. et al. 2015. Spatial and temporal changes in cumulative human impacts on the world’s ocean. - Nat. Commun. 6: 7615.

Hoegh-Guldberg, O. and Bruno, J. F. 2010. The Impact of Climate Change on the World’s Marine Ecosystems. - Science (80-.). 328: 1523–1528.

Hoegh-Guldberg, O. et al. 2007. Coral reefs under rapid climate change and ocean acidification. - Science 318: 1737–42.

Hof, C. et al. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. - Nature: 1–6.

Hughes, T. P. et al. 2003. Climate change, human impacts, and the resilience of coral reefs. - Science 301: 929–33.

IUCN 2015. The IUCN Red List of Threatened Species. Version 2015-4. <http://www.iucnredlist.org>.

Jetz, W. et al. 2007. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds (GM Mace, Ed.). - PLoS Biol. 5: e157.

Laborel, J. 1970. Madréporaires et hydrocoralliaires récifaux des cotes brésiliennes: systématique, écologie, répartition verticale et géographique. - Ann. l'Institut Ocean. Graph. Paris 47: 171–229.

Leão, Z. M. A. N. 1983. Abrolhos, o refúgio pleistocênico de uma fauna terciária de corais. - Rev. Biol. e Ciências da Terra 8: 22–24.

Leão, Z. M. A. N. et al. 2003. Corals and coral reefs of Brazil.

McAllister, D. E. 1988. Environmental, economic and social costs of coral reef destruction in the Philippines. - Galaxea 7: 161–178.

Moberg, F. and Folke, C. 1999. Ecological goods and services of coral reef ecosystems. - Ecol. Econ. 29: 215–233.

Moura, R. L. 2000. Brazilian reefs as priority areas for biodiversity conservation in the Atlantic Ocean. - 9th Int. Coral Reef Symp. 2: 917–920.

Nagelkerken, I. et al. 2000. Importance of Mangroves, Seagrass Beds and the Shallow Coral Reef as a Nursery for Important Coral Reef Fishes, Using a Visual Census Technique. - Estuar. Coast. Shelf Sci. 51: 31–44.

Neves, E. G. et al. 2010. Cnidaria, Scleractinia, Siderastreidae, Siderastrea siderea (Ellis and

Solander, 1786): Hartt Expedition and the first record of a Caribbean siderastreid in tropical Southwestern Atlantic. - Check List 6: 505–510.

Ogden, J. C. 1988. The influence of adjacent systems on the structure and function of coral reefs. - Proc. Int. Coral Reef Symp.: 123–129.

Pendleton, L. H. 1995. Valuing coral reef protection. - Ocean costal Manag. 26: 119–131.

Pimm, S. L. et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. - Science (80-.). 344: 1246752–1246752.

Reaka-Kudla, M. L. 1994. Biodiversity of coral reefs. - In: Science and a changing world. pp. 22.

Rosenzweig, C. et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. - Nature 453: 353–7.

Spurgeon, J. P. G. 1992. The economic valuation of coral reefs. - Mar. Pollut. Bull. 24: 529–536.

Thomas, C. D. et al. 2004. Extinction risk from climate change. - Nature 427: 145–8.

Chapter 1: Odds-and-evens: a new transferability-based framework to evaluate ecological niche models*

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Abstract

Ecological Niche Modelling (ENM) is widely used for conservation purposes, predicting species invasion, evolutionary aspects and a whole array of applications. However, for most cases, evaluating the efficiency of those models poses as problematic, as commonly used methods (i.e. random methods) do not assure the required independence between data used to create the model and data used to evaluate the model. We developed a new transferability-based framework that ensures the much-needed independence between subsets. We created an alternate approach that geographically splits occurrence datasets, while intrinsically controls issues related to previous transferability approaches, such as overfitting, extrapolation and sampling bias. We used 26 Atlantic coral species to perform three different geographical divisions quantifying the effect of different splits on model predictive efficiency. We demonstrate that transferability should be used as an effective method to evaluate ENMs. Geographical split of the area in deciles proved as a reliable evaluation method, assuring independence between datasets and being less prone to common transferability issues. Our odds-and-evens framework provides improvements to the ongoing debate of ENMs evaluating by its transferability. This new method corrects the issue of artificiality causing sampling bias and overfitting, common in previous methodologies, while also is less prone to extrapolation issues, a common problem in transferability approaches. Moreover, the framework appears as a feasible and useful alternative to the problematic and commonly used random partition of datasets evaluation.

Keywords: species distribution model; evaluation; ENM; SDM; Coral; independence; marine environments;

Introduction

Ecological niche modelling (ENM) had an exponential growth since its idealisation in the 1980s-1990s, with an average increase of over 20 published papers per year from 1995 to 2008 (Lobo et al. 2010). Such an incredible raise is due to the easy applicability of the method and availability of high resolution ready-to-use data, combined with the wide range of fields it is possible to apply ENM. As the applicability of ENMs expands into new fields (Pearman et al. 2010, Silva et al. 2014, Valladares et al. 2014) and new environments (Tyberghein et al. 2012, Riul et al. 2013) the growth trend is unlikely to change. Despite the significant growth and new applications, there are still old challenges that need to be addressed for ENM improvement. One recurrent issue, the evaluation of models is a major ongoing unresolved debate (e.g. Araújo and Guisan 2006; Hijmans 2012; Wenger and Olden 2012) and in spite of the best efforts, models still lack a reliable evaluation strategy.

Commonly used model evaluation methods are based on random sampling, in which occurrences are split randomly and a percentage is used to fit the model and the rest for evaluation (e.g. Riul et al. 2013; Silva et al. 2014). Another method is the k-fold cross validation, in which occurrences are randomly divided into blocks and several runs are performed, and at each run, one of these blocks are left aside for evaluating model fit (e.g. Randin et al. 2006; Braunisch et al. 2013). However, these techniques do not meet the assumption of independency between training and test subsets, a prerequisite for a valid evaluation process, which can lead to inflated measures of accuracy (Veloz 2009, Radosavljevic and Anderson 2014). In practical words, current random data partitioning methods may select as `training` or `test` two points that are very close in the geographical space, violating the independence assumption (Figure 1a, but see Fand *et al.* 2014; Iosif *et al.* 2014; Kelly *et al.* 2014; Trainor *et al.* 2014). The existence of high spatial autocorrelation observed in environmental datasets and proximity between such two points make them far from independence in a statistical sense. Therefore, there is a need for a geographical partitioning of the dataset (Figure 1b). However, a geographical partition may favour the arise of additional problems, such as the failure to make predictions from one to other regions (Peterson et al. 2007).

Transferability is not a completely new concept in modelling, many studies addressed the transferability problem even before the popularisation of ENMs (Thomas and Bovee 1993, Glozier et al. 1997, Schröder and Richter 2000), most of these studies involved projections to different regions (Kleyer 2002, Randin et al. 2006) or different time periods (Araújo and Whittaker 2005). Although being useful for testing transferability, those studies comprised data with a quality level that is not common to find, for example, Araújo & Whittaker (2005) had data of 116 bird species for two different well defined time periods with a sampling coverage of 98-100% for all Britain. Here, we advocate that the study of model transferability creates an opportunity to deal with problems in data partitioning for evaluation procedures. Since transferability analysis demand a geographical partition of the data, it intrinsically controls for problems of independence in model evaluation. However, despite this feature, due to the lack of an efficient and easy-to-use framework applicable to commonly available data, transferability analyses are not frequently used for evaluation purposes.

The first attempt to implement a framework to evaluate model’s transferability within the same region and time period was developed by Peterson and Shaw (2003), in which the authors divided the occurrences in four quadrants based on their median longitude and latitude and used a pair of quadrants to make predictions on the other pair (Peterson and Shaw 2003). Peterson also deepened the transferability discussion by applying the same framework in a comparison between two of the most widely used algorithms, GARP and MaxEnt, and concluded that both had issues that weakened their transferability (Peterson et al. 2007). In response, Phillips (2008) elaborated a study explaining some issues related to Maxent, where he stated that the main reasons behind such problems were: inappropriate background selection, which caused a sample selection bias, low number of species, and the option to use cumulative output, instead of logistic output. Additionally, Phillips (2008) demonstrated that using a mask to restrict background selection could solve the problem of creating a sampling bias.

A new major attempt to establish a framework to evaluate transferability was proposed by Wenger and Olden (2012), where evaluation of models was carried out by a non-random five- and ten-fold cross validation, in addition to the usual two-fold cross validation proposed by Peterson et al. (2007). Although there was a significant improvement in model's transferability, Wenger and Olden's framework still has the same issue of sampling bias, as the entire environmental space was used for creating models. More recently, Bahn & McGill (2013) and Radosavljevic & Anderson (2014) developed frameworks that geographically divided training and evaluation data, assuring independence between training and evaluation subsets, and did not cause sampling bias.

Another recurrent, but better resolved issue, is the variables choice. It is stated that collinearity among predictors is one of the main problems, as collinear predictors are not independent and, therefore, any extrapolations based on them has a chance of being erroneous (Dormann et al. 2013). In order to reduce model overfitting, causing discrepancies and errors in models projection, a common approach has been to simplify the predictor set by deriving principal components (PCs) (Jiménez-Valverde et al. 2011, Silva et al. 2014). Several studies reinforce that uncorrelated PCA derived variables give better predictions than original Bioclim variables (Warren et al. 2008, Dupin et al. 2011).

Here, we intend to advance even further in the challenge of evaluating ENMs using a transferability-based framework with independent training-testing subsets. For this, we propose a new method, in which we control the partition of background and occurrence data assuring independence between training and testing datasets, and also avoiding the creation of a sampling bias, a situation common to previous transferability studies (Peterson et al. 2007, Wenger and Olden 2012). We also evaluated the marine predictors from Bio-Oracle (Tyberghein et al. 2012), a relatively new environmental database, in respect to its collinearity.

We used Brazilian corals for applying our new transferability framework and also for improving species distribution models for marine environments. We opted for Brazilian corals because some species occur through the entire coast, which means they have a broad environmental tolerance, posing a great challenge for transferability. We also intended to reinforce the use ENM for marine ecosystems, considering that methodological discussions about ENM are disproportionally more common for terrestrial environments and little is discussed for aquatic species.

Methods

Species occurrence records and environmental information

We assembled basic information on the distribution of Brazilian coral species (orders *Alcyonacea*, *Antipatharia*, *Corallimorpharia*, *Scleractinia*, and families *Milleporidae*, *Stylasteridae*) from (1) online databases (GBIF and SpeciesLink) and (2) scientific literature records [Supplementary material 1]. In total, we gathered 4461 occurrence data from 173 species, from which we selected only those species with more than 20 unique occurrences to create the models. A unique occurrence was considered as an occurrence inside a pixel of 10 X 10 km, since additional occurrences at the same pixel would not be considered anymore. At the end, we had 26 species with 1174 unique records in South America, from those; approximately 32% were gathered from literature revision and 68% from online databases (Table S1).

There are many reported problems with using raw information from online databases (Giovanni et al. 2012). We tried to overcome these problems following a protocol that includes (a) searching for points positioned incorrectly; (b) use of Google Earth to acquire geographical information of occurrences that lacked georeferencing but had some basic information, for example the nearest coral reef from the city (c) checking for problems in synonimcs.

We assembled two different environmental datasets: (1) Bio-Oracle layers at 5km resolution (Tyberghein et al. 2012), and (2) principal components (PCs) derived variables from the previous dataset. The comparison of these results will help to evaluate the benefits of using PCA for reducing model complexity by reducing dimensionality and collinearity, in order to avoid model overfitting and related pitfalls in the Bio-Oracle database (Peterson and Nakazawa 2008, Jiménez-Valverde et al. 2011). We selected nine axes from PCA analysis that accounted for more than 95% of the variation of the original dataset (Fig 2b).

Modelling procedures

We used only MaxEnt (Mora and Sale 2011) as a modelling algorithm since it is the most widely used and considered as the best and more consistent in recent evaluations (e.g. Elith et al. 2006; Diniz-Filho et al. 2009; Silva et al. 2014). In spite of that, MaxEnt performed poorly in regard to transferability (Peterson et al. 2007), however, this happened possibly due to sampling bias because of the lack of background restriction, as suggested by Phillips (2008). MaxEnt models are created based on contrast between occurrence locations and background, creating response curves for each variable and a final suitability map (Merow et al. 2013). Since MaxEnt is sensitive to background selection, it is an optimum algorithm to evaluate model transferability.

In order to evaluate model transferability we performed a geographically structured cross validation, in which we divided the study area in quadrants, in a method that incorporates elements of several studies (Peterson et al. 2007, Phillips 2008, Wenger and Olden 2012, Bahn and McGill 2013, Radosavljevic and Anderson 2014). For each species we used the median/quartile/decile of its latitudinal variation to separate occurrence and environmental dataset in two, four or ten equal area quadrants, respectively. Since corals occur in specific areas and depths along the coast, we divided the distribution only latitudinally (Fig 2b). Whereas it is not recommended to create models with a relatively small number of occurrences, we only considered in our analyses those models that, after the split into quadrants, still had at least five occurrences in each quadrant subset (Pearson et al. 2007). It is important to note that this division represents the spatial structure of data but also reflects important environmental gradients (e.g. variations in temperature). In presence-background procedures (such as Maxent) a special care should be taken on the selection of background point, assuring to not include areas where the species is absent due to dispersal limitations (Barve et al. 2011). Additionally, when performing geographically structured k-fold division it is important to restrict background sampling to areas where the model will be fitted, in order to avoid creating sampling bias (Phillips 2008, Radosavljevic and Anderson 2014). To do so, we used a similar approach as the one used by Radosavljevic & Anderson (2014), where we created masks to restrict model background to fitted area. However, unlike the authors, who used a left-one-out evaluation method, we chose to recur to an alternate approach, where we fit the model on odd quadrants and projected onto even quadrants for evaluation, and vice versa.

Considering possible geographical bias and known overfitting problems in Maxent models, we used only linear and quadratic features, as suggested by Anderson & Gonzalez (2011). We fitted the model ten times to produce replicates using the same occurrence data but different generated background data, where we set to 10000 randomly selected sites.

Model Evaluation

We evaluated model transferability by the value of True Skill Statistics (TSS) value of ROC threshold of projections onto test dataset from models created with the training dataset. We conducted a Repeated Measures ANOVA to compare TSS values for data partitions in median/quartiles/deciles and differences between environmental databases. We assumed the dependency generated by the use of the same occurrence data in each species replicates, and used these replicates as a repeated measure in the ANOVA. We also took into consideration possible differences between odds and evens models, evaluating them separately.

A possible explanation for the low performance of analysis based on two-fold partition could be simply the underrepresentation of species environmental niche. This issue could be minimised by performing many-fold partitions, reducing environmental variability dissimilarity between fitted and predicted area. We evaluated the expected improvement of species model performance with the division in more quadrants and alternate picking of those quadrants by calculating niche overlap and niche subset similarity (Broennimann et al. 2012).Calculations were performed in R (The R Core Team 2014) using scripts developed by Broennimann et al. (2012) and Warren et al. (2008).

. We used the PCA environmental subset for this, fitted on the entire environmental space of the study background (PCA-env) to measure the niche overlap between odds and evens quadrants. The framework uses the first two axes of a PCA to estimate the limits of environmental space, and then it stablishes a comparison between the environmental conditions where the species occur and all available conditions to create a species niche (Broennimann et al. 2012). The method uses Schoener's D Metric (Schoener 1968) to calculate niche overlap between species, which varies from 0 to1. In our case, we used it to compare the niche of occurrences on the odd quadrants with the niche of occurrences on even quadrants. We also test differences in niche subset similarity among those occurrence data partition sets based on Peterson et al. (1999) null model approach implemented by Warren (2008). We compared the values of Schoener's D Metric using a Repeated Measure ANOVA. We also conducted linear regressions by quadrants between Schoener's D values and TSS values to test if the increase in niche overlap was one of the factors responsible for the increase in predictive accuracy.

Additionally, we took advantage of the fact that 13 of our species also occur in the Caribbean region to create models in South America and made predictions for Caribbean reefs.

Our main objective was to assess if models created with quadrants, particularly those created based on deciles, are able to predict coral occurrences in the Caribbean with the same accuracy as models created taking into consideration all Brazilian occurrences. Trying to predict geographically isolated areas is a common way of evaluating models by transferability, which is based on the ENMs assumption of niche conservatism. In practice, while trying to predict Caribbean occurrences with South America data, the real question is if all species niche is comprised within South America and how efficiently different methods of division within our framework represent the whole environmental range of the species.

All known measures of model efficiency are subject of some criticism, mostly related to its dependency on prevalence or number of records, but also possibly related to spatial autocorrelation in occurrence data (e.g. Manel *et al.* 2001; Lobo *et al.* 2008; Barve *et al.* 2011). To evaluate these effects, we performed linear regressions between TSS values for each species and (i) number of occurrences, (ii) spatial autocorrelation and (iii) prevalence. We calculated spatial autocorrelation in our occurrence data by using the first distance class of Moran's I to compare the resemblance among occurrences in regard to the first axis of the PCA dataset, which accounted for 36% of all the environmental variation. We calculated the prevalence in our models by the total number of cells predicted as presence when the ROC threshold is applied (size of predicted area). For situations i and ii, we performed regressions between average TSS and predictor i and ii, since there is no variation in those predictors within replicates and any internal variation in TSS values would not be related to those predictors and would possibly hinder any real correlation. Unlike previous situations, for iii there was a high variability in the size of predicted area within a species replicates. Therefore, to evaluate the effect of prevalence in TSS among quadrants we used all replicates, with its respective TSS and size of predicted area values, and not the average TSS.

Results

Transferability Assessment

We found a significant increase in model's accuracy for evaluating transferability with further area divisions, deciles were more transferable than quartiles and median, for both PCA and Bio-Oracle datasets ($F_{2,300}$=12.168, p<0.001). There was a pattern of progressive increase in model transferability when comparing division by median/quartile/decile for both PCA (TSS_{Med}=0.735 ± 0.229; TSS_{Quart}=0.791 ± 0.200; TSS_{Dec}=0.845 ± 0.132) and Bio-Oracle dataset (TSS_{Med}=0.792 ± 0.222; TSS_{Quart}=0.857 ± 0.130; TSS_{Decil}=0.881 ± 0.108). An exception was models created with the derived PCA dataset on odd quadrants, in which models divided by the median outperformed models divided by quartiles (Fig.3). This happened due to a higher accuracy of even median models, which caused a difference in odd and even patterns ($F_{2,300}$=3.177,p<0.05).

Division in deciles also greatly reduced variability within models. Both PCA and Bio-Oracle datasets presented a reduction of standard deviation with subsequent quadrant division, in addition to a sharp increase in the minimum TSS values. Maximum TSS values did not differ when comparing division methods, demonstrating that all division methods were able to produce accurate models. Division methods using the median and quartile division performed extremely poorly, while models for deciles had a reasonable increase while comparing the poorest performances, indicating its higher stability and lesser idiosyncrasy (Table 1).

Taking into account predictions for the Caribbean region, similarity against models created using all South America occurrences increased as the numbers of quadrants increased, with some exceptions. Models created with two quadrants scored worse than models created on the entire Brazilian area and all occurrences for both odd and even subsets ($F_{1,516}$=91.644, p<0.001). Models created with four quadrants were also worse, but with different intensities when comparing odds and evens ($F_{1,516}$=9.285,p<0.01), odd quadrants performed strongly worse ($F_{1,516}$=49.652, $p<0.001$), while at even quadrants the models were more similar to those created with all occurrences ($F_{1,516}$=12.646, $p<0.01$). As for models created with ten quadrants, there was a similar accuracy for those created on odd quadrants ($F_{1,516}$=1.201,$p>0.05$), but models created on even quadrants were worse than those created with the full range ($F_{1,516}$=5.028, $p<0.05$) (Fig. 4).

The gradual increase in TSS values could be related to increases in niche similarity, as dividing the area in ten quadrants significantly improved niche overlap among odds and evens (Schoener's D, $F_{2,67}$=4.973, $p<0.01$). As this pattern did not differ between models fitted on odd or even quadrants we evaluated both datasets together (Fig.5).

As a result of the increased overlap, there is also an improvement in the overall niche subset similarity, while the percentage of species that predicted opposite occurrences better than random was 56% for the models created on two quadrants and 40% on four quadrants, models for ten quadrants had a success rate of 75%.

Collinearity

We found no improvement in model results while using PCA variables derived from the original ones, on the contrary, there was a worsening for all the divisions when comparing the derived PCA dataset with the original Bio-Oracle variables for both models fitted on odd quadrants and even quadrants ($F_{1,300}$=10.259,$p<0.001$) (Fig.3). Besides underperforming, models created with PCA variables also presented a higher variation among odds and evens models, with a stronger effect in models created with two quadrants.

Other possible nuisance factors

TSS values were not affected by the number of occurrences for any division into quadrants, neither for models calibrated on even quadrants (Median: R^2=0.052, $p>0.05$ / Quartile: R^2=0.085, $p>0.05$ / Decile: R^2=0.114, $p>0.05$) nor for those calibrated on odd quadrants (Median: $R^2=0.0003$, $p>0.05$ / Quartile: $R^2=0.020$, $p>0.05$ / Decile: $R^2=0.0006$, $p>0.05$).

There was no effect of the spatial autocorrelation in our occurrence data in TSS values, again neither for models calibrated on even quadrats (Median: $R^2=0.002$, $p>0.05$ / Quartile: $R^2=0.009$, $p>0.05$ / Decile: $R^2=0.014$, $p>0.05$) nor for those calibrated on odd quadrants (Median: $R^2=0.037$, $p>0.05$ / Quartile: $R^2=0.009$, $p>0.05$ / Decile: $R^2=0.118$, $p>0.05$).

We found that further division in ten quadrants decreases the rate in which prevalence affects TSS values, both for those created on even quadrants (Median: $R^2=0.580$, slope=2.530, $p<0.05$ / Quartile: $R^2=0.598$, slope=3.380, $p<0.05$ / Decile: $R^2=0.178$, slope=2.359, $p<0.05$) (Fig 6) and for those created on odd quadrants (Median: $R^2=0.410$, slope=5.930, $p<0.05$ / Quartile: $R^2=0.147$, slope=3.380, $p<0.05$ / Decile: $R^2=0.357$, slope=3.057, $p<0.05$) (Fig.7). There is also an idiosyncratic behaviour on this pattern. While odd-based models demonstrated a gradual decrease in the slope, even-based models first had an increase in the slope from median to quartiles models with a subsequent decrease in deciles models. BioOracle models did not present the same pattern, median and quartiles division were less affected by prevalence than deciles, even if by little (Figs. S1 and S2).

Discussion

Evaluation of model fit demands a spatial partition of training and test datasets, in order to conduct a proper independent model evaluation. This is only truly achieved by using a geographical partition of training and test dataset. On the other hand, this geographical partition may cause poor transferability as a result of a lack of environmental similarity between training and test areas. Here we show that it is possible to combine these two different views to properly evaluate species distribution modelling. We argue that our odds-and-evens approach fulfils the requirement of spatial independence, while also reducing environmental differences – especially in the 10-fold partition – a desired property for model evaluation.

Unlike previous studies, which had poor results for transferability assessment (Peterson et al. 2007, Wenger and Olden 2012, Bahn and McGill 2013), we found evidences that dividing the area in several quadrants and using alternate calibration-fitting quadrants may deal with problems of overfitting and poor extrapolation. Nevertheless, we recognize that the number of odds-and-even partitions may be a complex choice, affected by the geographic distribution of occurrence points (*e.g.* the existence of aggregated clumps), the spatial distribution of environmental predictors and other spatial constrains. Our view is that an empirical evaluation of each dataset may be worthwhile in these circumstances. Therefore, we reinforce Wenger & Olden (2012) suggestion that transferability should be considered when creating models, and taking a step further, we recommend the assess of the environmental similarity among training and test datasets – the fundamental origin of the transferability problems – even when there is no desire to make projections to new regions, to guide the choice of the best partition number. Wenger & Olden (2012) suggested 3-10 fold division in a way that the fitting data should cover a large portion of the variability of the predictors. We agree with those authors in such point of view, but recommend restraining the division to more quadrants (8-10), as a smaller number may suffer from high variability, possibly due to extrapolation problems. As a final remark, we reinforce Phillips (2008) and Radosavljevic & Anderson (2014) recommendations about the importance of using a mask to restrict both background and occurrence data when performing transferability assessments. Mask creation solves the problem of artificial increase of sampling bias, since without a mask background data will be drawn from locations where occurrence data was intentionally excluded.

While most of the previous studies tested transferability based on one or two species (Peterson et al. 2007, Wenger and Olden 2012, Radosavljevic and Anderson 2014), we evaluated it on 26 species, giving us a solid support to build a broad overview about the use of transferability and explore the existence of variation among species. Moreover, our results show that many idiosyncratic results could come from single species approach to transferability. For example, if we only studied *Phyllangia americana* (Milne-Edwards and Haime, 1849) we would find an opposite response, in which division in ten quadrants underperformed division in two quadrants (Figure S3 and S4). Therefore, we recommend careful methodological assumptions construction when models are based on a single species. Additionally, we reinforce that ENM studies intending to explore new methodologies should take into consideration a large species database in order to avoid the effect of idiosyncrasy among species.

Another key feature is the restriction of the background to quadrants wherever the model was fitted, as demonstrated by Phillips (2008) and Radosavljevic & Anderson (2014). The restriction of background to accessible areas to the species over relevant time periods has a major effect on species prevalence, affecting model evaluation metrics (Barve et al. 2011). Additionally, background restriction has an effect on transferability, removing the effects of artificially increased sampling bias (Phillips 2008). Presence-background models, such as Maxent, are known to produce inflated measures of model accuracy due to biased occurrence data, which is spatially autocorrelated and, therefore, lacks independence (Veloz 2009). Our evaluation framework deals with the problem of sample bias by restricting the background to the same quadrants used to fit the model. Nevertheless, it should also be effectively applied to other algorithms that are not background-based, as another key feature of it is reducing issues of extrapolation and overfitting, a problem common to all algorithms (Elith & Graham 2009; Owens *et al*> 2013).

Background restriction, both when fitting and evaluating models, might also have another crucial role besides assuring independence and avoiding sampling bias in model fitting, which is minimizing spatial sorting bias. Spatial sorting bias, as discussed by Hijmans (2012), is the difference between geographic distances of training-testing and training-absence sites. If geographic distances of training-testing are larger than the training-absence one, AUC values would be highly inflated, being necessary to correct it by pairwise distance sampling or by the use of a null model (Hijmans, 2012). Another feature mentioned but not tested by Hijmans (2012) is the relative distribution of presence-testing sites in relation to presence-training sites, since it is important to assure that the first ones have a balanced distribution along species range. Our framework intrinsically deals with all those issues, as background restriction assures similar presence-absence distances in relation to training-testing distances, while ensuring that testing sites are distributed across all species range, what would not happen in a leave-one-out approach.

The gradual increase in TSS values from two to ten quadrants models with a high overall predictive accuracy in the last ones may be related to two key aspects; overfitting and extrapolation. Geographical division in several alternate areas, evens or odds quadrants, deals with extrapolation by better representing the whole spatial environmental variation, minimizing extrapolation into areas they were not fitted (Wenger and Olden 2012, Bahn and McGill 2013). This may be the reason why Radosavljevic & Anderson (2014) models performed poorly, since a division in four quadrants may cause the subsets to not fully represent the environmental variability, as was demonstrated by our models and visualised by a MESS analysis (Figure S5). The best representation of environmental variability among subsets might also contribute to reduce overfitting. As occurrence data is more diffuse, there is the possibility that our framework also minimizes overfitting problems stated by Peterson (Peterson et al. 2007) and Radosavljevic & Anderson (2014).

Apart from assuring better results in model evaluation, there is another attribute as important as the increase in TSS values; the variability of those values. Heterogeneity reduction in ten quadrant models could be related to lower uncertainty in predictions, as decile-based models had a higher overlap between training and test subsets, which reduces extrapolating problems. This means those models are more reliable as they reduce idiosyncrasy and, therefore, can be used as an evaluation method that fulfils all requirements: (1) independent test subset, (2) high transferability and (3) low variance.

The original variables from Bio-Oracle had an improved model performance compared to PCA axes, possibly meaning that multicollinearity among Bio-Oracle predictors is not extremely strong and deriving principal components from those variables result in a loss of information. Multicollinearity among predictors is known to affect models generality, hence, predictive power, due to over-parametrization; therefore, it is necessary to stablish methods to deal with this issue (Guisan and Zimmermann 2000). Several studies for terrestrial systems evaluated the influence of multicollinearity among predictors on ENMs and came up with the conclusion that controlling collinearity is essential for improving model accuracy (e.g. Dupin et al. 2011; Jiménez-Valverde et al. 2011; Silva et al. 2014). For marine studies, there were already attempts to control collinearity by using performance-based forward-stepwise selection, which proved to be an efficient way to enhance model accuracy and even model transferability (Tyberghein et al. 2012, Verbruggen et al. 2013). In this study we evaluated the efficiency of deriving principal components from the original dataset, but against our expectations we found a superior performance for raw variables compared to PCA axes. We presume that this result could be related to the overall lack of collinearity among Bio-Oracle variables, since Bio-Oracle can be derived in four different macroecological clusters and four singletons (Tyberghein et al. 2012), it is possible that multicollinearity does not poses as a serious issue to Bio-Oracle as it poses to the terrestrial BioClim database, where most variables are derived from two main macroecological predictors.

We recommend using this odds and evens framework to assess transferability whenever evaluating models built for widely distributed species, also recommending the use of background and data division in ten quadrants, due to its success in evaluating models while using independent datasets and without causing a sampling bias. We assume that possible limitations of this approach are related to species with a small number of records and biased information, which causes unbalanced distribution of occurrence points over the real range distribution of the species. Thus, we expect that this approach will more reliable for species with a reasonable number of occurrence data (>20 unique occurrences). Otherwise, the odds-and-evens approach is especially useful for modelling species in which the environmental variation is mostly related to a single dimension. Our case study with marine species of coastal areas of Brazil is a good example, with a higher latitudinal variation and only a small variation attributable to the distance to the coast. Although models were developed for marine species and take into consideration only a latitudinal gradient, there is no reason why this framework will not work in other situations and environments, as long as quadrant division follows the variability in environmental variables.

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References

Anderson, R. P. and Gonzalez, I. 2011. Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. - Ecol. Modell. 222: 2796–2811.

Araújo, M. and Whittaker, R. 2005. Reducing uncertainty in projections of extinction risk from climate change. - Glob. Ecol. Biogeogr. 14: 529–538.

Araújo, M. B. and Guisan, A. 2006. Five (or so) challenges for species distribution modelling. - J. Biogeogr. 33: 1677–1688.

Bahn, V. and McGill, B. J. 2013. Testing the predictive performance of distribution models. - Oikos 122: 321–331.

Barve, N. et al. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. - Ecol. Modell. 222: 1810–1819.

Braunisch, V. et al. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. - Ecography 36: 971–983.

Broennimann, O. et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. - Glob. Ecol. Biogeogr. 21: 481–497.

Diniz-Filho, J. A. F. et al. 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. - Ecography (Cop.). 32: 897–906.

Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. - Ecography 36: 27–46.

Dupin, M. et al. 2011. Effects of the training dataset characteristics on the performance of nine species distribution models: Application to Diabrotica virgifera virgifera. - PLoS One 6: e20957.

Elith, J. and Graham, C. H. 2009. Do they? How do they? WHY do they differ? on finding reasons for differing performances of species distribution models. - Ecography 32: 66–77.

Elith, J. et al. 2006. Novel Methods Improve Prediction of Species ’ Distributions from Occurrence Data. - Ecography 29: 129–151.

Fand, B. B. et al. 2014. Predicting the potential geographic distribution of cotton mealybug Phenacoccus solenopsis in Inda based on MAXENT ecological niche Model. - J. Environ. Biol. 35: 973–982.

Giovanni, R. et al. 2012. The real task of selecting records for ecological niche modeling. - Nat. Conserv. 10: 139–144.

Glozier, N. E. et al. 1997. Transferability of Habitat Suitability Curves for a Benthic Minnow, Rhinichthys cataractae. - J. Freshw. Ecol. 12: 379–393.

Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. - Ecol. Modell. 135: 147–186.

Hijmans, R. J. 2012. Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. - Ecology 93: 679–688.

Iosif, R. et al. 2014. Climate-induced shifts in the niche similarity of two related spadefoot toads (genus Pelobates). - Org. Divers. Evol. 14: 397–408.

Jiménez-Valverde, A. et al. 2011. Use of niche models in invasive species risk assessments. - Biol. Invasions 13: 2785–2797.

Kelly, R. et al. 2014. Combining global climate and regional landscape models to improve prediction of invasion risk. - Divers. Distrib. 20: 884–894.

Kleyer, M. 2002. Validation of Plant Functional Types across Two Contrasting Landscapes. - J. Veg. Sci. 13: 167–178.

Lobo, J. M. et al. 2008. AUC: a misleading measure of the performance of predictive distribution models. - Glob. Ecol. Biogeogr. 17: 145–151.

Lobo, J. M. et al. 2010. The uncertain nature of absences and their importance in species distribution modelling. - Ecography 33: 103–114.

Manel, S. et al. 2001. Evaluating presence absence models in ecology; the need to count for prevalence. - J. Appied Ecol. 38: 921–931.

Merow, C. et al. 2013. A practical guide to MaxEnt for modeling species’ distributions: what it does, and why inputs and settings matter. - Ecography 36: 1058–1069.

Mora, C. and Sale, P. 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. - Mar. Ecol. Prog. Ser. 434: 251–266.

Owens, H. L. et al. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. - Ecol. Modell. 263: 10–18.

Pearman, P. B. et al. 2010. Within-taxon niche structure: Niche conservatism, divergence and predicted effects of climate change. - Ecography 33: 990–1003.

Pearson, R. G. et al. 2007. Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. - J. Biogeogr. 34: 102–117.

Peterson, A. T. and Shaw, J. 2003. Lutzomyia vectors for cutaneous leishmaniasis in Southern Brazil: Ecological niche models, predicted geographic distributions, and climate change effects. - Int. J. Parasitol. 33: 919–931.

Peterson, A. T. and Nakazawa, Y. 2008. Environmental data sets matter in ecological niche modelling: An example with Solenopsis invicta and Solenopsis richteri. - Glob. Ecol. Biogeogr. 17: 135–144.

Peterson, A. T. et al. 1999. Conservatism of Ecological Niches in Evolutionary Time. - Science 285: 1265–1267.

Peterson, A. T. et al. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. - Ecography 30: 550–560.

Phillips, S. J. 2008. Transferability, sample selection bias and background data in presence-only modelling: A response to Peterson et al. (2007). - Ecography 31: 272–278.

Radosavljevic, A. and Anderson, R. P. 2014. Making better Maxent models of species distributions: Complexity, overfitting and evaluation. - J. Biogeogr. 41: 629–643.

Randin, C. F. et al. 2006. Are niche-based species distribution models transferable in space? - J. Biogeogr. 33: 1689–1703.

Riul, P. et al. 2013. Invasive potential of the coral Tubastraea coccinea in the southwest Atlantic. - Mar. Ecol. Prog. Ser. 480: 73–81.

Schoener, T. W. 1968. Anolis lizards of Bimini: resource partitioning in a complex fauna. - Ecology 49: 704–726.

Schröder, B. and Richter, O. 2000. Are habitat models transferable in space and time? - Zeitschrift für Ökologie und Naturschutz 8: 195–205.

Silva, D. P. et al. 2014. Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species Lithurgus huberi in South America. - Ecol. Modell. 273: 200–209.

The R Core Team 2014. R: A language and environment for statistical computing. - R Found. Stat. Comput.: 3407.

Thomas, J. a and Bovee, K. D. 1993. Transferability of Habitat Suitability Criteria. - Regul. RiversResearch Manag. 8: 285–294.

Trainor, A. M. et al. 2014. Enhancing species distribution modeling by characterizing predator-prey interactions. - Ecol. Appl. 24: 204–216.

Tyberghein, L. et al. 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. - Glob. Ecol. Biogeogr. 21: 272–281.

Valladares, F. et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. - Ecol. Lett. 17: 1351–1364.

Veloz, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. - J. Biogeogr. 36: 2290–2299.

Verbruggen, H. et al. 2013. Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. - PLoS One 8: e68337.

Warren, D. L. et al. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. - Evolution 62: 2868–2883.

Wenger, S. J. and Olden, J. D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. - Methods Ecol. Evol. 3: 260–267.

Figures and Tables

Table 1: Basic statistics for models true skill statistics (TSS)

Dataset	ODD/ EVEN	Quad	TSS	SD	Min	Max
PCA	***ODD***	2	0.661	0.236	0.001	0.978
		4	0.780	0.183	0.001	0.980
		10	0.833	0.138	0.130	0.983
	EVEN	2	0.808	0.194	0.096	0.990
		4	0.802	0.215	0.071	0.970
		10	0.856	0.124	0.352	0.994
Bio-Oracle	***ODD***	2	0.743	0.270	0.077	0.982
		4	0.823	0.166	0.000	0.978
		10	0.868	0.131	0.289	0.990
	EVEN	2	0.841	0.142	0.157	0.983
		4	0.891	0.064	0.548	0.979
		10	0.894	0.075	0.547	0.997

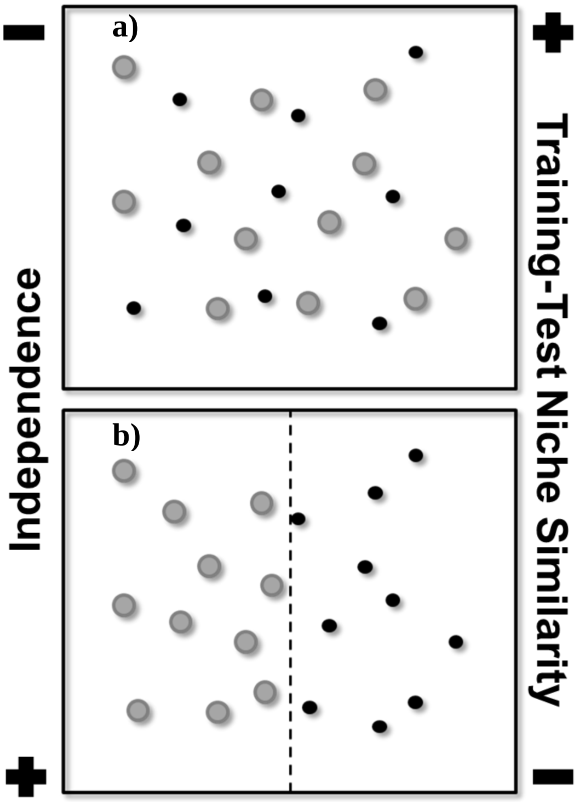
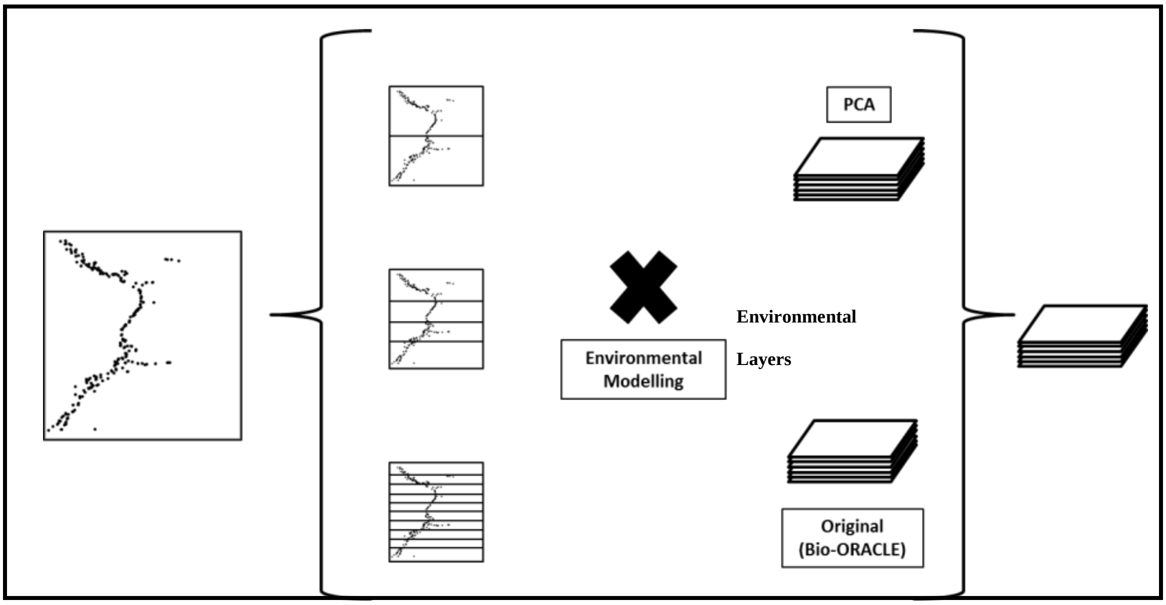


Figure 1: Framework comparing models created with random occurrence division (upper) and non-random division (bottom) and effects on model independence and transferability

Figure 2: Framework of modelling procedures, on the left side an exemplification of background and occurrence data division in two, four and ten quadrants; on the right side the two environmental databases used to create the models, one using PCA axes and one raw environmental data.


PCA
Environmental Modelling
Environmental
Layers
Original (Bio-ORACLE)

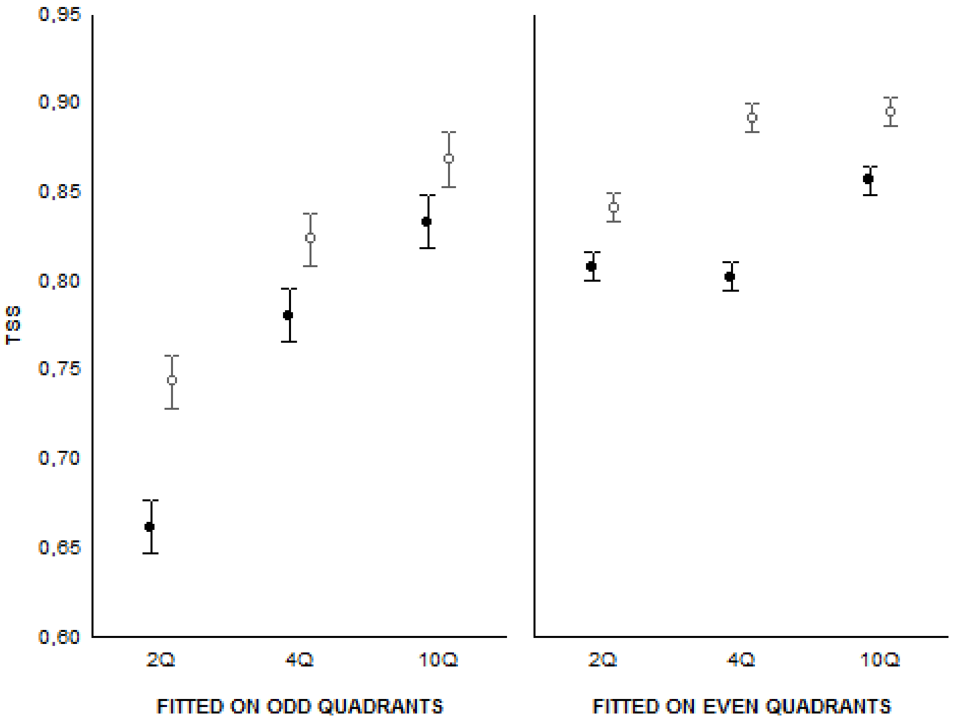


Figure 3: Repeated-measures ANOVA between quadrants comparing PCA (closed circles) and Bio-Oracle (open circles) databases for models fitted on odds (left) and evens (right) quadrants

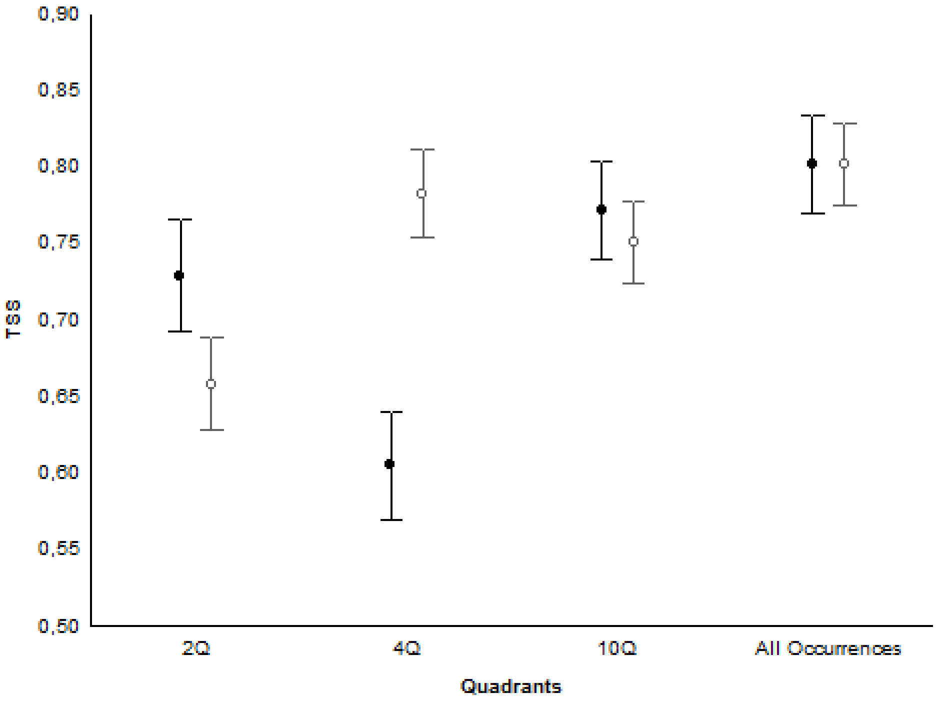


Figure 4: Repeated measures ANOVA contrasting Caribbean projection accuracy for models created with two, four and ten quadrants with models created without division, using all data from South America to fit the models. Models were created using the BioOracle database and fitted on both odds(open circles) and evens(closed circles) quadrants.

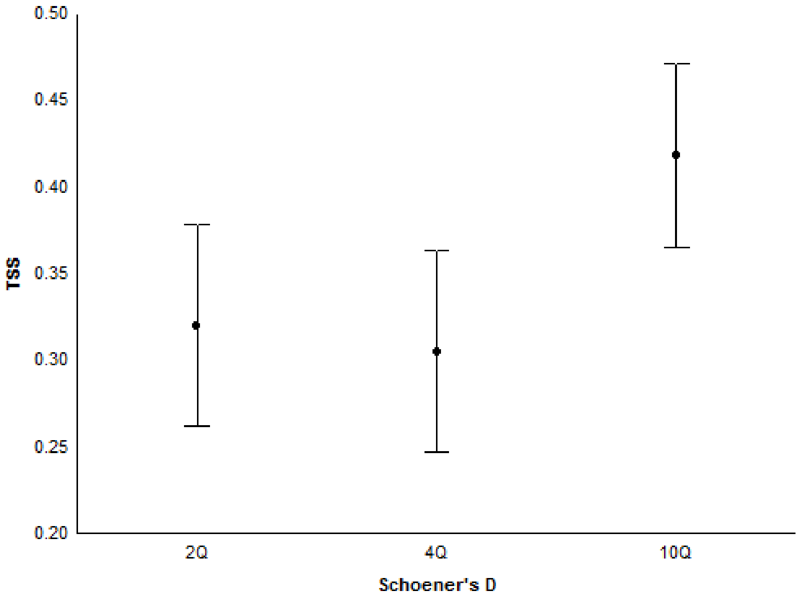


Figure 5: Schoener's D metric for niche overlap between odds and even quadrants for models created with two, four and ten division.

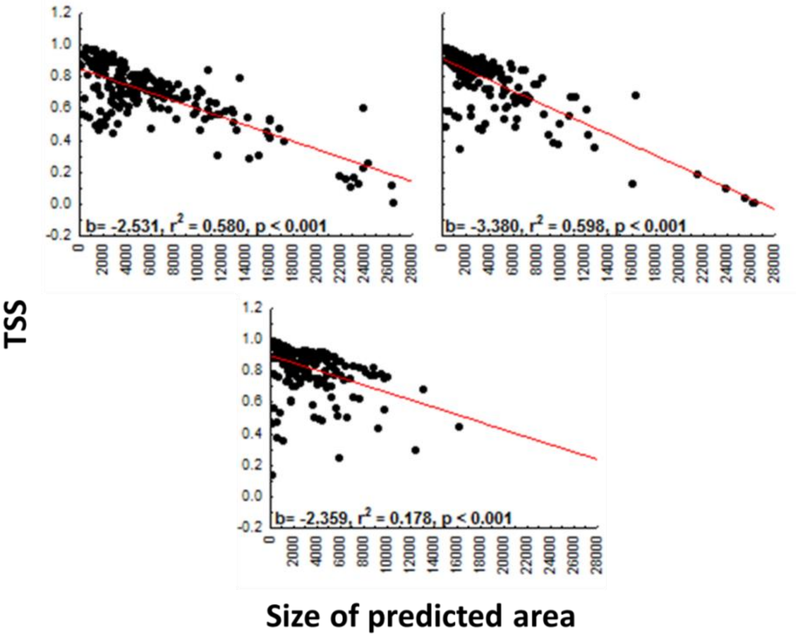


Figure 6: Effect of prevalence, measured as size of predicted area, on TSS values for models created with the PCA dataset and fitted on odd quadrants and divided by the median(top left), quartiles(top right) and deciles(bottom).

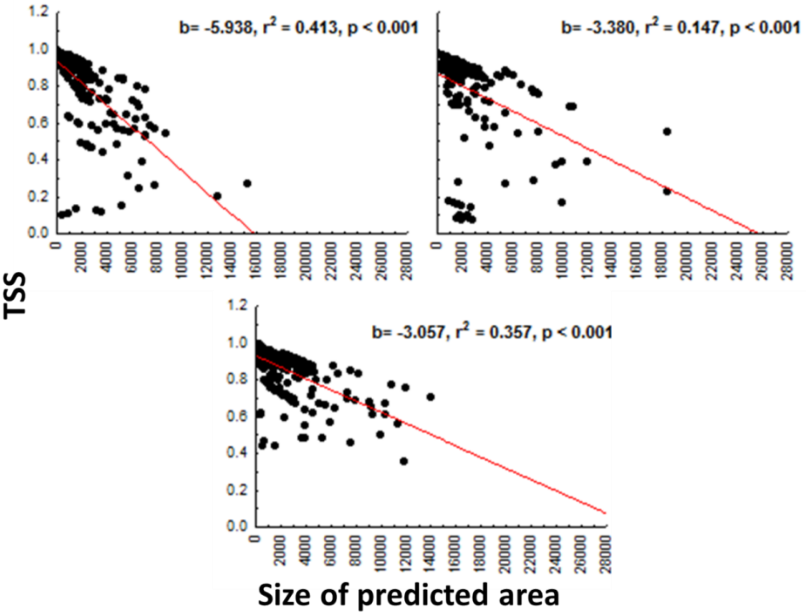


Figure 7: Effect of prevalence, measured as size of predicted area, on TSS values for models created with the PCA dataset and fitted on even quadrants and divided by the median(top left), quartiles(top right) and deciles(bottom).

Chapter 2: Protecting the irreplaceable and vulnerable future of Brazilian corals

(Planejado para ser submetido à Marine Ecology Progess Series)

Abstract

Coral reefs are of extreme importance to both nature and society, due to being responsible for several services and harbouring hundreds of species. Despite such critical importance, reef corals current suffered heavy losses since the Anthropocene, with 20% of world´s corals damaged beyond recovery due to human pressure and coastal development. This scenario is even worse, since corals are especially vulnerable to climate change and the entire ecosystem could go extinct by 2050. In this study we focus on comparing the already established impacts from human development and the yet happen losses from climate change on Brazilian corals, a unique fauna that still have gaps in knowledge. We created environmental suitability models for 24 species and quantified individual losses from both climate change and human activities. From the individual results we derived an overall pattern, in which we found out that future losses from climate alteration are equivalent to current losses from human activities. We then used the spatial distribution of those activities and key areas for conservation, determined with software Zonation, to select six areas in the Brazilian exclusive economic zone where proactive and reactive conservation strategies should be implanted, given its importance to biodiversity and concentrated anthropogenic impacts. Overall suitability losses were of approximately 30% for both sources and 60% of the areas will continue to be suitable in the future. Therefore, Brazilian corals will experience heavy losses from climate, especially the loss of highly suitable areas, which are compared to effects from human economic activities. Coral situation is likely to be even worse, if we were to consider bleaching, ocean acidification and diseases, events expected to increase with the rising temperature.

Keywords: climate change, anthropogenic impacts, seascape ecology, prioritisation, coral reefs, environmental niche modelling

Introduction

Human alterations on the environment are so striking that it is already possible to see reflects in species extinction rates, now 1000 times greater than before humans (Pimm et al. 2014). Given the velocity and proportion of human activities, there is an urge for actions to mitigate or prevent those impacts. Climate change is one of the main concerns among human related impacts, in a way that there has been countless efforts to understand and predict the effects of climate alterations on species and ecosystems (e.g. Araújo & Pearson 2005; Gosling *et al.* 2011; Lemes *et al.* 2013; Alagador *et al.* 2014). However, processes with a much shorter time-span, such as direct impacts from human activities, may affect species persistence and interfere with future available areas, and pose a threat even more serious than climate change (Jetz et al. 2007, Hof et al. 2011).

Current environment modifications and future climate changes may represent different challenges to conservation biologists. Prioritising key areas and creating protected areas is one of the most common and a worldwide strategy for preserving and protecting biodiversity from human expansion (e.g. Nagendra 2008; Molloy *et al.* 2009). From a general view, prioritization proposals can fit in two different categories: reactive and proactive. The reactive school prioritises highly vulnerable locations, mostly by mapping locations that experienced intense habitat loss. The proactive school, on the other hand, focuses on prioritising irreplaceable areas, which are areas with an extreme importance to world biodiversity, given its high endemism, before they experience excessive human impacts (Brooks 2006). Thus, the reactive school may be more adequate to respond to current environmental changes, since much has already been lost due to human activities, while there is enough space to proactive action in response to climate change problems, as most of threats related with climate alteration are yet to occur and a key aspect to it will be acting to preserve climate refugia. In spite of this obvious simplification, those challenges are not independent since current environmental changes may redirect possible proactive solutions in prioritisation efforts. Regardless of the chosen strategy, one take in account, the velocity and trend of environmental alterations and related species vulnerability.

Species vulnerability can be split in three dimensions: exposure, sensitivity and adaptive capacity (Dawson et al. 2011, Foden et al. 2013). The exposure component is configured by a species experience impacts or alterations in the environment, for example a species is in an area that is undergoing a temperature increase, and could be characterised as the first step of a vulnerability assessment. From this step it is necessary to account for biological characteristics of each species, such as how this alteration will impact the species survival (sensitivity) and capacity to adapt and bear those impacts (adaptive capacity) (Foden et al. 2013). Therefore, it is possible to apply this three dimensional framework to estimate a species vulnerability to any impact, whether it is a climatic alteration or impacts from human activities. Let us take for example a species that is in an area where the temperature is increasing or the natural vegetation in being replaced by pasture; to allege if the species will continue or perish one needs to understand some important ecological aspects. Key questions are: Will these alterations have any effect on the species fecundity or mortality rates? Can the species change its behaviour to mitigate the negative effects of those changes? Is it possible that the species could avoid the nuisances by modifying its behaviour? Obviously, these questions highlight the importance of basic natural history knowledge, demography and other important ecological aspects. Unfortunately, for the majority of tropical threatened species this knowledge is not available. This is why, the majority of species vulnerability studies focus only on the exposition component.

Species vulnerability analysis also has issues related to spatial scales. Two major threats to diversity, climate change and human activities, occur at two different extensions; while the first happens at broad areas, the second occurs at a landscape scale. The concept of landscape, seascape in marine environments, is originally a terrestrial intellectual construct, but has the merit of highlighting the importance of the connection of different sites mediated by spatial phenomena. We apply a view developed by De Marco et al (unpublished manuscript) that intends to estimate species vulnerability of individual species based on the integration of the view of environmental impacts at a landscape scale and modelling species climatic suitability over broad areas. ENMs of species suitability to climate are estimated at large scales while within a cell finer-scale pixelated human activities cause the loss of suitability up to a point in which the cell is no longer viable to sustain the species. In this way De Marco (unpublished manuscript) evaluates both sources of threats in a method that resembles the hierarchical theory, that proposes that upper scales (such as climate) constrain the focal level, while lower scales (such as human activities) provide important details that help understand the response (O'Neill et al. 1986, Turner et al. 2001). Therefore, while climate is important in constraining the broad extent of a species occurrence, human activities affects landscape processes that occur in a specific area and may make such location unavailable for this species occurrence.

Coral reefs are one of the most endangered ecosystems, due to its high vulnerability to both climate change and human activities (Hughes et al. 2003, Hoegh-Guldberg et al. 2008, Halpern et al. 2008, Foden et al. 2013). Several corals rely on symbiotic zooxanthellae photosynthesis for food production. When corals experience extreme temperatures, those zooxanthellae are expelled interrupting the process. This dynamic makes corals extremely sensitive to abrupt temperature increases, as the loss of symbionts cuts off corals main energetic source (e.g. Harriott 1985; Miranda *et al.* 2013). Although there is some evidence that corals may adapt to bleaching (Palumbi et al. 2014), history demonstrated that this recovery might not be so simple and effects might be catastrophic (Glynn et al. 2001, Kelmo & Attrill 2013). Other than temperature, corals will also experience changes due to increases in atmospheric carbon dioxide, as CO_2 dissolves into water and binds with carbonate, an ion essential for coral accretion, what makes this ion unavailable for corals and interferes in coral growth (Hoegh-Guldberg et al. 2008).

Located on one of the most impacted environments, corals also face major anthropogenic impacts, especially from pollution, overfishing and mining (Cesar 2002, Halpern et al. 2008). One of the major threats to corals, fishing pressure and capture efficiency has increased since the Industrial Revolution and post-World War II technological novelties, in a way that, in a period of 50 years, exploitation of coastal areas around the world more than doubled and now there are few pristine areas (Myers & Worm 2003, Swartz et al. 2010, Watson et al. 2011). Fishing affects directly coral reef fauna by causing the loss of large predators, leading to unbalances that can lead to drastic alterations of the whole community (Hughes 1994, Hawkins & Roberts 2004). In addition to direct losses, local activities also cause reduction in corals fitness, which can lead to major regime shifts, where a coral-dominated community shifts into a seagrass-dominated community (Folke et al. 2004, Bellwood et al. 2004, deYoung et al. 2008). Corals situation is even more worrisome, as land-use alterations and local impacts are still increasing in most coastal areas around the world (Halpern et al. 2015).

In this study we intend to use De Marco *et* al (unpublished manuscript) approach to quantify impacts from climate change and human alterations and propose new priorities areas for Brazilian reef corals, composed of highly endemic and vulnerable species with major importance from both economic and social aspects (Laborel 1970, Frost 1977, Leão 1983, Sousa 1994, Leão et al. 2003). We address both reactive and proactive strategies, by evaluating the impact of climate change and human activities over irreplaceable and vulnerable areas. We also evaluate which one of those factors, climate or human activities, is more harmful to Brazilian corals and analyse the interaction between factors to establish priority areas for conservation.

Methods

Environmental Niche Modelling

We used the same occurrence database from chapter one to create niche models, however, we restricted our analysis exclusively to those species that achieved True Skill Statistics (TSS) values above 0.7 in any case. We once more used a comparative approach between BioOracle and PCA derived datasets as variables for the future are restricted to Sea Surface Temperature and Salinity, which could result in an increase in collinearity and, therefore, reduce the performance of models created from the original BioOracle dataset. We took care of maintaining the relation between PCA axis and present environmental variables when deriving principal components for future environmental layers. As the comparison of datasets is not the objective of this chapter, we present here only the results of models created with the dataset that had higher accuracy in its predictions, based on TSS values. Models for the future were created based on emission scenarios A1B and A2 for the year 2100, used on IPCC 3rd and 4th Assessment Reports on Climate Change (IPCC 2001, 2007). To stablish a comparison among them, A1B is a more optimistic scenario, where there is rapid economic growth and replacement for more efficient fuels, while A2 is a more pessimistic scenario, with slower and local economic growth and a fragmented development of alternative fuels (IPCC 2000).

We used five different algorithms to create niche models: (i) Envelope Score, a quantitative version of Bioclim (BIO) (Piñeiro et al. 2007), (ii) Generalized Linear Models (GLM) (Guisan et al. 2002), (iii) Mahalanobis Distance (MAHA) (Farber & Kadmon 2003), (iv) MaxEnt (MAX) (Phillips et al. 2006), (v) Support Vector Machine(SVM) (Guo et al. 2005); and (vi) Random Forest (RF) (Prasad et al. 2006). Since algorithms establish the correlation between occurrence and climate in different ways, it is important to account for uncertainty in results caused by this difference (Diniz-Filho et al. 2009). In order to account for algorithm uncertainty, we derived principal components from the distinct suitability maps, in which each algorithm had a different weight in the principal component calculation, according to its TSS value, for each species and used the first axis as an ensemble model. Ensemble purpose is to highlight common areas among all algorithms, therefore, ensemble models allows for the accounting of uncertainty caused by the algorithms, as areas predicted similarly by all algorithms are less likely to be an artefact caused by different modelling methods (Araújo & New 2007, Benito et al. 2013, Crimmins et al. 2013).

We assured our projections for the future were not being affected by extrapolation issues by performing a multivariate environmental similarity surface (MESS) analysis, which identifies which cells contain future environmental conditions that are outside the current range. MESS analysis were performed inside the software MaxEnt (Elith et al. 2010, Owens et al. 2013).

Anthropogenic activities

Anthropogenic impacts happen on a landscape scale and, therefore, there is a need for a more refined approach and different theoretical basis when considering the impact of such activities on species distribution. We quantified the effect of those local disturbances within a cell by using two different scales and applying the landscape theory of extinction threshold (Fahrig 2001). For this we started from the ENMs outputs of 10x10km suitability maps and rescaled this map into a 1x1km map, where all 1km^2 pixels within a 10km^2 cell would have the same suitability value. Then we identified which of those pixels were already altered by human activities and considered those pixels as unsuitable for species occurrence. We then calculated the amount of pixels lost to human activities and evaluated those results based on the principles of extinction threshold theory (Fahrig 2001). Based on the amount of pixels lost to human activities a cell would lose suitability, up to a threshold (50%) where the cell would be considered inappropriate for the occurrence of the species (Fig.1). This process results in a new suitability map for each species in which we can identify the most vulnerable species, what are the most vulnerable locations and what are the most problematic activities.

Anthropogenic impacts database is comprised of activities related to Programa de Aceleração do Crescimento (PAC), a development program proposed by the Brazilian government. Marine enterprises addressed in the database are harbours, fishing areas of several targets (shrimp, lobster, pelagic fishes, octopus) and methods (drag, seine and gillnetting), oil rigs and ducts. In order to represent the area affected by each enterprise we created a 10km buffer around the point location. This data was made available to us thanks to Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO).

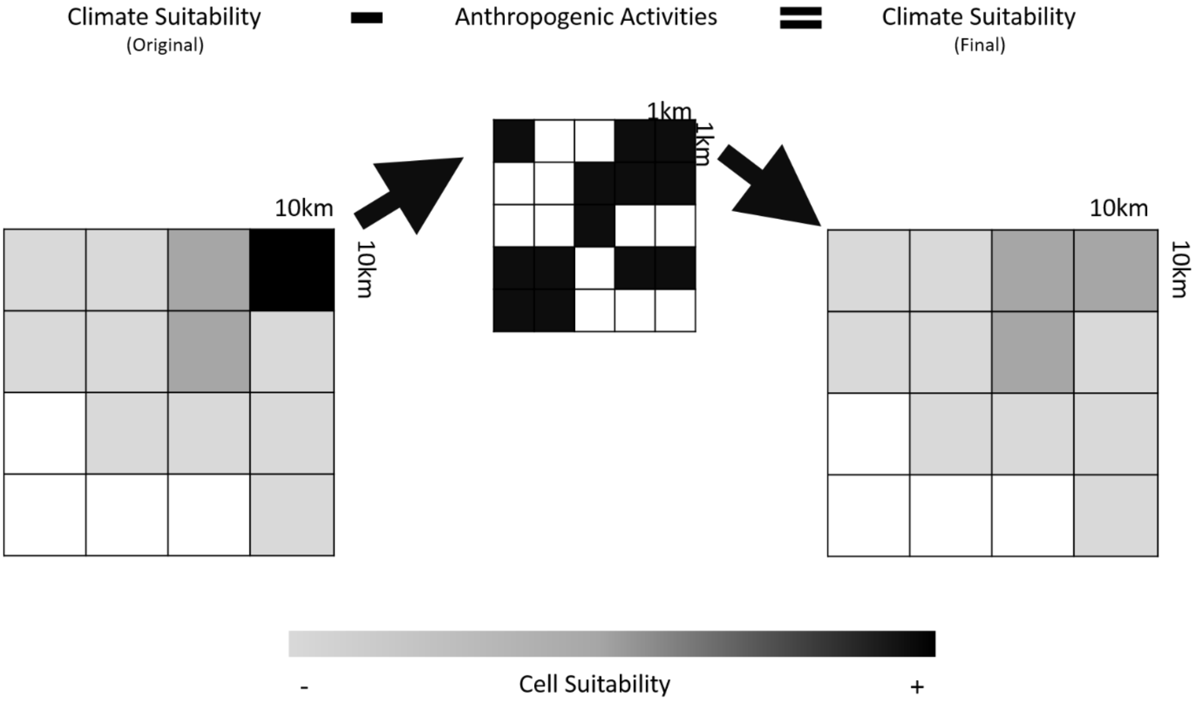


Figure 1: Anthropogenic activities framework. The presence of anthropogenic activities within the upper right cell changes it suitability from high to average.

Index for Suitability Analysis of Remaining Area (SARA)

Species vulnerability was ranked by the use of a Suitability Analysis of Remaining Area (SARA), where cells lost are weighted by the relative importance based on their original suitability (Equation [1]).

$$Index\ of\ Lost\ Area\ Suitability = \frac{(\sum_{su=1}^{SU} lost\ area_{su}\ \times suitability_{su})}{(\sum_{su=1}^{SU} original\ area_{su}\ \times suitability_{su})} \qquad [1]$$

Where SU is a suitability class, which varies from 0-1 in intervals of 0.05.

The index calculates, for each suitability class above the threshold, the number of lost cells and multiplies this value by the midpoint suitability value of that interval. Results for each interval are then summed and divided by the sum of the total number of cells in each class multiplied by the midpoint suitability value of that class. The result of this division is the SARA index, a number that varies from 0-1, in which the closer a species index is to one the higher is the loss of suitability. The key aspect of this index is that more suitable cells have a higher weight in the final result, as each class is multiplied by its midpoint suitability.

Climate and Human Activities Comparison

In order to summarize and compare the effects of climate and human activities we used two approaches: number of lost cells and SARA index. To do this we compared for each species the total number of cells lost due do climate and anthropogenic activities and also calculated the SARA index for both climatic and human activities alterations on the raw suitability. We opted to use both approaches as they account for two different key metrics for conservation, total number of cells represents the total area lost, while the index incorporates the quality of those areas in the calculations. We proceeded by conducting a paired t-test on both metrics to evaluate if one of the sources (climate change or human activities) is more threatening to Brazilian corals persistence.

Climate Change Effects

We further investigated the effects of climate change on corals by categorizing present and future areas in three categories: (i) Lost, the cell will not be suitable for the species in the future; (ii) Novel, the cell is not currently suitable, but will be adequate for the species in the future or (iii) Overlap, the cell is suitable for the species now and will remain in the future. We further quantified and spatialized each category in order to highlight which of the species are more vulnerable to climate changes and how to plan conservation efforts in order to ensure the survival of those species.

Conservation Priorities

We approached prioritisation taking into account both strategies: proactive and reactive. Areas considered as priority according to the reactive school are the ones that already experienced heavy habitat loss. According to our framework, based on fragmentation ideas developed by Fahrig (2001), a cell is no longer suitable for a species occurrence when it loses 50% or more of its pixels due to human activities. Therefore, we based reactive prioritisation on activities to recover pixel losses on cells that are on the edge of the 50% threshold, as any increase of impacts within the cell would cause it to be unsuitable for species survival.

Priority areas, according to proactive ideas, are the ones considered irreplaceable, such as areas with high diversity or endemism rates. We calculated those areas using the software Zonation (version 4.0; Moilanen *et al.* 2014) with the variant core-area Zonation(CAZ), which best represents rare species (Dobrovolski et al. 2013). We calculated species weights taking into account its endemism and IUCN Red List classification (Lemes *personal communication,* IUCN 2015) (Equation 2).

$$Species\ Weigth = \left(\frac{1}{Nspecies}\right) * endemism * IUCN\ category \quad [2]$$

An endemic species scores two in endemism, while a common species receives one. For Brazilian corals, we considered as endemic those species that occurred only in Brazil; 10

species were considered endemic and 14 occurred both in Brazil and Caribbean. As for the IUCN classification, Near Threatened and Least Concern species score one, Vulnerable and Data Deficient 1.25, Endangered 1.5 and Critically Endangered two (Lemes *persn. comm.*). Of all 24 coral species, 17 were Data Deficient or did not appeared at the IUCN Red List, 6 were classified as Least Concern and only one (*Porites branneri*) was classified as Near Threatened. All Brazilian endemic coral species in our study were classified as Data Deficient or are not at the IUCN Red List.

Individual human activities weights were the result of the sum of all species weights divided by the number of activities multiplied by -1, therefore, all activities had the same negative weight. We also considered existing protected areas, inputting them as a mask.

We defined as highly critical for conservation those cells in which human impacts are close to the 50% threshold and categorised as priority according to the Strategic Plan 2011–2020 of the Convention on Biological Diversity (CBD 2012), which defines as goal the conservation of the most important 10% of coastal and marine areas. We used an ensemble to combine present and future areas, in a way that high priority areas are those with high values for both time periods and, regarding human impact, selected cells marked as threatened (close to 50% threshold) for any time period. In our view, these areas meet the requirements for both reactive and proactive strategies and should be the focus of any conservation planning.

All analysis were restricted to the Brazilian Economic Exclusive Zone (EEZ), as the EEZ is the area in which a state has rights of exploration and use of marine resources, and, therefore, in which any conservation plans would be applied.

Results

Climate-Human Activities Comparison

Average suitability loss, according to SARA index, was 28% considering human activities and 27% and 32% considering climate change, scenarios A1B and A2 respectively.

Idiosyncrasy was high within all three situations, with human activities losses varying from 3-97% and climate change varying from gains of 17% up to losses of 81% for both scenarios (Fig.2).

Climate and human activities had the same effect in suitability loss according to SARA index for both A2 (paired-t_{23}: -0.428, $p>0.05$; Avg_{Dif}: 0.033) and A1B scenarios (paired-t_{23}: 0.124, $p>0.05$; Avg_{Dif}: -0.009). Climatic differences between scenarios A2 and A1B caused differences in suitability loss among scenarios, in which losses were higher in A2 scenario (paired-t_{23}: 2.119, $p<0.05$; Avg_{Dif}: 0.043).

Apart from the lack of overall difference, there was large variance among species. While the average SARA index for both climate change and human activities was around 0.3, there were critical situations for both threats, in which the index reached critical loss values of over 0.8 (*Astrangia rathbuni*, 98% loss due to Human Activities; *Neospongodes atlantica*, 82% future loss due to Climate Change; Figs.3 and 4).

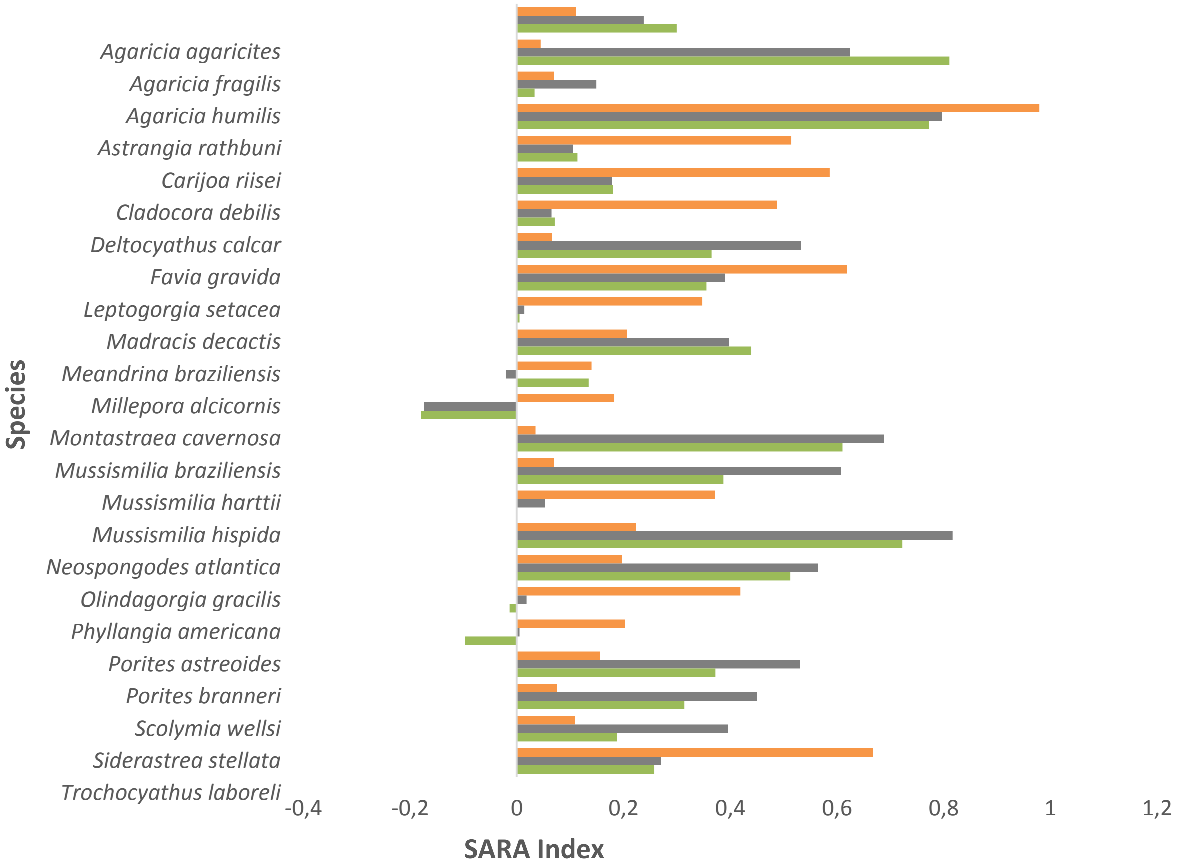


Figure 2: Species specific SARA index for areas lost due do climate change, scenarios A2 (grey) and A1B(green), and human activities (orange).

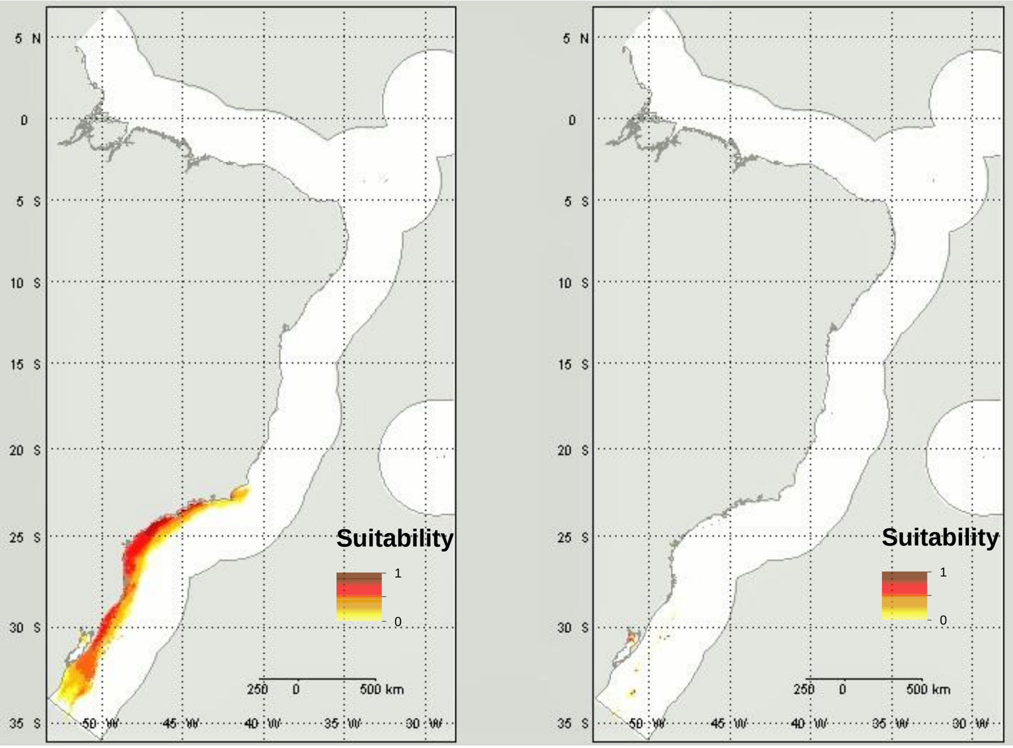


Figure 3: *Astrangia rathbuni* loss of suitable areas due to human activities (SARA index 0.979)

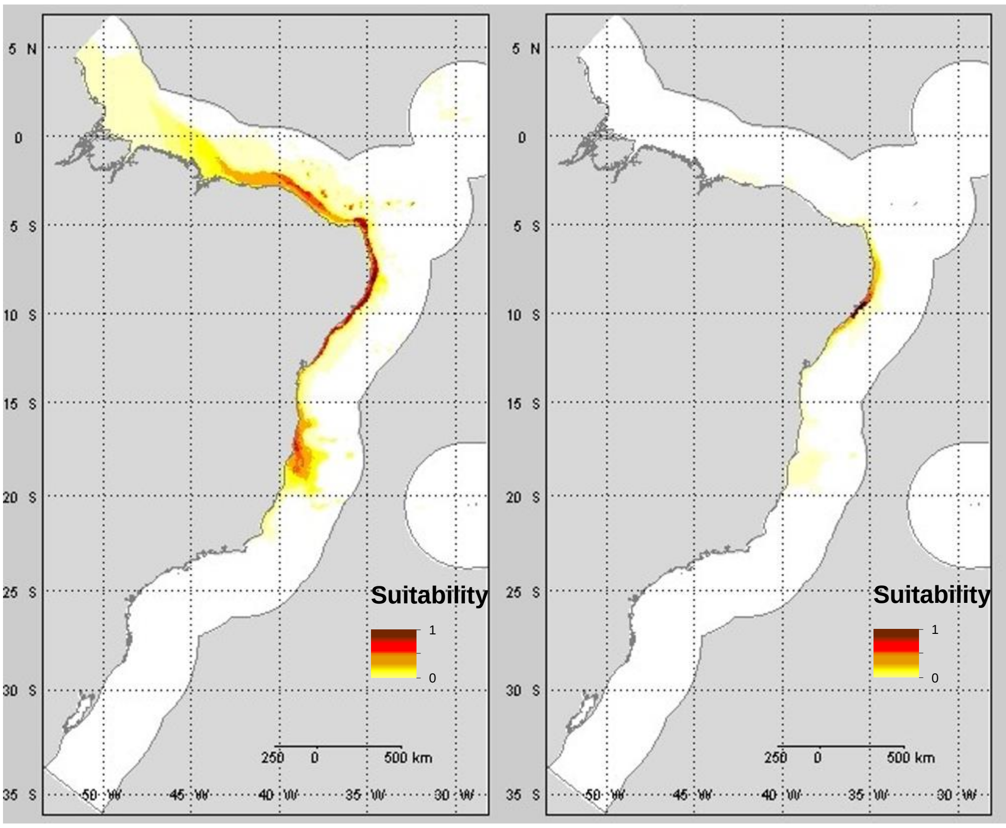


Figure 4: *Neospongodes atlantica* loss of suitable areas due to climate change(A2) (SARA index 0.817)

When we considered the raw number of cells, without giving weights for their suitability, there was an average loss of 31% cells lost due to human activities, and 21 and 27% from climate changes scenarios A1B and A2 respectively. There was again a high variation among species with human activities causing losses of 4-97% and climate change having an even higher variation, in which some species gained over 60% of suitable cells and others lost 80% of its area (Fig.5). There was also no difference in the amount of lost cells when comparing human activities and climate change for both the pessimistic scenario A2 (paired-t_{23}: 0.444, $p>0.05$; Avg_{Dif}: -0.039 % of lost cells), and the optimistic A1B (paired-t_{23}: 1.153, $p>0.05$; Avg_{Dif}: -0.096 % of lost cells).

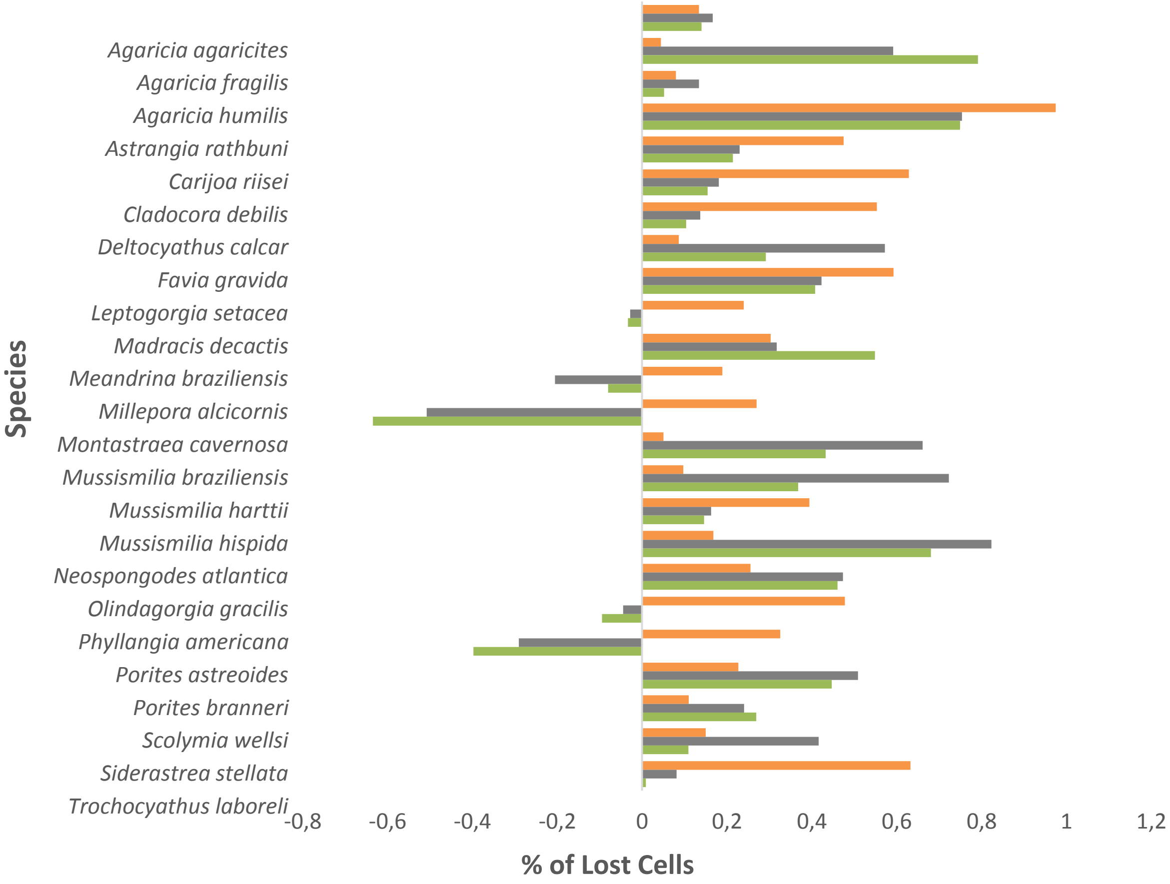


Figure 5: Species specific percentage of lost cells for areas lost due do climate change, scenarios A2 (grey) and A1B(green), and human activities (orange).

We also compared the percentage of lost cells and the SARA index in order to evaluate if the loss of cells caused by climate change and human activities also represents a proportional loss of suitability. We found different patterns, which means climate and activities are affecting species suitability in different ways. Climate change, for both scenarios, has higher index values than expected if the index and the loss of cells escalated on a 1:1 relation for species that experience little area loss (<0.4%) and relation closer to 1:1 on species that experienced higher total losses (b_{A1B}:0.740, r^2_{A1B}:0.841/ b_{A2}:0.784, r^2_{A2}:0.887). Human activities, on the other hand, scales close to expected, regardless of the amount of area loss by the species (b_{HA}:1.018, r^2_{HA}:0.955) (Fig.6). Those different patterns indicate that climate may be causing the loss of, primarily, high suitable cells, and as the total amount of cells lost increases, this effect is no longer visible as all areas are affected. Human activities have a more homogeneous effect, causing the loss of cells with both high and low suitability, regardless of the amount of lost cells.

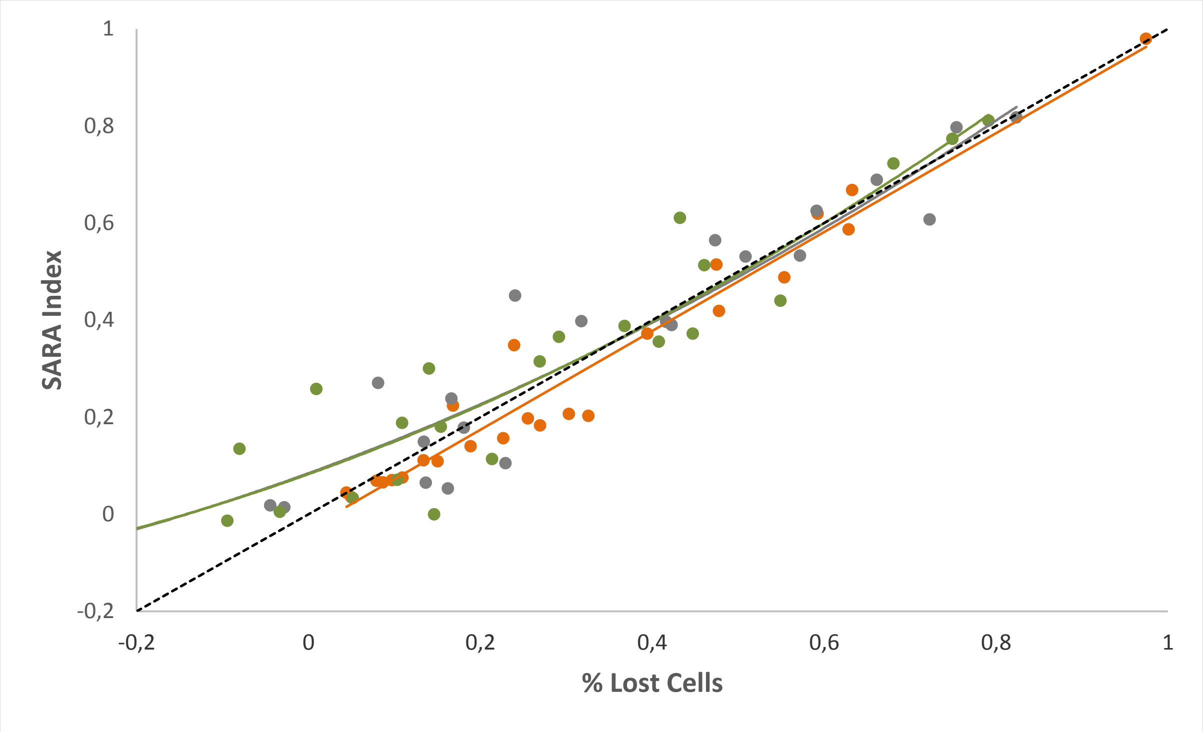


Figure 6: Relation between percentage of lost cells and SARA Index for coral species considering climate change, A1B(Green) and A2(Grey) scenarios, and human activities (Orange). Black dotted line represents the expected scenario if the index has a 1:1 scale with the percentage of lost cells. Human Activities (R^2:0.955): 1.018x-0.029; Climate A1B (R^2:0.892): $0.3806x^2 + 0.6339x + 0.0828$; Climate A2 ($R^2$:0.913): $0.3314x^2 + 0.643x + 0.0847$

Corals future situation

In order to discuss prioritisation of areas for corals we considered the future situation of corals in regard to both climate change and human activities. For this we split future areas, regarding climate change, in three categories: Lost, Novel and Overlapping areas. Overall, average overlapping was 58% in scenario A2 and 64% in scenario A1B, with the maximum value of 95% (*Porites astreoides* and *Millepora alcicornis*) and minimum of 19% (*Astrangia rathbuni* and *Neospongodes atlantica*). Average area gain (Novel) was of 15% for both scenarios, with species with the most gain being *Montastraea cavernosa* (66-77%) in both scenarios and species with fewer gains being *Mussismilia hartii* (0.5%) and *Olindagorgia gracilis* (0.5%). As for area loss (Lost), maximum values were of approximately 80% (*Astrangia rathbuni*,*Mussismilia braziliensis* and *Neospongodes atlantica*), and minimum losses were of approximately 5% (*Milepora alcicornis* and *Porites branneri*). Overall, 80% of our species lost area in the end, being most critical *Astrangia rathbuni*, *Mussismilia braziliensis*, *Mussismilia hartii* and *Neospongodes atlantica*, species with high losses, few area gains and reduced remaining area. On the opposite site, some species experienced gain of area with the changing climate, which was the case for *Montastraea cavernosa*, *Porites astreoides* and *Millepora alcicornis* (Fig.7).

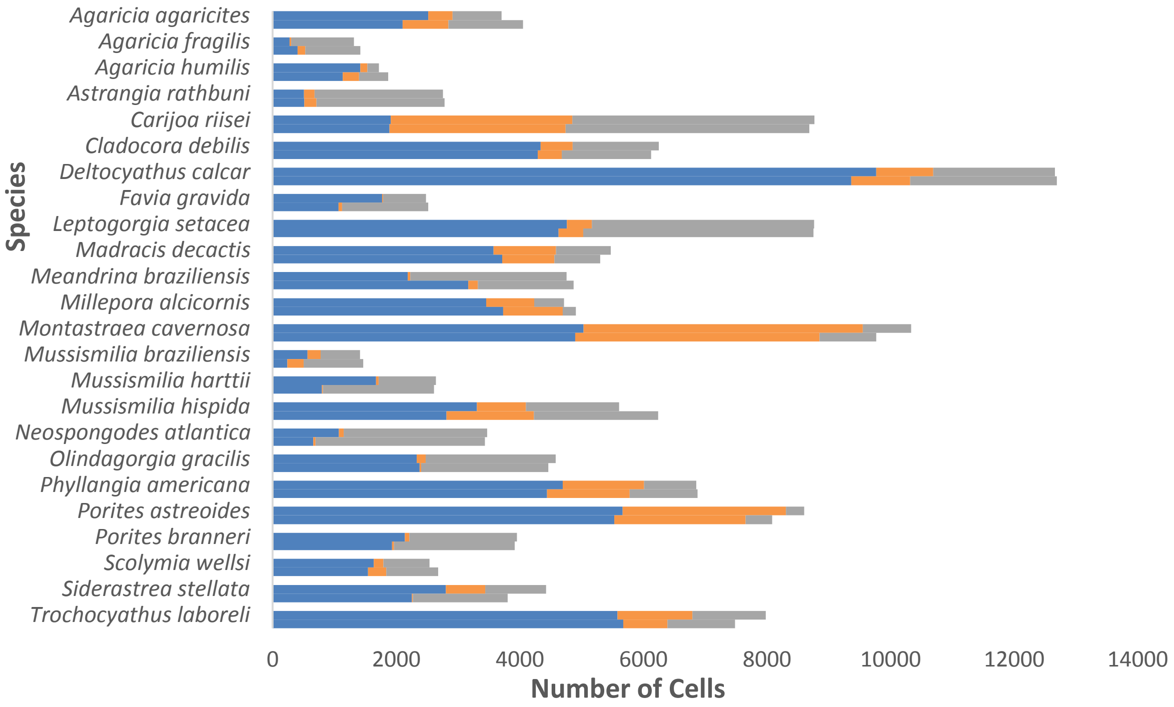


Figure 7: Species specific situation of areas suitable for corals in the year 2100 for both scenarios A1B (Upper bars for each species) and A2 (Lower bars for each species), areas are categorised in Overlapping(Blue), Novel (Orange) and Lost(Grey) areas.

In regard to areas affected by human activities, there was no difference between actual losses and future losses for both scenarios, either by considering the index (A1B, paired-t$_{23}$: -0.826, p>0.05; Avg$_{\text{Dif}}$: -0.014/ A2, paired-t$_{23}$: -0.826, p>0.05; Avg$_{\text{Dif}}$: -0.014) or considering the percentage of total cells lost (A1B, paired-t$_{23}$: -0.170, p>0.05; Avg$_{\text{Dif}}$: -0.003/ A2, paired-t$_{23}$: -0.696, p>0.05; Avg$_{\text{Dif}}$: -0.013). Some species had higher losses in their future distribution but this was not the predominant pattern and only occurred on those species in which suitable areas expanded or shifted towards the southern or the northern region, where human activities are more intense (Fig.8).

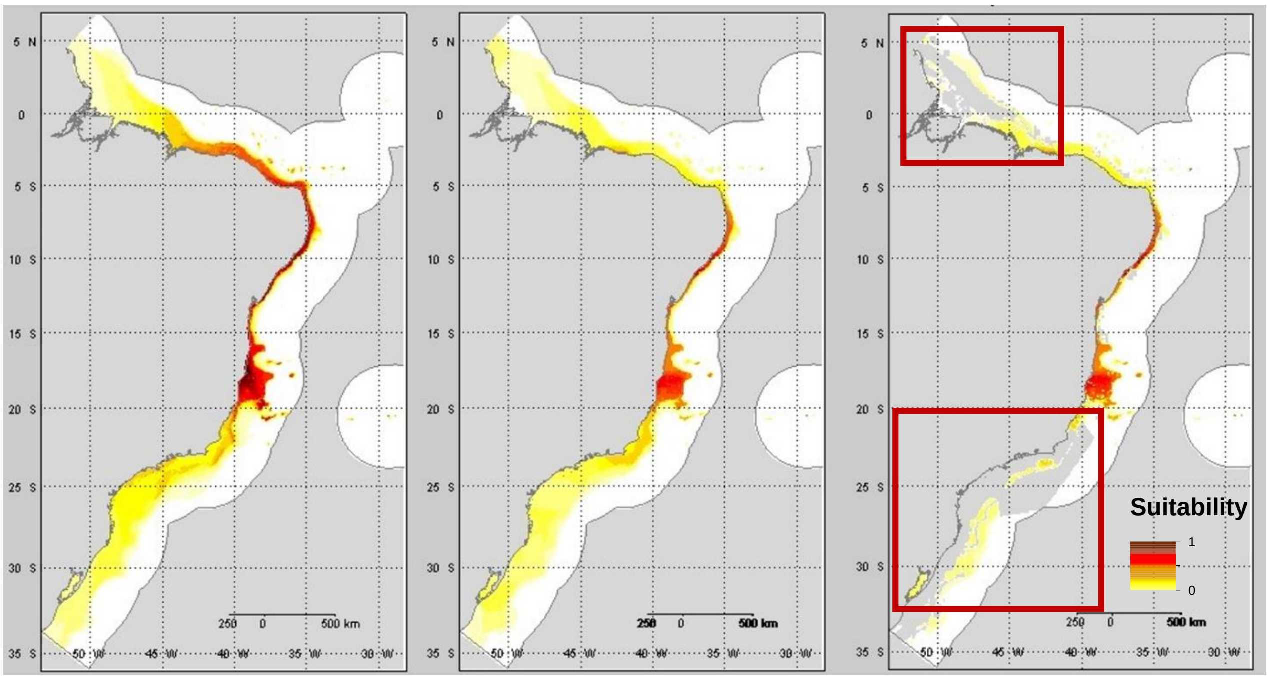


Figure 8: Progression of lost areas due to climate and human activities. On the left the actual suitability considering all coral species. On the middle the suitability for 2100, A1B optimistic scenario, and on the right the suitability for 2100 with the losses from human activities (grey areas inside red rectangle).

Priority Areas

We followed the framework of irreplaceability relative to vulnerability to identify priority areas. Key areas are those irreplaceable and also highly vulnerable, in a way that there is a need for intervention in order to assure the persistence of important aspects of biodiversity (Margules & Pressey 2000). We used combined present and future outputs produced by Zonation in a way to ensure long-term protection and selected the 10% most irreplaceable cells, in accordance to Aichi Biodiversity Targets. Areas of major importance (top 5% cells) for biodiversity are concentrated between the states of Maranhão and Espírito Santo and considering the desired 10%, there is a little extension towards the whole coast of Maranhão and Espírito Santo and regions in the coast of Rio de Janeiro, São Paulo and Rio Grande do Sul (Fig.9).

We discussed the reactive approach regarding the vulnerability of cells to human activities. We defined as priorities those cells that suffer from significant human impact but are not yet lost, in a way that the cell is still suitable for species, but there is a need for protection and recovery to ensure those cells will not be lost. Such areas are widespread all over the Brazilian coast, with an apparent concentration on Southern and Northern regions (Fig.9). There is little difference between present and future areas, possibly due to slight overall variation in the suitability patterns.

We then overlapped irreplaceable areas with vulnerable areas, and selected six major grand areas of concern: south of Rio De Janeiro and north of São Paulo, Espírito Santo, central Bahia, Pernambuco, Ceará and Maranhão (Fig. 9). All those areas are areas considered as priority according to the Aichi Biodiversity Targets and comprise a considerable aggregate of cells threatened by human activities, and should, therefore, be the focus for conservation discussions and both proactive and reactive actions.

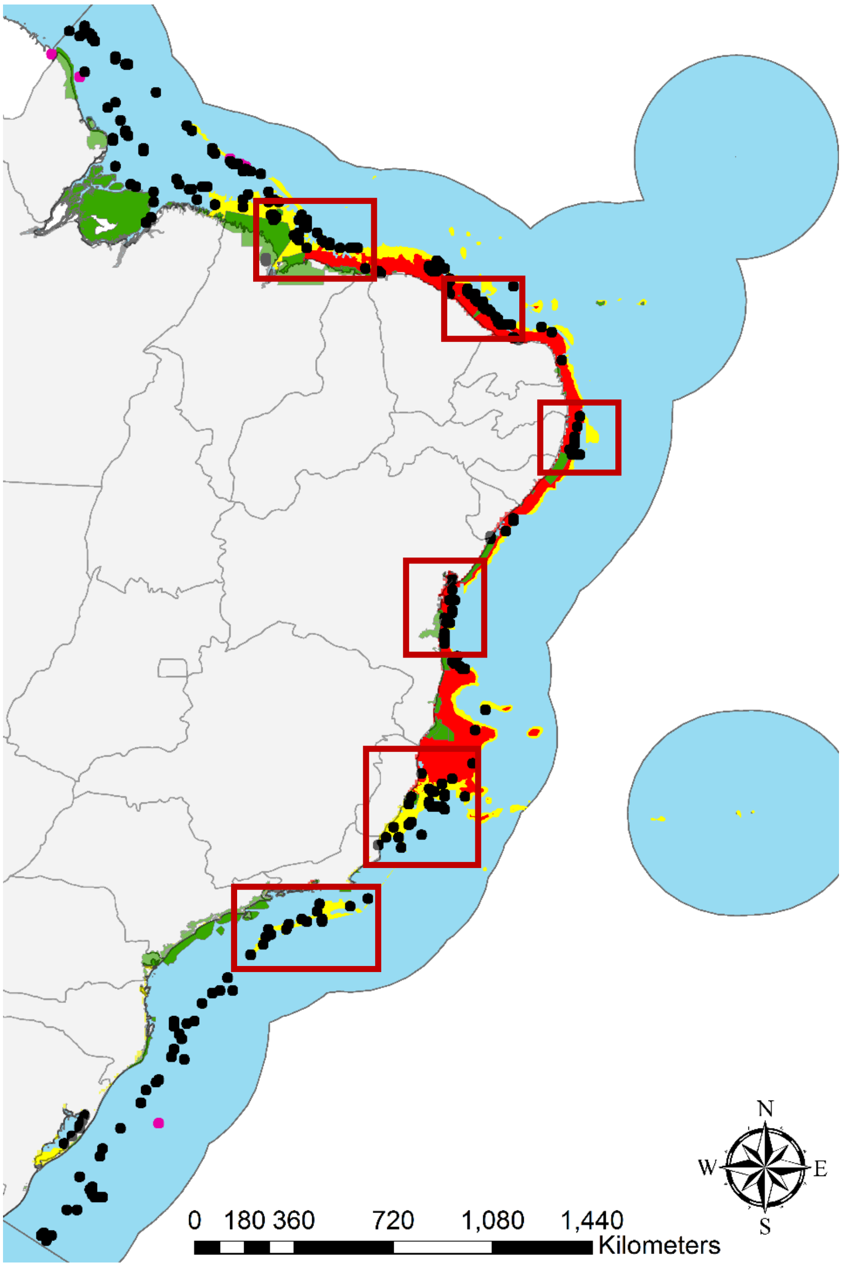


Figure 9: Priority areas for coral conservation in the Brazilian Economic Exclusive Zone. Black (present) and purple (future) dots represent areas threatened by human activities (close to 50% threshold); Green areas are the existing protected areas; Yellow areas are the top 10% regarding biodiversity conservation and Red areas are the top 5%.

Discussion

Climate change has received major concern over the last decade as one of the major factors driving future extinctions and area loss (Thomas et al. 2004, Hoegh-Guldberg & Bruno 2010, Foden et al. 2013). Among all studies, coral reefs are one of the ecosystems that received considerable efforts and studies (Hoegh-Guldberg et al. 2008, Carpenter et al. 2008, Foden et al. 2013). In our study we demonstrate that, despite occurring on smaller scales, human activities can have an effect as high as climate change on species area loss and, therefore, should be considered when discussing a species overall vulnerability and when defining priority areas.

Concerns regarding human activities impacts on the marine ecosystem is not something new (Hodgson 1999, Nyström et al. 2000, Halpern et al. 2008), however, assessing and comparing the effects of both climate and human activities is not easy, and even for terrestrial systems, is somewhat infrequent due to data required and different spatial extents. Nevertheless, several studies for terrestrial groups that compared the effects of climate and land-use concluded that land-use alterations may be as important as, or even more important than climate change when discussing species area loss (Jetz et al. 2007, Hof et al. 2011, Reece et al. 2013). A novelty in our study is that we were able to quantify and spatialize species losses in a combined manner, according to the framework from De Marco et al. (unpublished manuscript), paving the way for a direct comparison, which allows us to identify priority areas and related climatic and anthropogenic threats.

Another key factor to consider is that different species suffer from different threats in different ways. This was already discussed by Jetz *et al.* (2007), as a latitudinal gradient, in which tropical species were more vulnerable to anthropogenic threats, while temperate species might be more vulnerable to climate change. In our study we found no average difference between climate and anthropogenic threats within species of tropical corals, however we found species that are critically affected by at least one of them or even both. Therefore, it is important to emphasize that the lack of difference does not represent a lack of effect, and some species, for example *Astrangia rathbuni* and *Neospongodes atlantica*, are in great peril.

Despite the lack of overall difference, our results indicate that climate change and human activities might cause suitability loss in different ways, which could only be perceived due to SARA's index property of taking suitability in account when calculating a species vulnerability. Climate change appears to have a stronger effect in highly suitable cells, which could prove critical for species, as those areas would become less suitable being even at risk of becoming unsuitable for species occurrence. Human activities, on the other hand, do not appear to have a pronounced effect on any specific class of suitable cells, which could be related to the fact that such activities have no direct connection to the environmental tolerances of species, while climate change is directly related to physiological boundaries.

Such difference in effects should be considered while discussing conservation priorities. Climate change major effects are yet to happen, however the temperature rise is already observable and, although it is possible to reduce the rate of increase, it is unlikely that this trend will change (IPCC 2014). Therefore, prioritization should be discussed based on the assumption that corals will experience a loss of suitability and proactive actions should be taken in order to try to mitigate those impacts. A key action is to identify priority areas, such as climate refugia, and prevent further impacts on those already sensitive areas. In our study, we highlighted six critical areas along the Brazilian coast, due to their importance to overall biodiversity and intense threats from human activities. One of the major barriers for conservation is the limited availability of resources, especially in less developed countries, such as Brazil (James et al. 2001, Balmford et al. 2003). Therefore, we recommend that those six areas should be marked as priorities, in a way that development of new activities should be treated with extreme care, current disturbances must be monitored and efforts should be made in order to recover those regions.

Brazilian government, via the Projeto da Conservação e Utilização Sustentável da Diversidade Biológica Brasileira (PROBIO), developed between 1997-2000 a project to define priority areas for conservation for all ecosystems, in which priority areas were designed based on literature and surveys to all researchers related to the focal taxon. In relation to corals, the project established key areas due to their high diversity and anthropogenic pressure, metrics we also used in our study. Our results endorse the areas highlighted by PROBIO, as five of six areas we defined as extremely important were also mentioned in the final report. Regions in the state of Maranhão, Ceará, Central Bahia and the north coast of Espírito Santo were defined as priority due to poor knowledge and fishing pressure, our models confirm the intense pressure in the region and also the expectancy of a high biodiversity. The entire coast of Pernambuco was also highlighted as having extreme importance due to the existence of extensive coral reefs that are prone to human impacts, due to the proximity to the coast. For last, we also defined as priority an offshore area comprising the south coast of Rio de Janeiro and north coast of São Paulo, while this area is not mentioned in the PROBIO report, we believe it is worth taking this area in consideration as it is the only one in the Southern Brazilian coast and is surrounded by areas with heavy anthropogenic impacts.

Areas that overlap in the present and future scenarios are particularly important for conservation due to its ecological meaning towards climate change, acting as a refuge from changing climate. When facing climate change a species will experience one of three scenarios: disperse, adapt or perish. Overlapping areas are those where a species already is occurring and will experience minimal alterations in climate, therefore it is more likely that a species will be able to maintain itself in those areas without any need of intervention. While the average amount of overlapping areas is considerably high (55-60%), species like *Neospongodes* *atlantica*, *Astrangia rathbuni* and *Mussismilia braziliensis* have less than 20% overlapping areas and should be closely monitored. The loss of overlapping areas is especially important due to corals dispersal by a pelagic larval stage, what makes them subordinates to ocean currents, and due to Brazilian corals being partially isolated from other Atlantic coral reefs, in a way that larvae recruitment depends mostly on native populations (Nunes et al. 2009). Brazilian coral populations along the coast are connected by larvae dispersed in ocean currents, which in turn are restricted by the mouth of major rivers (Nunes et al. 2009, SISBIOTA-MAR 2014). The existence of such dynamics must be taken in consideration as it creates subpopulations that will suffer distinct effects from climate change. Besides, due to ocean currents direction and differential suitability, there are regions and subpopulations that act as source of propagules to other locations, for example subpopulations of *Mussismilia hispida* in the northeast are source of larvae for other subpopulations (SISBIOTA-MAR 2014). Therefore, in addition to the percentage of overlapping area, the location of those areas is also an important factor, as the loss of areas that act as source of larvae might cause the disrupture of the entire system.

Seascape ecology is a relatively new method, with its origins in the early 1990s the field had 118 papers until 2010, with only approximately 10% related to coral reefs (Boström et al. 2011). The vast majority of those studies treat corals and other ecosystems as patches and evaluate the influence of patch size, connectivity, patch shape and edge effect on the dynamics of fishes (Boström et al. 2011). The concept of habitat amount, one of the landscape metrics that best explains a species survival probability in a landscape (Fahrig 1997, 2001), is poorly discussed in seascape ecology, with the few studies reaching different conclusions (Rakocinski et al. 2008, Macreadie et al. 2009). Population size changes with habitat loss, has even fewer and more contrasting evidence, all considering the effect of seagrass fragmentation on fishes. While some studies indicate the existence of a threshold (Pittman et al. 2004, Reed & Hovel

2006), other indicate the existence of a parabolic relationship, in which the suboptimal coverage is between 55-65% (Salita et al. 2003). In our study we chose to consider a cell as unsuitable for a species when it loses 50% of its area to human activities. The 50% remaining area is an average and conservative threshold for several terrestrial species, therefore, as this issue is not resolved for the marine environment, we opted to recur to this well-established terrestrial metric (Fahrig 2001, Swift & Hannon 2010). We are aware that the marine environment has differences on mobility, dispersal and ecological processes, but we chose to keep a safe approach as this subject is still incipient in seascape ecology.

One could say we are being pessimistic by adopting the existence of a threshold and not a parabolic relationship, however, the reality is that coral reefs situation is likely to be even worse (IPCC 2014). First, our models only consider the effects of climatic tolerances while leaving out of the analysis climatic related threats such as bleaching and ocean acidification, likely to increase in the future, which are major causes of coral degradation (Cao & Caldeira 2008, Donner 2009). Second, we do not consider biological interactions. It is known that corals have a dynamic competition with macro algae that can have its equilibrium altered by human impacts, such as overfishing of herbivores and nutrient input, that reduce corals resilience up to a point that allows macro algae to dominate the system (Nyström et al. 2000, Bellwood et al. 2004). Despite not taking such factors in consideration, our results demonstrate that, even from an optimistic point of view, Brazilian corals are already in peril from climate changing to conditions outside of their tolerances and loss of area to human activities.

Finally, our study also enlightens vulnerability status for Brazilian corals. From our species, 70% had no information on IUCN Red List, 25% were classified as species of Least Concern and only one was considered Near Threatened. The SARA index and total lost area are reliable metrics of a species situation and could be used as an indicative of its vulnerability. Our results indicate an existing average loss of suitability of 30% due to human activities and a further loss of 30% due to climatic alterations, with 80% of the species being prone to experience suitability loss to climate change. Since we produced species-specific index of suitability loss, we provide additional data and interpretation to discuss the vulnerability of those species. At least critical species such as *Trochocyathus laboreli*, endemic Brazilian species that already experienced high losses from human activities, *Astrangia rathbuni,* endemic Atlantic species that suffered high losses from human activities and is also expected to experience heavy losses from climate change and *Neospongodes atlantica*, endemic Brazilian species predicted to have the most significant suitability loss due to changing climate, deserves further discussion about its vulnerability status since all three do not even appear in the Red List.

Therefore, it is essential to include both impacts from climate and anthropogenic sources when discussing corals conservation as they are equally harmful. It was already well established that both sources were extremely impactful to corals, however, the comparison of such impacts is still quite rare in the literature, even for other taxon. As for conservation strategies, we acknowledge that an overall perspective is the optimal strategy for conserving a taxon as designing an individual plan for each species is unfeasible, however some species are especially vulnerable and a general strategy might not be sufficient for their maintenance. In addition, some areas might be more important than others as they act as propagules sources and, therefore, might be essential for the maintenance of whole subpopulations. In our study we opted to prioritise areas with a high biodiversity and heavily impacted by human activities as a way of combining proactive and reactive strategies. Those regions highlighted by our models were also defined as priorities by experts, what reinforce the value of these locations and could be a way of validating the accuracy of our models. Considering this accuracy, we believe this study can be useful to clarify Brazilian corals vulnerability.

References

Alagador D, Cerdeira JO, Araújo MB (2014) Shifting protected areas: scheduling spatial priorities under climate change. J Appl Ecol 51:703–713

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–7

Araújo M, Pearson R (2005) Validation of species–climate impact models under climate change. Glob Chang Biol 11:1504–1513

Balmford A, Gaston KJ, Blyth S, James A, Kapos V (2003) Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. Proc Natl Acad Sci 100:1046–1050

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–33

Benito BM, Cayuela L, Albuquerque FS (2013) The impact of modelling choices in the predictive performance of richness maps derived from species-distribution models: Guidelines to build better diversity models. Methods Ecol Evol 4:327–335

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: Advances , gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Brooks TM (2006) Global Biodiversity Conservation Priorities. Science (80-) 313:58–61

Cao L, Caldeira K (2008) Atmospheric CO 2 stabilization and ocean acidification. Geophys Res Lett 35:L19609

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore J a, Obura DO, Ochavillo D, Polidoro B a, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. Science 321:560–563

CBD (2012) Strategic Plan for Biodiversity 2011 – 2020 and the Aichi Targets.

Cesar HSJ (2002) Coral Reefs : Their Functions, Threats and Economic Value. In: Collected essays on the economics of coral reefs.p 14–39

Crimmins SM, Dobrowski SZ, Mynsberge AR (2013) Evaluating ensemble forecasts of plant species distributions under climate change. Ecol Modell 266:126–130

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions:

biodiversity conservation in a changing climate. Science 332:53–8

deYoung B, Barange M, Beaugrand G, Harris R, Perry RI, Scheffer M, Werner F (2008) Regime shifts in marine ecosystems: detection, prediction and management. Trends Ecol Evol 23:402–9

Diniz-Filho JAF, Mauricio Bini L, Fernando Rangel T, Loyola RD, Hof C, Nogués-Bravo D, Araújo MB (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography 32:897–906

Dobrovolski R, Loyola RD, Guilhaumon F, Gouveia SF, Diniz-Filho JAF (2013) Global agricultural expansion and carnivore conservation biogeography. Biol Conserv 165:162–170

Donner SD (2009) Coping with commitment: projected thermal stress on coral reefs under different future scenarios. PLoS One 4:e5712

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Fahrig L (1997) Relative Effects of Habitat Loss and Fragmentation on Population Extinction. J Wildl Manage 61:603

Fahrig L (2001) How much habitat is enough ? Biol Conserv 100:65–74

Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecol Modell 160:115–130

Foden WB, Butchart SHM, Stuart SN, Vié J-C, Akçakaya HR, Angulo A, DeVantier LM, Gutsche A, Turak E, Cao L, Donner SD, Katariya V, Bernard R, Holland R a, Hughes AF, O’Hanlon SE, Garnett ST, Şekercioğlu ÇH, Mace GM (2013) Identifying the World’s Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. PLoS One 8:e65427

Folke C, Carpenter S, Walker B (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581

Frost SH (1977) Cenozoic reef system of the Caribbean. Prospects for Paleoecologic Synthesis. In: Reef and Related Carbonates, Ecology and Sedimentology Studies in Geology No. 4.p 93–110

Glynn PW, Maté JL, Baker AC, Calderón MO (2001) Coral Bleaching and Mortality in Panama and Ecuador During the 1997 – 1998 El Niño – Southern Oscillation Event : Spatial / Temporal Patterns and Comparisons With the 1982 – 1983 Event. Bull Mar Sci 69:79–109

Gosling SN, Taylor RG, Arnell NW, Todd MC (2011) A comparative analysis of projected impacts of climate change on river runoff from global and catchment-scale hydrological models. Hydrol Earth Syst Sci 15:279–294

Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Modell 157:89–100

Guo Q, Kelly M, Graham CH (2005) Support vector machines for predicting distribution of Sudden Oak Death in California. Ecol Modell 182:75–90

Halpern BS, Frazier M, Potapenko J, Casey KS, Koenig K, Longo C, Lowndes JS, Rockwood RC, Selig ER, Selkoe KA, Walbridge S (2015) Spatial and temporal changes in cumulative human impacts on the world’s ocean. Nat Commun 6:7615

Halpern BS, Walbridge S, Selkoe K a, Kappel C V, Micheli F, D’Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science 319:948–52

Harriott V (1985) Mortality rates of scleractinian corals before and during a mass bleaching event . Mar Ecol Prog Ser 21:81–88

Hawkins JP, Roberts CM (2004) Effects of artisanal fishing on Caribbean coral reefs. Conserv Biol 18:215–226

Hodgson G (1999) A global assessment of human effects on coral reefs. Mar Pollut Bull 38:345–355

Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World’s Marine Ecosystems. Science 328:1523–1528

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2008) Coral Reefs Under Rapid Climate Change and Ocean Acidification. Science 318:1737–1742

Hof C, Araújo MB, Jetz W, Rahbek C (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature:1–6

Hughes TP (1994) Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. Science 265:1547–1551

Hughes TP, Baird a H, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–33

IPCC (2000) IPCC Special Report Emissions Scenarios.

IPCC (2001) IPCC Third Assessment Report: Climate Change 2001 (TAR) - Synthesis Report.

IPCC (2007) IPCC Fourth Assessment Report: Climate Change 2007 (AR4) - Synthesis Report.

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)].

IUCN (2015) The IUCN Red List of Threatened Species. Version 2015-4. <http://www.iucnredlist.org>.

James A, Gaston KJ, Balmford A (2001) Can We Afford to Conserve Biodiversity? Bioscience 51:43

Jetz W, Wilcove DS, Dobson AP (2007) Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLoS Biol 5:e157

Kelmo F, Attrill MJ (2013) Severe impact and subsequent recovery of a coral assemblage following the 1997-8 El Niño event: a 17-year study from Bahia, Brazil. PLoS One 8:e65073

Laborel J (1970) Madréporaires et hydrocoralliaires récifaux des cotes brésiliennes: systématique, écologie, répartition verticale et géographique. Ann l'Institut Ocean Graph Paris 47:171–229

Leão ZMAN (1983) Abrolhos, o refúgio pleistocênico de uma fauna terciária de corais. Rev Biol e Ciências da Terra 8:22–24

Leão ZMAN, Kikuchi RKP, Testa V (2003) Corals and coral reefs of Brazil.

Lemes P, Melo AS, Loyola RD (2013) Climate change threatens protected areas of the Atlantic Forest. Biodivers Conserv 23:357–368

Macreadie PI, Hindell JS, Jenkins GP, Connolly RM, Keough MJ (2009) Fish Responses to Experimental Fragmentation of Seagrass Habitat. Conserv Biol 23:644–652

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–53

Miranda RJ, Cruz ICS, Leão ZMAN, Metropolitana U, Educação D, Luis A, Pontes T (2013) Coral bleaching in the Caramuanas reef (Todos os Santos Bay , Brazil) during the 2010 El Niño event Blanqueamiento de corales en el arrecife de Caramuanas (Bahía de Todos los Santos , Brasil) durante el evento El Niño 2010. 41:351–360

Moilanen A, Pouzols FM, Meller L, Veach V, Arponen A, Leppänen J, Kujala H (2014) Zonation - Spatial conservation planning methods and software v4.0 and user manual.

Molloy PP, McLean IB, Côté IM (2009) Effects of marine reserve age on fish populations: A global meta-analysis. J Appl Ecol 46:743–751

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Nagendra H (2008) Do parks work? Impact of protected areas on land cover clearing. Ambio 37:330–337

Nunes F, Norris RD, Knowlton N (2009) Implications of isolation and low genetic diversity in peripheral populations of an amphi-Atlantic coral. Mol Ecol 18:4283–4297

Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol 15:413–417

O'Neill R V, DeAngelis A, Waide J, Allen TFH (1986) A hierarchical concept of ecosystems.

Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, Ingenloff K, Lira-Noriega A, Hensz CM, Myers CE, Peterson AT (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol Modell 263:10–18

Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. Science 344:895–8

Phillips S, Anderson R, Schapire R (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190:231–259

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752–1246752

Piñeiro R, Aguilar JF, Munt DD, Feliner GN (2007) Ecology matters: Atlantic-Mediterranean disjunction in the sand-dune shrub *Armeria pungens* (Plumbaginaceae). Mol Ecol 16:2155–2171

Pittman SJ, McAlpine C a., Pittman KM (2004) Linking fish and prawns to their environment: A hierarchical landscape approach. Mar Ecol Prog Ser 283:233–254

Prasad AM, Iverson LR, Liaw A (2006) Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. Ecosystems 9:181–199

Rakocinski CF, Moncreiff C a, Peterson MS, Vanderkooy KE, Randall T a (2008) Habitat condition and associated macrofauna reflect differences between protected and exposed seagrass landscapes. Gulf Caribb Res J 20:11–19

Reece JS, Noss RF, Oetting J, Hoctor T, Volk M (2013) A Vulnerability Assessment of 300 Species in Florida: Threats from Sea Level Rise, Land Use, and Climate Change. PLoS One 8:e80658

Reed BJ, Hovel K a. (2006) Seagrass habitat disturbance: How loss and fragmentation of eelgrass Zostera marina influences epifaunal abundance and diversity. Mar Ecol Prog Ser 326:133–143

Salita JT, Ekau W, Saint-Paul U (2003) Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. Mar Ecol Prog Ser 247:183–195

SISBIOTA-MAR (2014) Relatório Final.

Sousa SH de M e (1994) Estudo microbiofaciológico da Formação Amapá (Terciário), Bacia da Foz do Amazonas: Interpretações bioestratigráficas e paleoecológicas

Swartz W, Sala E, Tracey S, Watson R, Pauly D (2010) The spatial expansion and ecological footprint of fisheries (1950 to present). PLoS One 5:3–8

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biol Rev 85:35–53

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Siqueira MF De, Grainger A, Hannah L, Hughes L, Huntley B, Jaarsveld AS Van, Midgley GF, Miles L, Ortega-Huerta M a, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–8

Turner MG, Gardner RH, O’Neill R V. (2001) Landscape Ecology in theory and practice.

Watson R, Zeller D, Pauly D (2011) Spatial expansion of EU and non-EU fishing fleets into the global ocean , 1950 to the present.