SYSTEMATIC CONSERVATION PLANNING FOR ECOSYSTEM SERVICES: OPPORTUNITIES FOR IMPROVING SPATIAL TARGETING OF ECOSYSTEM SERVICE PAYMENTS IN COSTA RICA

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AUTHORIZATION TO SUBMIT DISSERTATION

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ABSTRACT

Tropical forests are of high conservation priority world-wide due their high value for harboring biodiversity and providing ecosystem services from the local to global scale. Financial resources for conservation are scarce. This challenges practitioners to design conservation networks encompassing spatial synergies between biodiversity and ecosystem services. Furthermore, conservation networks need to be robust to climate change impacts and the unpredictability of biodiversity response to these impacts. Methodologies for selecting locations that can help achieve multiple conservation objectives and can be easily integrated in current conservation practices are urgently needed. The first chapter of this study was focused on exploring the effect of integrating into conservation assessments two climate adaptation approaches based on environmental heterogeneity, as well as the effect of the selection of planning unit size on resultant conservation networks. With Costa Rica as planning region, our results showed that protecting the representation of the geophysical diversity resulted in conservation networks with over 25% more internal environmental heterogeneity, but more fragmented. Incorporating cross-environmental connectivity, on the other hand, resulted in low increases in environmental heterogeneity. Increasing the planning unit size reduced the effect of emphasizing connectivity between environmentally different locations. These results highlight the importance of testing environmental-heterogeneity-based approaches in each context due the specific characteristics of planning regions prior integrating them into formal conservation assessments. The second chapter focused on exploring synergies between biodiversity and carbon storage priorities, when integrating environmental-heterogeneity-based climate adaptation approaches. Results revealed very low synergies between targeting the representation of regional biodiversity and areas of high carbon content. However, spreading out across the country the selection of carbon priority areas by adding stratification improved the synergies with biodiversity priorities, and revealed locations that could be considered priorities for carbon storage in the distribution range of Dry Tropical Forests; one of the most threatened tropical ecosystem. The extent of gains for co-benefits between carbon-related ES and biodiversity conservation will depend in part on how priority areas are selected for implementing strategies, such as PES and REDD, and will determine the location and amount of tropical forest to be conserved. As indicated by the recent development of the spatial data used in Chapter 2, improving spatial datasets for supporting ES targeting is critical in tropical dry forests. As a result, we developed new phenological approaches to map tropical dry forest type using multitemporal Landsat 8 Operational Land Imager data. The major gains in mapping accuracy realized by the multitemporal analysis bodes well for the future of landscape level ES planning in tropical dry forest. Finally, the promising progress in the detection of functional traits through remote sensing offers further opportunities to improve on the quality of the inputs for the mapping of ES, a topic covered in Chapter 4.

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DEDICATION

To Bastiaan, Evan and Erin who endured with me throughout these years. This work has truly become a family achievement.

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CHAPTER 1. CAPTURING SPATIAL ENVIRONMENTAL HETEROGENEITY IN CONSERVATION PLANNING WHEN INTEGRATING CLIMATE ADAPTATION APPROACHES AND THE INFLUENCE OF PLANNING UNIT SIZE

ABSTRACT

Numerous approaches have been proposed to incorporate the effects of climate change in conservation assessments. Those approaches that conserve environmental heterogeneity can also promote species diversity by providing diverse niche spaces and opportunities to adapt under changing climate conditions. However, few studies have yet evaluated how planning unit size and input data affect the amount of environmental heterogeneity captured in conservation networks and other resultant conservation assessment outcomes. In this study, we used Costa Rica as planning region to explore the effect of (1) promoting cross-environmental connectivity (i.e. connectivity between different environmental conditions) and (2) conserving various geophysical settings (i.e. geophysical diversity based on topographic and soil attributes) on total internal environmental heterogeneity, efficiency, and spatial patterns of resultant conservation networks. We examined the influence of planning unit size and cost measure on these outcomes. We found that (a) promoting connectivity between environmentally different adjacent planning units had, in our study region, a limited effect on increasing network's environmental heterogeneity, likely due to the combination of the extent of the study region, the resolution of the underlying environmental data, and the environmental characteristics of the region; (b) generally the effect on capturing environmental heterogeneity decreased as the size of the planning unit increased; (c) the cost measure influenced the effect of promoting cross-environmental connectivity, because it reduced the flexibility in the selection of sites, and (d) adding the geophysical diversity increased the network environmental heterogeneity

without representing a major compromise with the network efficiency and degree of fragmentation. These results agree with previous studies supporting the inclusion of environmental-heterogeneity based approaches in conservation assessments, but highlight the importance of testing their effect in each context due the specific characteristics of planning regions prior to integrating them into formal conservation plans.

INTRODUCTION

Accelerating impacts of climate change underscore the urgency that conservation networks be designed to consider the response of biodiversity to altered climates (Groves et al., 2012). Different approaches have been proposed for incorporating climate change into systematic conservation planning. An overarching goal of these approaches is to provide opportunities for biodiversity to adapt over space and time (*see* Groves et al., 2012). Among these approaches, those focusing on environmental heterogeneity are based on the hypothesis that spatial environmental heterogeneity promotes species diversity by increasing available niche space, providing refuge from adverse environmental conditions, and providing opportunities for adaptation and speciation (Comer et al., 2015; Stein et al., 2014). The inclusion of such approaches into conservation assessments can help to design conservation networks that represent the range of physical environments of a region, hence capturing inside these networks the heterogeneity necessary to sustain regional biodiversity patterns regardless of changes in species composition as result of climate change (Anderson et al., 2015). However, secondary effects on the efficiency and spatial patterns of the selected priority areas may result in outcomes that may unduly limit conservation goals, for instance resulting in highly fragmented networks. Furthermore, because conservation assessments require that the planning region be divided into units of analysis, the selection of the size of such units can have important implications.

Systematic conservation planning is widely used for designing on- and off- reserve systems and ecological networks at local, national, or regional scales (Carwardine et al., 2009; Kukkala and Moilanen, 2013; Margules and Pressey, 2000). The reserve system design process involves several steps (Fig. 1), in which planning units (i.e. the spatial unit of analysis) are used to summarize biodiversity status (i.e. the amount of a conservation feature within a planning unit), cost data (i.e. the associated cost of including a planning unit in the reserve network), as well as other input data for conservation assessments. Hence, their characteristics (e.g. shape, size, location) will influence the spatial pattern of conservation networks (i.e. a set of sites that collectively achieve conservation goals), such as total area, location, level of fragmentation, and distribution of planning unit irreplaceability values (i.e. importance for meeting biodiversity conservation targets) (Nhancale and Smith, 2011; Pressey and Logan, 1998). In Table 1.1 can be found the definition of terms used along this document.

Previous work to study the influence of planning unit size on conservation assessments found specific implications arising from (1) changes in the apparent spatial distribution of input data, (2) trade-offs between efficiency (i.e. minimizing cost while also meeting targets) and the level of fragmentation of the conservation network, and (3) tradeoffs between efficiency and the viability for implementation on the ground (e.g. flexibility in the definition of conservation site boundaries) (Nhancale and Smith, 2011; Pressey and Logan, 1998, 1995). One of the main conclusions drawn from such analyses is that smaller planning units generally produce more efficient outcomes as they provide more flexibility for selection, but at the expense of creating more fragmented networks. On the other hand, larger planning units will produce larger total network areas, but typically include locations not required for achieving conservation targets (Nhancale and Smith, 2011; Pressey and Logan, 1998, 1995; Shriner et al., 2006). A recent study by Nhancale and Smith (2011) found that the influence of planning unit size on trade-offs between efficiency and unwanted fragmentation could be reduced using real-world constraints (e.g. by implementing cost metrics) and by clustering smaller planning units.

Integrating biodiversity climate adaptation approaches in conservation planning that are based on environmental heterogeneity is considered scientifically sound (Bonn and Gaston, 2005; Comer et al., 2015; Hodgson et al., 2009), with widespread empirical evidence showing positive relationships between environmental heterogeneity and biodiversity (Stein et al., 2014). Hence, approaches to conserving the geophysical diversity (Anderson and Ferree, 2010; Beier and Brost, 2010; Hunter et al., 1988) and promoting cross-environmental connectivity (Game et al., 2011) may preserve wider ranges of ecological and evolutionary settings and enhance the likelihood of species populations dispersing across suitable habitat conditions (e.g. across geological, altitudinal, or precipitation gradients) as climate changes (Anderson and Ferree, 2010; Game et al., 2011; Groves et al., 2012).

Conserving geophysical diversity is intended to protect the regional diversity of geophysical attributes that will not vary under climate change. The geophysical diversity (or geodiversity) is used to describe geologic, geomorphologic, and soil features (Anderson et al., 2015) and is considered a significant driver of biodiversity patterns, representing the arenas of biological activity (e.g. ecological processes, evolution, and range shift) (Anderson and Ferree, 2010; Beier and Brost, 2010; Hunter et al., 1988). This geophysical diversity can be represented by *land facets*, which are defined as “recurring landscape units with homogeneous topographic and soil attributes” (Beier and Brost, 2010). Therefore, protecting interspersed, representative samples of land facets increases the probability of conserving biodiversity patterns under current and future climate conditions (Anderson and Ferree, 2010; Beier and Brost, 2010; Game et al., 2011; Possingham et al., *in* Lovett et al., 2005).

Cross-environmental connectivity refers to promoting connectivity between habitats that differ in their environmental characteristics (e.g. cooler and warmer, drier and moister) (Game et al., 2011; Hodgson et al., 2009). This approach relates to landscape structural connectivity (i.e. the physical characteristics of the landscape between resource patches), which contributes significantly to functional connectivity (i.e. the degree to which movement of individuals actually occurs) by determining movement potential through a landscape (Doerr et al., 2011).

Both approaches are used to increase internal environmental heterogeneity of conservation networks and can be integrated relatively easily in current conservation assessment practices (see Game et al., 2011). However, the influence of the selection of planning unit size when these climate adaptation approaches are integrated in conservation assessment has not been explored. Planning unit size may affect the apparent environmental distance between adjacent planning units and, hence, the amount of internal environmental heterogeneity captured in conservation networks. Increasing planning unit size could lead to decreased heterogeneity between planning units (Shriner et al., 2006) due to the underlying spatial resolution of input data (i.e., a given environmental heterogeneity). Furthermore, the integration of both climate adaptation approaches (i.e. cross-environmental connectivity and conserving the geophysical diversity) can affect the efficiency and spatial patterns of conservation networks (Game et al., 2011). Because efficiency characterizes the extent to which a conservation network meets targets while minimizing cost, the cost associated with planning units can greatly influence the resulting spatial patterns of priority areas (Nhancale and Smith, 2011), and could consequently limit the internal environmental heterogeneity captured in conservation networks by reducing the number of satisfactory solutions.

Here, conservation planning design software (i.e. MARXAN, Ball and Possingham, 2000; Ball et al., 2009) was used for exploratory conservation assessments across the full range of landscapes occurring in Costa Rica. The main goals were to determine: (i) the effect of integrating the two approaches of (a) promoting cross-environmental connectivity and (b) conserving the geophysical diversity on environmental heterogeneity, efficiency, and spatial pattern of conservation networks; (ii) the effect of changing planning unit size on the internal environmental heterogeneity of conservation networks when integrating the approaches; and (iii) the influence of the associated planning unit cost metric on outcomes. Two sets of conservation features were used: (1) 31 terrestrial ecosystems based on vegetation distribution; and (2) a set of 84 features, comprising the terrestrial ecosystems and 53 land facets defined here based on geological and topographical attributes. We hypothesized that (i) integrating cross-environmental connectivity and geophysical diversity approaches will increase internal environmental heterogeneity of conservation networks but will produce trade-offs with their degree of fragmentation and efficiency, (ii) increasing planning unit size will reduce the effect of promoting cross-environmental connectivity, and (iii) introducing constraints with planning unit cost measure will reduce opportunity for increasing environmental heterogeneity.

INTEGRATING ENVIRONMENTAL HETEROGENEITY IN CONSERVATION ASSESSMENT

Environmental heterogeneity can be integrated into conservation assessment through two components: composition and configuration. Compositional heterogeneity refers to the variability of environmental conditions or elements, while configurational heterogeneity refers to the spatial configuration of those elements (Dufour et al., 2006; Possingham et al., *in* Lovett et al., 2005).

Conserving geophysical diversity by identifying *land facets* (Anderson and Ferree, 2010; Beier and Brost, 2010; Hunter et al., 1988) is analogous to conserving compositional spatial heterogeneity (Possingham et al., *in* Lovett et al., 2005). Land facets are defined as "recurring landscape units with homogeneous topographic and soil attributes" (Beier and Brost, 2010). Land facets are intended to capture the regional diversity of invariant, geophysical attributes under the assumption that they represent the arenas of biological activity (e.g. ecological processes, evolution, and range shift). Therefore, protecting interspersed, representative samples of land facets increases the probability of conserving biodiversity under current and future climate conditions (Anderson and Ferree, 2010; Beier and Brost, 2010; Game et al., 2011; Possingham et al., *in* Lovett et al., 2005).

An advantage of using land facets is that they may be defined using globally available, free access datasets, therefore providing new opportunities to undertake conservation assessments in particularly data poor regions. The relative success of using land facets vs. not using this approach when undertaking conservation assessments (Game et al., 2011) underscores this opportunity. However, land facets can underrepresent or fail to capture some elements of biodiversity, mainly due to the patchy distribution of some species or communities (i.e. rare, endemic, or narrow-range species) (Game et al., 2011; Hermoso et al., 2013). Hence, it is advisable to integrate geophysical diversity in conservation assessments as a complementary approach to more direct biodiversity surrogate approaches (Beier and Brost, 2010; Game et al., 2011; Lombard et al., 2003).

Here, the geophysical diversity is represented by defining land facets based on surface lithology classes, elevation, and the division between the Pacific and Atlantic slopes. Geology can shape species diversity patterns through its influence on the chemical and physical properties of soil and water, as well as on shaping the topography (Anderson and Ferree, 2010). Elevation gradient has significant influence on animal and plant variations and has been strongly associated to the distribution of ecological communities and species turnover in Costa Rica (Chain-Guadarrama et al. 2012; Lieberman et al. 1996; Garcia-Lopez et al. 2012).

Configurational heterogeneity can be integrated into conservation planning by considering the spatial relationships among planning units (Possingham et al., *in* Lovett et al., 2005). Landscape connectivity, defined as ‘the degree to which the landscape facilitates or impedes movement among resource patches’ (Taylor et al., 1993), is currently one of the most considered biodiversity conservation strategy to respond to climate change and other global changes (Heller and Zavaleta, 2009). Structural connectivity refers to the physical characteristics of the landscape between habitat patches, while functional connectivity is more complex and refers to the degree to which movement of individuals actually occurs (Doerr et al., 2011). Empirical research on movement behaviour have shown that structural connectivity contributes significantly to functional connectivity by determining movement potential through a landscape (Doerr et al., 2011).

However, due the lagged and uncertain responses of species to climate change, one approach to support climate adaptation is facilitating range shifts by plants and animals across different environmental gradients, for instance promoting connectivity between cooler and warmer and drier and moister environments, instead of connectivity between similar habitats (Hodgson et al., 2009). Therefore, cross-environmental connectivity is aimed to promote structural connectivity between habitats that differ in their environmental characteristics, and will be most efficiently accomplished, as Game et al., (2011) stated, by prioritizing the protection of locations with high environmental heterogeneity.

Using MARXAN planning design software, structural connectivity is taken into account by using the boundary length variable. This variable along with the Boundary Length Modifier (BLM) parameter are used to control the level of compactness of a solution (increasing BLM value reduces the overall boundary length of the network) (Game and Grantham, 2008). Here, we used Game et al., (2011) method. They proposed that cross-environmental connectivity could be easily incorporated in conservation assessment as the boundary length variable in MARXAN by substituting (or combining) the actual physical length of the boundary shared by adjacent planning units (geographic distance), which is the measure typically used, with the environmental distance between adjacent planning units. The environmental distance is measured as the Euclidean distance in environmental space between adjacent planning units (Game et al., 2011) (see methods section).

METHODS

Study Area

Costa Rica (Fig. 1.2), with approximately 51,000 square kilometers of territory, is located in Central America and is part of the Mesoamerican biodiversity hotspot (Myers et al., 2000). The country is characterized by high species richness as consequence of the variety of topographic, climate, and soil conditions originating from volcanic mountain ranges typical of Central

America, and as consequence of its location as a bridge between North and South America (Castro et al., 2003; SINAC-MINAE, 2007).

We first subdivided the country into hexagonal planning units using four different sizes: 500 ha, 1000 ha, 2500 ha, and 5000 ha. However, analyses for 5000 ha size were not continued as preliminary analyses showed no statistical difference in internal environmental heterogeneity between network solutions using geographic and environmental distances. Planning units were created using the Repeating Shape ArcGIS extension (Jenness 2012). For research purposes, we decided to use hexagonal planning units because they often produce more efficient and less fragmented network solutions, in comparison to square or irregular shapes, due to the lower edge-to-area ratios of hexagons (Ardron et al., 2010; Nhancale and Smith, 2011). Planning units were clipped to the national boundaries of Costa Rica and then combined with a layer containing the boundaries of Biological Reserves and National Parks, resulting in a set of mostly equal sized planning units and some irregular planning units neighboring these protected areas and international borders.

Data

Conservation features. - A national conservation planning assessment was already undertaken for Costa Rica, known as GRUAS II (SINAC-MINAE, 2007). In GRUAS II, terrestrial ecological systems called Phytogeographic Units (from now on referred to as floristic regions, in order to avoid confusion) were used as the coarse-filter surrogate of biodiversity. These floristic regions were defined based on the distribution of floristic patterns from field data, previous vegetation maps, and expert knowledge, as well as the use of abiotic factors for helping their delimitation (Zamora, 2008). Here, we used the 31 continental floristic regions as the main conservation features. Each floristic region was analyzed relative to a 2012 forest map obtained from the

Forest National Inventory map (Programa REDD/CCAD-GIZ - SINAC. 2015) and the amount of forest area of each floristic region was calculated within each planning unit.

Here, we mapped 53 land facets. The land facets were created by performing a categorical overlap of three maps representing surface lithology (nine classes), elevation (four classes), and the division between Pacific and Atlantic slopes of Costa Rica (USGS et al. 1987; ASTER-GDEM validation team, 2011; Watershed map in Atlas of Costa Rica 2008; respectively). Each land facet was analyzed relative to a 2012 forest map obtained from the Forest National Inventory map (Programa REDD/CCAD-GIZ - SINAC. 2015) and the amount of forest area of each land facet was calculated within each planning unit. Instead of using soil attributes, we used surface lithology classes describing age and origin of the rocks, because surface lithology resulted one of the most important variables for predicting the distribution of the floristic regions in Costa Rica (Fung et al., 2015).

Feature targets. - The feature targets were defined based on the CBD (Convention of Biological Diversity) (CDB, 2010), which aims to protect at least 17% of the original extent of each terrestrial ecosystem. The contribution of Biological Reserves and National Parks (Protected Areas for now on) to meeting each target was calculated, and then we calculated the proportion of additional forest cover out of the protected areas needed for each floristic region and land facet to complete the CBD targets. Other protected areas, such as Forest Reserves and Wildlife Refuges, were considered as part of the planning region, because the majority of these lands are privately owned and therefore subject to off-reserve conservation policies unique to Costa Rica, such as payments for ecosystem services (PES).

Planning unit cost. –Two alternative cost measures were used in order to compare between conservation assessments and test the effect of planning unit cost on the outcomes. First, for all planning units the cost value was set to 1, and thus the total cost of the conservation network was expressed as the total number of selected planning units. This was named Cost Objective 1. Second, the cost associated to each planning unit was the sum of planning unit's probability of the land being cover by forest, which was termed Cost Objective 2. The forest probability map, in raster format, was obtained from Bárcena et al., (2011). Planning units with low values would be preferred for selection, as they were considered at more threat of losing biodiversity by deforestation or forest degradation related to human activities. On the contrary, it was assumed that those planning units with high values would be less susceptible to forest conversion or degradation. These assumptions are based on the fact that Costa Rican Forest Law No. 7575, in force since 1996, bans forest conversion to other land uses, which in practice has preserved forest cover. However, studies on PES impact on deforestation in Costa Rica have shown that targeting towards areas with some deforestation pressure (for instance areas closer to urban areas, national roads, and lower slopes) would have significant potential gains (Pfaff et al., 2009; Robalino et al., 2008).

Environmental distance and geographic distance. – In general, we followed the method from Game et al. (2011) for integrating cross-environmental connectivity into Marxan-based landscape analysis. We used eleven environmental variables of climate and topography (Table 1.2). Using the mean value of a planning unit for each of the 11 environmental variables, we calculated the Euclidean distance in environmental space among all adjacent planning units. Therefore, the environmental distance is a measure of the degree of environmental dissimilarity between two sites; the higher the value the greater the dissimilarity and vice versa. The geographic distance is the actual geographical length of the boundary between two adjacent planning units (Game and Grantham, 2008) and was produced using the add-in tool Marxan Boundary for ArcGIS 10.x (ABPmer marine environmental research). Both distances were rescaled to a range from 1 to 100. We assigned the geographic distance and environmental distance as alternative boundary length in MARXAN analyses.

The boundary length variable in MARXAN is also referred to as boundary cost or penalty, because it represents the cost that must be paid if a pair of adjacent planning units are not included together. Hence, a high boundary length between adjacent planning units increases the likelihood that if one of the planning units is selected, the other will be selected too (Game and Grantham, 2008). Producing more compact conservation networks can be accomplished by minimizing the boundary length, which is controlled by the Boundary Length Modifier (BLM). Larger BLM values will produce solutions with smaller overall boundary length (Game and Grantham, 2008). Any change to the boundary file will change the influence of the BLM on the MARXAN objective function (Game et al., 2011). As a result, the BLM was calibrated to keep relatively constant the boundary penalty added to the MARXAN objective function and to make outcomes from conservation assessments comparable to each other. The Zonae Cogito decision support software for MARXAN (Segan et al., 2011) was used to calibrate the BLM in each conservation assessment by testing 20 BLM values (20 repeated runs in each test) and then compared boundary penalties between assessments using analysis of variance and a Tukey test. When necessary, the BLM was calibrated manually. Those BLM values where the boundary penalty means were not statistically different were selected. Statistical analyses were performed using R 3.1.2 (The R Development Core Team, 2014) and InfoStat statistical package (Di Rienzo et al., 2014).

Analysis

MARXAN. - 24 different conservation assessments were run in the widely used conservation software MARXAN (Ball and Possingham, 2000; Ball et al., 2009). MARXAN uses input data to select a set of priority areas (planning units) that jointly constitute a conservation network within the planning region. Each conservation assessment was run independently 10 times with simulated annealing followed by iterative improvement (20 repeated runs, 10,000,000 iterations) (For details of the algorithm used by MARXAN see Game and Grantham, 2008). The different conservation assessments resulted from combining the two boundary distances, three planning unit sizes, two sets of conservation features, and two measures of planning unit cost (Table 1.3). Correlation analysis and spatial pattern comparisons were performed on outcomes from analyses using 1000 repeated runs. This, allowed to use the selection frequency of a planning unit as a measure of its importance in contributing to achieve targets. Hence, the irreplaceability value for each site is represented by the proportion of solutions containing it, in a range of values between 0 and 1, where sites with values of 1 are considered the most important (Carwardine et al., 2006).

MARXAN outcomes are primarily: (a) the ‘best solution’, which is the solution that meets targets with the lowest score (i.e. the lowest objective function value, representing the sum of the network total cost, penalties for not meeting conservation targets, and boundary penalty); (b) the ‘summed-solution’, which comprises the selection frequency of each planning unit; and (c) the ’summary information’, which contains information on each run, such as the score, the total cost, and penalties (Ball and Possingham, 2000; Game and Grantham, 2008).

Network internal environmental heterogeneity. – Conservation networks were compared among assessments using geographic and environmental distances as alternative boundary lengths, and when targeting the representation of the geophysical diversity by integrating the land facets, within and across three different planning unit sizes: 500 ha, 1000 ha, and 2500 ha. The internal environmental heterogeneity was calculated as the sum of all planning unit environmental distances for each conservation network (i.e. best solution). Because the number of environmental distances change with the total number of planning units, the summed internal environmental heterogeneity values were not directly comparable among the three different sizes. Instead, we used for comparison purposes the average proportional increase of internal environmental heterogeneity from the best network solutions, based on 10 independent MARXAN analyses for each conservation assessment.

Network efficiency and spatial patterns. –The efficiency, level of fragmentation, and spatial congruency between assessments were compared. Efficiency was compared using the total cost incurred in best solutions for meeting targets and the ratio between forest area and total area in each best solution. This ratio helped to explore the efficiency of networks in terms of the relationship between areas required for achieving targets and additional areas. The level of network fragmentation was interpreted with the total external boundary length; higher values indicated more fragmentation.

Spatial congruency was measured in two ways: proportional overlap analysis and irreplaceability similarity (e.g. Chan et al., 2006; Egoh et al., 2011). Proportional overlap analysis quantified the area shared (i.e. number of planning units) between two conservation networks as a percentage of the conservation network area with a smaller total area. The irreplaceability value of a planning unit was calculated as the number of times, out of 1000, that the planning unit was in a solution. Using these planning unit irreplaceability values, we performed correlation analysis (Pearson's r) as a measure of irreplaceability similarity between solutions. In other words, we looked at the similarity between conservation assessments in terms of patterns of the importance of each planning in its contribution for efficiently meeting biodiversity targets (Carwardine et al., 2006).

The effect of cost measure. – Comparisons between outcomes from analyses using Cost Objective 1 and Cost Objective 2 were performed. When no statistical differences in internal environmental heterogeneity between networks were found, no further comparisons were done.

RESULTS

Internal Environmental Heterogeneity

When comparing best solutions between assessments using either geographic or environmental distance as boundary length, the average increase in internal environmental heterogeneity was low for all planning unit sizes, generally about 1% to 3%. This result occurred regardless of the suites of conservation features used in the analysis. Nonetheless, the internal environmental heterogeneity between solutions were statistically different for both 500 ha and 1000 ha planning unit sizes. On average, the higher increases in environmental heterogeneity occurred at the 1000 ha size. But, increasing the planning unit size to 2500 ha reduced the effect of promoting cross-environmental connectivity, as at this size there was no statistical difference on internal environmental heterogeneity between network solutions. Looking at the effect on the overall boundary length, using environmental distance showed higher increases in the degree of fragmentation in general for all planning unit sizes, but particularly at smaller planning unit size (Table 1.4 and 1.5).

Comparisons among network solutions that used geographic distance were performed to explore the effect of targeting jointly the representation of floristic regions and land facets (geophysical diversity) versus only targeting the representation of floristic regions. We calculated the internal environmental heterogeneity in the same fashion as it was done for cross-environmental connectivity (see analysis section in methods). Considerable gain in internal environmental heterogeneity for all planning unit sizes was found when adding land facets as conservation features (mean = 31%, range = 25% to 38%). Larger planning unit sizes showed larger increases in internal environmental heterogeneity when comparing with not-including land facets, regardless of the boundary distance used. The effect of integrating the cross-environmental connectivity to these scenarios slightly improved the average increase in internal environmental heterogeneity (3% more, on average).

Network Efficiency and Spatial Patterns

In all best solutions identified by MARXAN all conservation features targets were achieved. Because the cost associated with each planning unit was consistent (i.e. set to 1), the total cost of the network represented the total number of planning units that comprised the best solution. In order to compare among planning unit size classes, however, total area (ha) and the ratio between forest area and total area were used as measures of efficiency. Results showed that increasing planning unit size reduced the efficiency of conservation networks. In the same fashion, incorporating either or both cross-environmental connectivity (environmental distance) and conserving geophysical diversity (land facets) reduced network efficiency. These additions required more total area in order to meet targets; therefore, there was an increase in areas that were not necessary for achieving targets (Table 1.4).

The level of fragmentation within network solutions was varied. Results showed that network solutions were more fragmented (i.e. had longer boundary lengths) when both environmental distance and land facets were included (Fig. 1.3). Including land facets, in particular, produced larger increases of external boundary length values, mostly over 50% (Table 1.5, c). While using the environmental distance increased the external boundary length mostly below 20%, irrespective the suite of conservation features targeted (Table 1.5, a and b).

When comparing between conservation assessments using geographic and environmental distances, spatial congruency and irreplaceability similarity between network solutions were generally high (Table 1.7; Fig. 1.4). However, comparing between network solutions targeting only the representation of floristic regions and those including land facets reduced the overlap and irreplaceability similarity values. Increasing the size of the planning unit slightly increased the overlap between compared pair of networks.

The Effect of Cost Measure

The results showed that the type of planning unit cost had a large influence on the conservation assessment results. When assigning, to all conservation assessments, the summed forest probability as planning unit cost (Cost Objective 2), it was found that the type of boundary distance used had no effect on changes in the internal environmental heterogeneity of conservation networks. In other words, interchanging the geographic distance with the environmental distance (i.e. integrating the cross-environmental connectivity approach) did not increase the internal environmental heterogeneity of the conservation networks. These results were regardless of the suite of conservation features used and consistent across sizes.

DISCUSSION

As climate change proceeds, successful conservation of biodiversity will depend on creating conservation networks that are robust to uncertainties related to how species and community responses to climate forcing (Groves et al., 2012). Integrating climate adaptation approaches in systematic conservation planning is therefore important. Climate adaptation approaches of particular utility will be those that can be (1) easily incorporated in current conservation assessment practices, (2) based on well-established ecological principles, and (3) can be applied using freely available datasets with consistent accuracy assessments (Game et al., 2011). Approaches based on environmental heterogeneity are therefore promising because they can increase the internal environmental heterogeneity of conservation networks and can be relatively easy integrated into conventional conservation assessments (Bonn and Gaston, 2005; Game et al., 2011).

While approaches based on environmental heterogeneity may be effective in planning for climate-related habitat change, results here demonstrated that outcomes are affected by the spatial distribution of input data and choices related to specific planning unit characteristics. In the present study, we explored the effect of including both cross-environmental connectivity and conservation of geophysical diversity on the internal environmental heterogeneity, efficiency, and spatial patterns of the conservation network solution. We studied the effect of planning unit size on capturing environmental heterogeneity when including these approaches. In addition, we explored the influence of the cost measure on the outcomes. Results revealed the importance of understanding the effectiveness of the approaches in each conservation planning context.

Climate adaptation approaches based on increasing environmental heterogeneity are promising because they (1) provide opportunities for diverse sets of species to move through different environmental conditions and (2) are supported by widespread empirical evidence showing positive relationships between environmental and biological diversity (Groves et al., 2012; Stein et al., 2014). It is intuitive that integrating climate adaptation approaches based on environmental heterogeneity will increase the internal environmental heterogeneity of conservation networks, however, in our study including cross-environmental connectivity approach resulted in low values of average increase in internal environmental heterogeneity. These results differed from those of Game et al., (2011), which obtained conservation networks with over 40% more internal environmental heterogeneity.

The difference of gains in network internal environmental heterogeneity when integrating the cross-environmental connectivity approach between our results and those of Game et al. (2011) could be explained by the combination of the small size of our planning region (ten times smaller than in Game et al., 2011), the resolution of the underlying environmental data, the geophysical heterogeneity of the country, and the spatial distribution of conservation features. Costa Rica has highly heterogeneous physiography mainly due its topography created by volcanic mountain ranges, and currently most forest areas are located in these mountainous regions. Geographic and environmental distances were very similar in their influence on site selection; showing high spatial congruency between solutions with ~70% of spatial overlap between best solutions and very high irreplaceability similarity (>0.90 Pearson's *r* correlation between planning unit selection frequencies).

On the other hand, our results showed that incorporating geophysical diversity (i.e. land facets) increases the internal environmental heterogeneity of conservation networks by an overall average of 31%. However, as expected, this also resulted in more fragmented solutions by promoting maximum dispersion of locations selected in conservation networks (52% increases in total external boundary length in average). The inclusion of land facets in addition to vegetation-based coarse-filter surrogates (i.e., floristic regions), using for instance 500 ha, resulted in conservation networks that on average were roughly 13% more expensive (i.e., more planning units selected), but required just under 6% more forest area to achieve targets. Incorporating the geophysical setting in national conservation assessments will increase the likelihood of conserving present and future biodiversity because geophysical gradients foster high amounts of species richness (Anderson and Ferree, 2010; Stein et al., 2014). In addition, conservation networks that encompass broad environmental gradients will allow organisms to adjust their local distributions in response to changing climate (Hunter et al., 1988).

Selecting an appropriate planning unit size is critical for implementing conservation plans. Our results agree with previous works that found that increasing planning unit size reduced the efficiency of the network (Nhancale and Smith, 2011; Pressey and Logan, 1998; Shriner et al., 2006). Specifically, our results showed that smaller planning units were more efficient in terms of less total area and less additional areas; the latter indicated by the relation between the total forest area and total area of the network. However as also noted in these other studies, our results showed that networks using smaller planning units resulted in more fragmented solutions, what can be controlled with the BLM parameter.

Here, we investigated the tradeoff between habitat fragmentation and the amount of environmental heterogeneity captured in the conservation solutions. When quantifying environmental distance between adjacent planning units (under scenarios targeting both the floristic regions and land facets), we found that by increasing planning unit size from 500 ha to 1000 ha it was possible to capture more internal environmental heterogeneity with relatively lower rates of fragmentation. Selecting the appropriate planning unit size also depends on the conservation policy to be implemented and other considerations of ecological viability of protected areas. Nhancale and Smith (2011) argued that in order to maintain flexibility and maximize efficiency in selection of priority areas, it is better to use small planning units and then to reduce their fragmentation levels by increasing BLM (Boundary Length Modifier) values or other methods. Hence, an alternative approach for future research would be to test different BLM values and find a level of compactness with the desired results.

Comparisons between conservation assessments using geographic or environmental distances can add insight to the potential effectiveness of conservation planning strategies. We found that the cost metric largely influenced the spatial pattern of network solutions. This resulted in no differences between the network environmental heterogeneity when the probability of forest was used as a cost measure (Cost Objective 2). This result was consistent across all planning unit sizes. Nhancale and Smith (2011) found that using a socio-economic cost metric reduced the influence of planning unit characteristics on assessment results, because variation in costs reduced flexibility in the selection of priority areas. MARXAN will tend to select the lower cost planning units and, consequently, the same locations repeatedly. This effect of cost metric is generally desired for producing more robust results (Carwardine et al., 2010). However, for this particular study, where setting the planning unit cost metric to 1 resulted in low increases, the reduction in flexibility, by using other cost metric, limited the efficacy of integrating approaches aimed at preserving environmental connectivity.

Although it is intuitive that integrating climate adaptation approaches that are based on environmental heterogeneity in conservation assessment will produce conservation networks that capture more environmental heterogeneity versus not integrating the approaches, our results showed that the degree of increase depend on each planning context and available data (e.g. extent of the planning region, resolution of the underlying environmental data, cost measure used). Particularly, for integrating cross-environmental connectivity approach, we highlight the importance of assessing the influence of integrating the approaches on conservation assessment outcomes in each planning context. Adding geophysical diversity allowed to increase networks environmental heterogeneity without compromising the achievement of floristic region targets and without incrementing significantly the amount of forest necessary for meeting targets, important from the point of view of implementation. Making of this approach, as Game et al., (2011) stated, a not-regret way to improve the likelihood of biodiversity persistence under climate change. Further research is needed for supporting decisions about the selection of the planning unit size in concordance with the resolution of the underlying environmental data, as well as for evaluating the way that the environmental heterogeneity is characterized and integrated in conservation assessment, in order to capture the environmental heterogeneity necessary for sustaining current and future biodiversity.

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Table 1-1: Definition of some terms related to Systematic Conservation Planning and Marxan analysis

Systematic Conservation Planning (SCP)	A multidisciplinary science; a discipline of decisions supported by spatial analyses; and a stage-wise operational model concerning "the prioritisation of sites for their biodiversity value and the participatory planning and collaborative implementation of strategies, decisions and actions that secure the long-term survival and favorable conservation status of biodiversity in general" (Kukkala et al., 2013; first described by Margules and Pressey, 2000).
Conservation assessment	A quantitative assessment for the identification of spatial priorities for conservation action, i.e., site selection (Egoh et al., 2007; Kukkala et al., 2013).
Conservation feature	A measurable, spatially definable component of biodiversity that is to be conserved within a reserve network (Ardron et al., 2010)
Conservation feature target	The amount of the conservation feature to be included within the reserve network (Ardron et al., 2010)
MARXAN	A software that delivers decision support for reserve system design, aiming to identify a combination of planning units or reserve network that will meet user-defined biodiversity targets for the minimum cost (Game and Gratham, 2008).
Planning Units	The unit of analysis where input data is summarized or compiled, principally the amount of a conservation feature in a planning region. The planning region is subdivided into a number of planning unit polygons, which can be of regular or irregular shape (Nhancale and Smith, 2011).
Cost (of a planning unit)	A measure of the cost (or suitability) of including each planning unit in the reserve system (Game and Gratham, 2008).
Conservation network	Also can be found as reserve system, reserve network, or conservation portfolio. It is a set of sites that collectively contribute to the achievement of conservation objectives.
Best solution	The reserve network with the lowest Marxan objective function value (i.e., the most efficient solution) from a series of Marxan solutions (Ardron et al., 2010)

Species Penalty Factor (SPF)	A multiplier that represents the penalty that must be paid for not meeting a conservation feature target in the current reserve scenario. The higher the value, the greater the relative penalty (Game and Grantham, 2008).
Irreplaceability value	A measure of how important is each planning unit in its contribution for efficiently meeting biodiversity conservation targets. Using MARXAN, the irreplaceability value of a planning unit is measured as the proportion of solutions containing it; how often a planning unit is selected over the total number of solutions per scenario (Ardron et al., 2010; Carwardine et al., 2006).
Boundary length	A variable used in MARXAN that represents a measure of the spatial relationship or connectivity between two planning units, which may or may not be adjacent to each other. Typically, the boundary length is the geographic length of the shared boundary between adjacent planning units, and it is considered as the cost that must be paid if a pair of adjacent planning units are not included together in the reserve network solution. (Game and Grantham, 2008; Possingham et al., in Lovett et al., 2005).
Boundary Length Modifier (BLM)	A multiplier used to determine how much emphasis should be place on minimizing the overall reserve network boundary length (Game and Grantham, 2008).

Table 1-2: Environmental data and sources

No.	Environmental attributes	Source
	Climate attributes	
1	Precipitation of the coldest quarter	Climate attributes from Hijmans et al., 2005; available on-line htpp://worldclim.org/download. Potential annual evapotranspiration from Trabucco et al., 2009; available on-line http://csi.cgiar.org/Aridity/
2	Precipitation of the warmest quarter	
3	Precipitation seasonality	
4	Potential evapotranspiration	
5	Precipitation/Potential evapotranspiration	
6	Minimum temperature of the coldest month	
7	Temperature annual range	
8	Temperature seasonality	
	Topographic attributes	
9	Elevation	Aster-GDEM2 validation team (2011). Slope tool of spatial analyst ArcMap 10.3 (©2009-2014 ESRI Inc.). CTI ArcGIS tool Evans et al., (2014)
10	Slope in degrees	
11	Compound topographic index (CTI)	

Table 1-3: Planning unit sizes and input data used in conservation assessments

Code	
Planning unit size	
A	500 ha
B	1000 ha
C	2500 ha
Set of conservation features	
FR	Floristic regions
LF	Land facets
Boundary distance	
geo.	Geography distance, the physical boundary shared by two adjacent planning units
env.	Environmental distance, the environmental differences (Euclidean distance) between two adjacent planning units
Cost metric	
1	Cost Objective 1, the cost value of a planning unit set to 1
2	Cost Objective 2, the cost value of a planning unit as the summed probability of the planning unit been covered by forest

Table 1-4: Average values of conservation network attributes for each size evaluated, when a planning unit cost is set to 1. Averages were calculated using the best solution from 10 independent analyses (20 repeated runs in each analysis).

Network	Total cost (number of planning units)	Total boundary length (km)	Total area (ha)	Total forest area (ha)	Forest area / Total area
A) 500 ha					
FR geo.	**1412**	**3583**	**692765**	**464897**	**0.67**
FR env.	1442	4191	708657	464353	0.66
FRLF geo.	1586	5415	781696	492720	0.63
FRLF env.	1617	5906	797375	492924	0.62
B) 1000 ha					
FR geo.	**748**	**2665**	**726282**	**467724**	**0.64**
FR env.	763	2962	745377	467020	0.63
FRLF geo.	845	4163	827073	501761	0.61
FRLF env.	863	4511	846373	501388	0.59
C) 2500 ha					
FR geo.	**325**	**2113**	**772118**	**472272**	**0.61**
FR env.	329	2336	790008	472769	0.60
FRLF geo.	377	3162	909813	523156	0.58
FRLF env.	380	3383	921721	523004	0.57

FR: floristic regions, LF: land facets, geo.: geographic distance, env.: environmental distance, Bold: reference network solutions

Table 1-5: Proportional average increases in attribute values of networks when comparing: (a) geographic versus environmental distances targeting 31 floristic regions, (b) geographic versus environmental distances targeting both floristic regions and land facets, and (c) geographic distance targeting floristic regions versus geographic distance targeting both floristic regions and land facets. For all assessments the cost of a planning unit was set to 1. Values using the best networks from 10 independent analyses (20 repeated runs within each analysis). Analysis of variance (ANOVA), with p-value < 0.0001 (otherwise stated), indicating that the averages are different. R square (adjusted) are presented, indicating the strength of ANOVA results (% of variation explained). See standard deviations in Table 1.6.

	(a) FR geo. *vs* FR env.			(b) FRLF geo. *vs* FRLF env.			(c) FR geo. *vs* FRLF geo.		
	500 ha	1000 ha	2500 ha	500 ha	1000 ha	2500 ha	500 ha	1000 ha	2500 ha
% increase									
Environmental heterogeneity	2.72	2.86	1.21	2.70	3.21	0.73	28.63	30.02	36.22
Boundary length	17.10	11.22	10.65	9.09	8.39	7.02	51.22	56.23	49.70
Total area	2.30	2.63	2.32	2.01	2.34	1.31	12.84	13.88	17.84
Forest area	-0.12	-0.15	0.11	0.04	-0.07	-0.03	5.98	7.28	10.78
R^2 (adjusted)									
Environmental heterogeneity	0.59	0.73	_	0.78	0.64	_	1.00	0.99	1.00
Boundary length	0.92	0.86	0.82	0.92	0.88	0.74	0.99	0.99	0.99
Total area	0.83	0.91	0.75	0.93	0.86	0.67	1.00	1.00	1.00
Forest area	0.32 (i)	_	_	_	_	_	0.99	0.99	0.99

(i) p-value = 0.0057, (_) no statistical difference

Table 1-6: Standard deviations of proportional average increases in network attribute values when comparing: (a) geographic versus environmental distances targeting 31 floristic regions, (b) geographic versus environmental distances targeting both floristic regions and land facets, and (c) geographic distance targeting floristic regions versus geographic distance targeting both floristic regions and land facets (see Table 1.5).

	(a) FR geo. *vs* FR env.			(b) FRLF geo. *vs* FRLF env.			(c) FR geo. *vs* FRLF geo.		
	500 ha	1000 ha	2500 ha	500 ha	1000 ha	2500 ha	500 ha	1000 ha	2500 ha
% increase									
Environmental heterogeneity	1.23	1.18	1.88	1.02	1.73	1.27	2.11	1.5	1.57
Boundary length	5.36	4.44	4.71	2.16	2.31	2.7	3.51	3.02	4.84
Total area	0.62	0.49	0.93	0.32	0.6	0.53	0.82	0.56	0.61
Forest area	0.14	0.27	0.43	0.53	0.54	0.86	0.37	0.47	0.81

Table 1-7: Results from proportional overlap analysis of best solutions and correlations (Pearson's r) between solutions patterns of planning unit irreplaceability values based on their selection frequencies ("summed-solution"). For all assessments the cost of a planning unit was set to 1.

Planning unit size	Compared networks	Overlap	Correlation
Comparing geographic versus environmental distance			
500 ha	FR geo. *vs* FR env.	69.29	0.96
	FRLF geo. *vs* FRLF env.	68.90	0.96
1000 ha	FR geo. *vs* FR env.	73.47	0.95
	FRLF geo. *vs* FRLF env.	71.93	0.96
2500 ha	FR geo. *vs* FR env.	78.64	0.95
	FRLF geo. *vs* FRLF env.	71.96	0.94
Comparing excluding versus including land facets			
500 ha	FR geo. *vs* FRLF geo.	59.94	0.76
	FR env. *vs* FRLF env.	57.82	0.73
1000 ha	FR geo. *vs* FRLF geo.	64.00	0.74
	FR env. *vs* FRLF env.	60.80	0.72
2500 ha	FR geo. *vs* FRLF geo.	67.18	0.73
	FR env. *vs* FRLF env.	62.85	0.69

FR: floristic regions, FRLF: floristic regions and land facets, geo.: geographic distance, env.: environmental distance

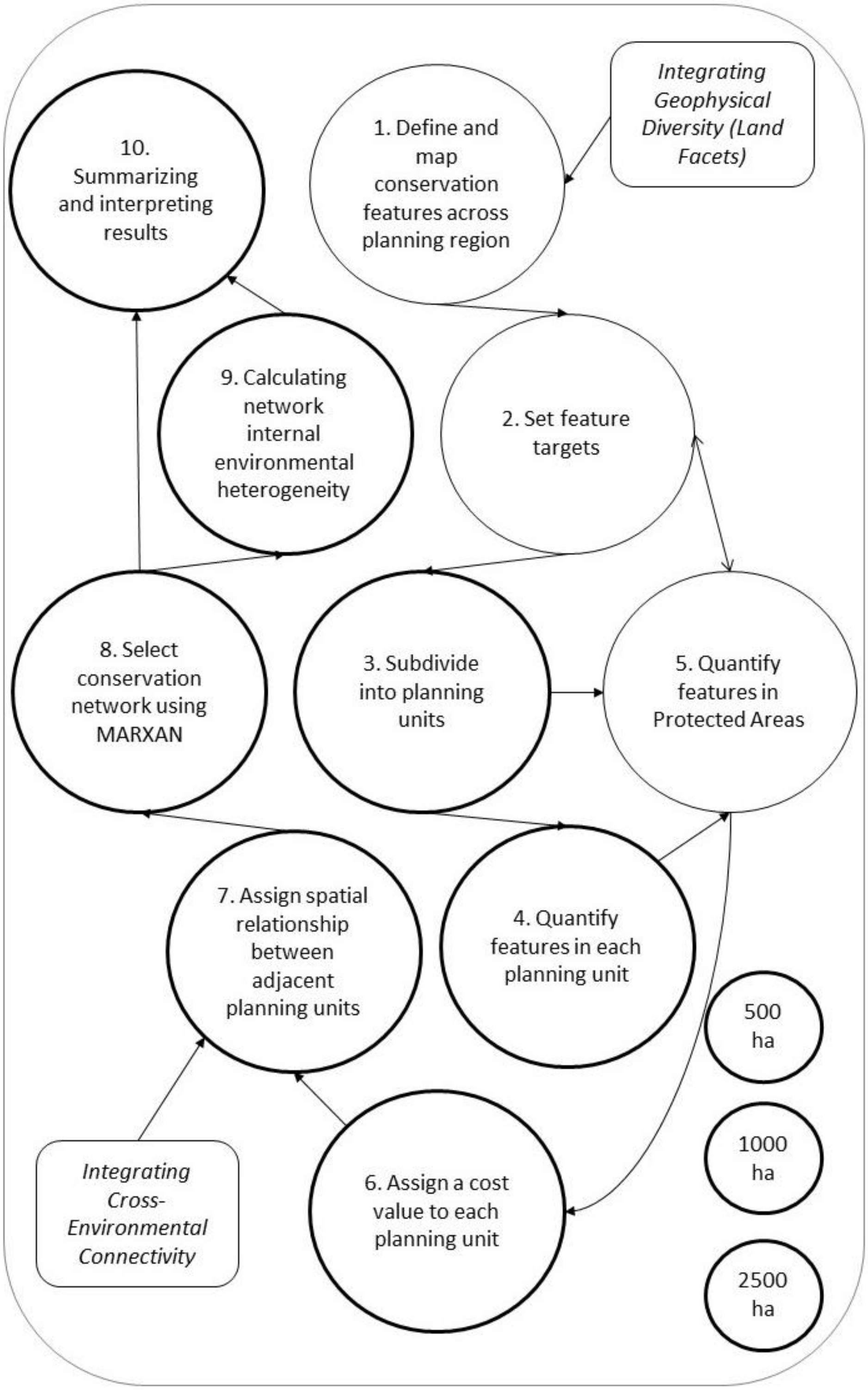

Figure 1-1: Steps followed for conservation assessments in this study based on Systematic Conservation Planning framework. Conservation assessments were done using three different sizes (small bold circles) and some steps required to be repeated for each size (big bold circles). The climate adaptation approaches (in boxes) and the steps in where they were integrated are shown.

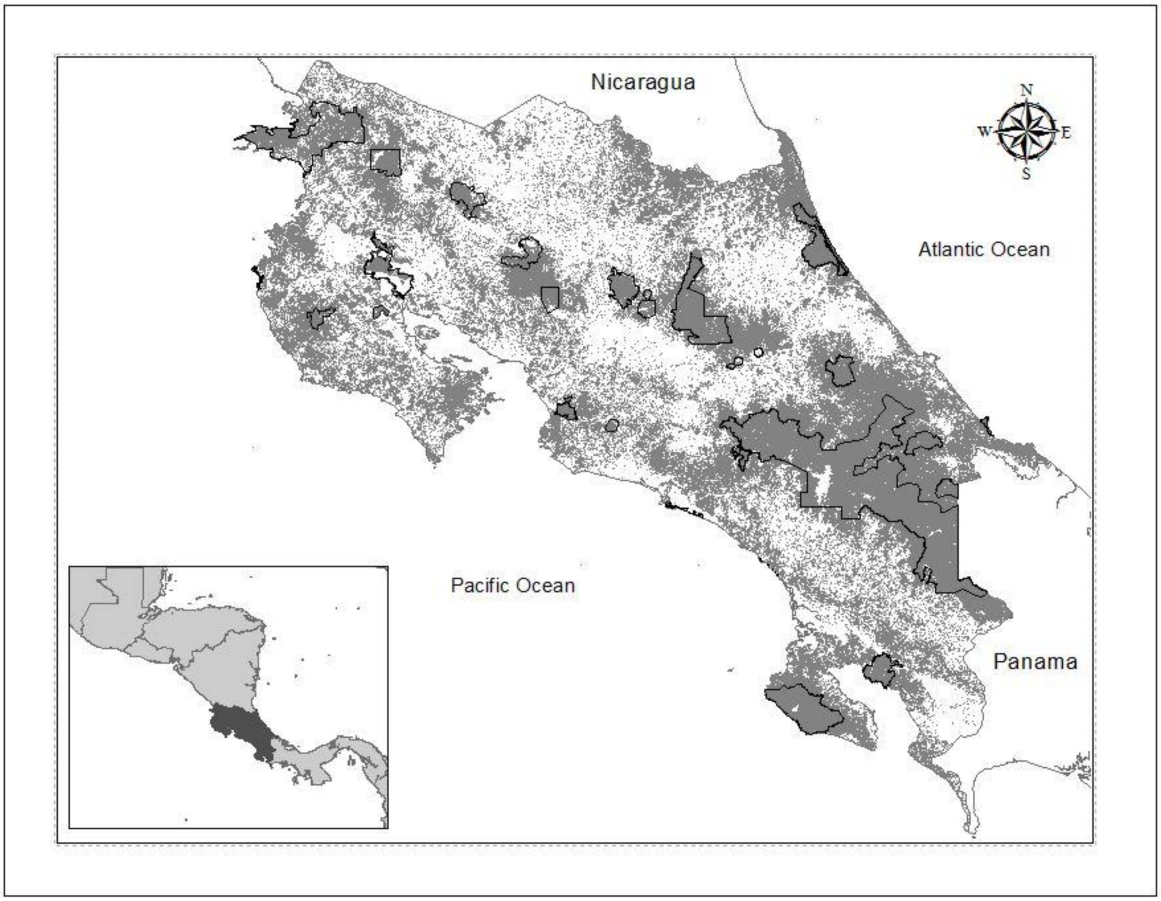

Figure 1-2: Study area, Costa Rica, and its location in Central America (small box at left lower corner). Current forest cover presented in gray and strict protected areas (terrestrial Biological Reserves and National Parks) in black lines.

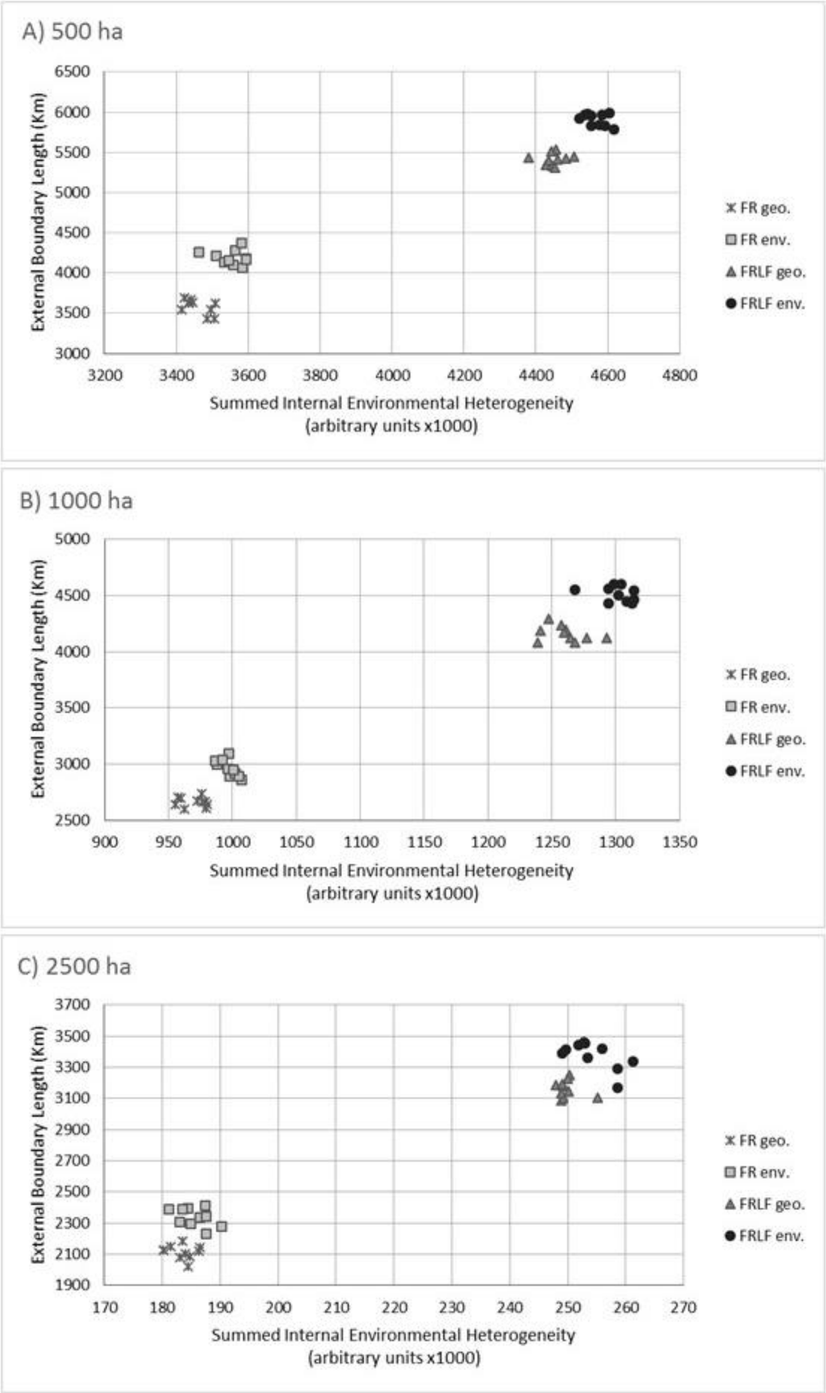

Figure 1-3: Comparison of the total internal environmental heterogeneity (x-axis) and the total external boundary length (y-axis) of best network solutions when using planning unit size of (A) 500 ha, (B) 1000 ha, and (C) 2500 ha, and two different boundary length formulations: 100% geographic distance (geo.) and 100% environmental distance (env.). All planning unit cost values set to 1. Two set of conservation features were used: (i) 31 floristic regions (FR), and (ii) 84 features (FRLF) comprising the 31 floristic regions and 53 land facets. Summed internal environmental heterogeneity values across sizes are not comparable as number of total planning units and boundaries changes when changing planning unit size.

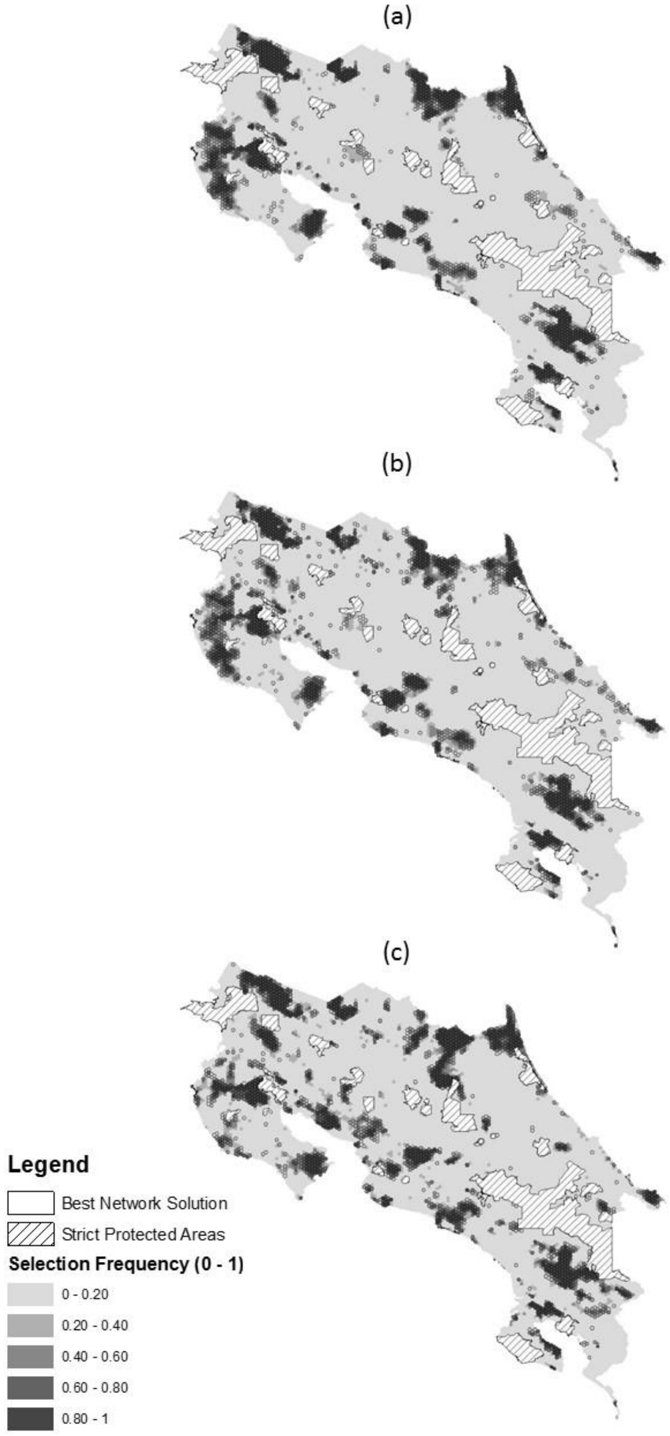

Figure 1-4: Example of network solutions. Planning unit size of 500 ha and cost set to 1: (a) reference network solutions, in which only the representation of floristic regions were targeted and geographic distance was used; (b) integrating cross-environmental connectivity approach by using environmental distance, while targeting the representation of floristic regions; (c) integrating conserving geophysical diversity approach by targeting the representation of land facets jointly with floristic regions, while using geographic distance as boundary length.

CHAPTER 2. CLIMATE, CARBON, AND BIODIVERSITY: POTENTIALS FOR CLIMATE-RESPONSIVE CONSERVATION MANAGEMENT IN COSTA RICA

ABSTRACT

Tropical forests are a high conservation priority world-wide due their high value for harboring biodiversity and providing ecosystem services. However, financial resources for conservation are scarce, challenging practitioners to design conservation networks encompassing spatial synergies among priorities for biodiversity and ecosystem services. Hence, methodologies for selecting locations that can help achieve multiple conservation objectives are urgently needed. Due to climate change, spatial synergies between biodiversity conservation and carbon storage are of particular interest. However, uncertainties of how species will respond to climate change make it paramount to design conservation networks that are robust to these uncertainties and, moreover, are easily to integrate in current conservation planning practices. In this study, using a commonly used conservation planning tool for site selection, we explored spatial synergies between biodiversity conservation and carbon storage priorities in Costa Rica, integrating into biodiversity conservation assessments two climate adaptation approaches: (1) conserving the geophysical settings, and (2) promoting cross-environmental connectivity. Both seeking greatest environmental heterogeneity in conservation networks. We also compared three free-access, pantropical above-ground biomass datasets for Costa Rica in order to investigate the effect of the dataset selection on conservation assessment outcomes for carbon-storage. Additionally, we explored whether adding conservation assessment for carbon storage as a stratification element could improve the level of synergies between priorities for carbon storage and biodiversity conservation. We used as a stratification element the national division of Conservation Areas in order to spread out across the country the selection of sites for carbon

storage. Our results revealed that promoting cross-environmental connectivity, by explicitly considering environmental heterogeneity between adjacent planning units, increased the internal EH of conservation networks, but only by 2% more. Conserving the representation of the geophysical diversity (i.e. land facets) increased over 25% internal EH in conservation networks, but the level of fragmentation increased, even in some cases over 50%. These results were expected, because conservation networks harboring more environmental heterogeneity would be more spread out across the country. Synergies between biodiversity conservation and carbon storage priorities were very low, but they improved when including the Conservation Areas into carbon-storage conservation assessment. The selection of AGB dataset affected the location of carbon priority areas, particularly in the North-Central and North-West part of the country, but comparing networks where Conservation Areas were included these differences were reduced, and revealed locations that could be considered priorities for carbon storage in the distribution range of Dry Tropical Forests. Our study, highlights the importance of exploring the effects of integrating environmental-heterogeneity-based approaches for the planning region of interest before incorporating them in formal conservation assessments, because factors related to the characteristic of the region and input data might affect the results. Synergies between carbon and biodiversity priorities could be improved by adding meaningful stratification for carbon in conservation assessments, in order to spread carbon-storage priority areas across the country. The extent of gains for co-benefits between carbon-related ES and biodiversity conservation will depend in part on how priority areas are selected for implementing strategies, such as PES and REDD, and will determine the location and amount of tropical forest to be conserved.

INTRODUCTION

Conservation of tropical forests is a global priority. Their conservation importance lies not only on their high value for harboring biodiversity, but also on the ecosystem services they provide (Harvey et al., 2010; Venter et al., 2009). Because financial resources for conservation are scarce, analyses of spatial synergies and trade-offs among biodiversity conservation and ecosystem services priorities have emerged throughout the world. Optimizing methodologies for preserving locations that can help achieve multiple conservation objectives is thus a high priority (Anderson et al., 2009; Chan et al., 2006; Egoh et al., 2011; Locatelli et al., 2013).

Recognition that climate change impacts must be incorporated into international and national conservation agendas is maturing. In particular, it is of growing interest to identify opportunities for spatial synergies between carbon-related ecosystem services and biodiversity conservation (Venter et al., 2009). Just as carbon storage affects climate change, climate change also will impact the current distribution of ecological communities and species diversity patterns. The unpredictability of these impacts makes crucial the identification of conservation networks that are robust to uncertainties (Game et al., 2011; Groves et al., 2012). Climate adaptation approaches have been proposed that can be incorporated as complementary strategies into conservation assessment (Groves et al., 2012). However, few examples of the integration of such approaches in conservation assessment exist (e.g. Fung et al., 2015; Game et al., 2011; and see Anderson et al., 2015), and to our knowledge, their effect on patterns of spatial synergies between ecosystem services has not yet been explored.

Here, we analyzed the spatial synergies between biodiversity conservation and carbon storage priorities when incorporating in conservation planning assessment two climate adaptation approaches based on environmental heterogeneity. Specifically, we explore ways to conserve geophysical diversity and promote cross-environmental connectivity. Conserving the geophysical diversity relates to the protection of environmental settings describing geologic, geomorphologic, and soil attributes (Anderson et al., 2015). Geophysical diversity is considered a significant driver of biodiversity patterns and, hence, the arenas of biological activity, such as evolution and range shifts (Anderson and Ferree, 2010; Beier and Brost, 2010; Hunter et al., 1988). The geophysical diversity of a region can be represented by 'land facets', which generally are defined as "recurring landscape units with homogeneous topographic and soil attributes" (Beier and Brost, 2010). Promoting cross-environmental connectivity (Game et al., 2011) aims to favor the selection of adjoining sites that differed in their environmental characteristics. This approach is based on the concept of structural connectivity, relating to the physical characteristics of the landscape between resources patches, which contributes significantly to functional connectivity (i.e. the actual degree of movement of individuals between resources patches) by determining the movement potential through a landscape (Hodgson et al., 2011).

Because the inclusion of conserving geophysical diversity and promoting cross-environmental connectivity approaches into conservation assessments will influence which locations are selected as priorities, they may also affect the spatial relationship between biodiversity and carbon storage. In addition, simultaneously considering both carbon and biodiversity when setting conservation priorities could influence the amount of internal environmental heterogeneity captured in the selected conservation networks and increase the synergies and efficiency of multiple conservation efforts.

Biodiversity Conservation Planning Approaches

Enhancing the environmental heterogeneity of conservation networks is typically well suited for achieving biodiversity goals. This approach is based on ecological principles that show that increasing available niche spaces as well as the opportunities for organisms to move through a wide range of environmental conditions are favorable for many organisms (Groves et al., 2012). These approaches rely on the hypothesis that habitat heterogeneity largely underpins species diversity patterns (Anderson and Ferree, 2010). Environmental heterogeneity can be considered in maintaining or restoring structural connectivity between habitats to favor the movement of individuals along environmental gradients, such as connectivity between cooler and warmer and between drier and moister habitats, for allowing range shifts under changing climate conditions (Hodgson et al., 2009) and increasing the resilience of populations under pressure due to threats caused by or intensified by climate change (Doerr et al., 2011). One additional advantage of these approaches is that they typically make use of freely available and (in many cases) systematically validated environmental data sets, of particular importance in developing countries with high biodiversity yet scarce biological data.

The spatial environmental heterogeneity of a region can be captured and integrated in conservation assessment by considering its two components: composition and configuration. The first relates to the diversity of environmental attributes in a region, while the second relates to the spatial arrangement of those attributes (Dufour et al., 2006; Possingham et al., in Lovett et al., 2005).

The approach of conserving geophysical diversity is based on protecting regional compositional heterogeneity, which can be characterized by recurring landscape units with homogeneous topographic, geological and/or soil attributes, called land facets or units (Beier and Brost, 2010; Hunter et al., 1988). Land facets are meant to capture the representation of underlying geophysical conditions, which are considered to drive to a greater extent the distribution of terrestrial ecological communities and species diversity in the long term than climate (Anderson and Ferree, 2010; Beier and Brost, 2010; Hunter et al., 1988). By preserving the ecological and evolutionary settings, it may be possible to increase the likelihood of conserving biodiversity in both present and future climate (Anderson and Ferree, 2010). In this study, we defined land facets by combining surface lithology classes, elevation, and the division between de Pacific and Atlantic slopes. In Costa Rica, surface lithology resulted to be a good predictor of coarse-vegetation distribution patterns (Fung et al., 2015), and elevation has been associated with animal and vegetation distribution and turnover (Chain-Guadarrama et al., 2012; García-López et al., 2012; Lieberman et al., 1996).

Promoting cross-environmental connectivity relates to configurational heterogeneity. Here, we followed the methodology proposed by Game et al., (2011), which is intended to favor the selection of adjoining locations that differ in their environmental characteristics (e.g. topography, climate). In conservation assessment, this approach can be incorporated by considering the spatial relationship between adjacent locations available for conservation (Possingham et al., in Lovett et al., 2005).

Carbon Storage

To help quantify carbon storage as ecosystem service, considerable recent effort has produced freely available global wall-to-wall aboveground biomass datasets for the pan-tropics in a spatial resolution relevant for national analysis (Avitabile et al., 2016; Baccini et al., 2012; Saatchi et al., 2011). Saatchi et al. (2011) and Baccini et al. (2012) published remote sensing derived databases at high resolution, 1 km and 500 m, respectively. However, disagreements between these two aboveground biomass maps and field data estimates and spatial patterns have been reported (e.g. in Amazonia: (Mitchard et al., 2014)). In response, Avitabile et al., (2016) published a fused map at 1 km resolution, that combined these two carbon maps with national reference maps and additional field datasets. While Avitabile et al. (2016) reported the lowest error estimate of the three efforts to date, there are nonetheless considerable differences in spatial patterns between these databases. As a result, it is currently challenging for practitioners and countries to compare the outcomes (i.e. selected conservation priority areas) derived from previous spatial analyses using either of the Baccini et al. (2012) or Saatchi et al. (2011) datasets with analyses using the more recent fused map from Avitabile et al. (2016).

Here, we explored synergies between conservation planning outcomes while prioritizing retention of both carbon and biodiversity in Costa Rica. We used the conservation design software MARXAN (Ball and Possingham, 2000) to investigate the effects of incorporating the above mentioned climate adaptation approaches on the spatial synergies between biodiversity conservation and carbon storage, as well as on the amount of internal environmental heterogeneity selected in the resultant conservation network. In addition, we investigated differences in spatial patterns among the three maps of aboveground biomass, and how the selection of a particular input map will affect the location of selected priority areas. We hypothesized that: (1) the inclusion of environmental-heterogeneity-based approaches will result in tradeoffs with the level of aggregation of the conservation networks (i.e. more fragmented solutions) as the solution needs to be more spread out across the planning region; (2) there will be modest levels of spatial synergy between biodiversity and carbon storage priority areas due to differences in the way these conservation features are targeted, but that synergies can be improved by stratifying the selection of priority areas for carbon storage; and finally, (3) summarizing the carbon storage data into planning units (i.e. units of analysis) will reduce spatial pattern differences between databases, unless markedly spatial pattern differences existed.

METHODS

Study Area

We focused our work on the Central American country of Costa Rica (Fig. 2.1). At around 51 100 Km^2 in size, Costa Rica spans the Mesoamerican isthmus between the Pacific and Atlantic Oceans and therefore is both a biodiversity hotspot and an important corridor for species dispersal and movement (Myers et al., 2000). Currently, 52% of the country is covered by forest (Programa REDD/CCAD-GIZ-SINAC, 2015). The high diversity is related to the varied topography, variety of climates, and different soil conditions originated mainly from volcanic mountain ranges characteristic of this region, as well as for species dispersion processes resulting from the regional bridge effect between North and South America (Castro et al., 2003; SINAC-MINAE, 2007).

The country is divided into 11 Conservation Areas that together constitute the National System of Conservation Areas (SINAC) (Coco Island Marine Conservation Area was excluded from this study). In Costa Rica, SINAC is the national authority in matters of policy, conservation, and management of natural resources, and the Conservation Areas are the administrative units. Approximately 26% of Costa Rica continental territory is under some category of Protected Area (SINAC 2007). Moreover, in 1996 a blanket ban to forest conversion was put in place by the Forest Law 7575 (Art. 19). This law also established a pioneering nationwide program of payments for environmental services (PES) that provides options for conservation action on privately owned lands (Pagiola, 2008).

In this study, we subdivided the country into hexagonal planning units of 500 ha using the Repeating Shape extension in ArcGIS (ESRI, Redlands, CA; Jenness 2012). The planning units were clipped to the boundaries of Costa Rica as well as with a map of protected areas represented Biological Reserves and National Parks. The resultant dataset was a map of planning units that were mostly equally sized hexagons, with some irregular, truncated hexagons neighboring the protected areas and national borders.

Generalities of Conservation Assessment and MARXAN

A systematic conservation planning (SCP) framework is commonly used for designing on- and off- reserve systems and ecological networks at different spatial scales (Carwardine et al., 2009; Kukkala and Moilanen, 2013; Margules and Pressey, 2000; Nhancale and Smith, 2011). Within an SCP framework, conservation assessment is the process of identifying priority areas (i.e. area selection) for conservation action (Egoh et al., 2007). This process involves several steps, generally: (1) selecting and mapping *conservation features* (in the case of this study, biodiversity and carbon storage); (2) setting *conservation targets* for the conservation features (i.e. a minimum amount or proportion of the feature to be captured in the network); (3) sub-dividing the planning region into spatial units of analysis, termed *planning units*; (4) calculating the *amount* of each conservation feature within each planning unit; (5) assigning a *cost* (or suitability value) to each planning unit based generally on constraints or opportunities for conservation relevant to the planning region (e.g. ecological condition, opportunity cost of the land, amount of area); (6) evaluating the *contribution of existing protected areas* to achieving conservation targets; and (7) using a computer software for selecting a set of planning units (i.e. *conservation network*) that meet targets at minimal cost, which defines the level of *network efficiency* (Ardron et al., 2010; Ball et al., 2009; Chan et al., 2006; Margules and Pressey, 2000; Nhancale and Smith, 2011). In Fig. 2.2 we presented the steps that were followed for this study.

We used the software MARXAN (v1.8.2, (Ball and Possingham, 2000)) to develop the conservation networks. Each assessment was run with simulated annealing followed by iterative improvement (1000 repetitions, 10,000,000 iterations). In additional to the steps outlined above, when using MARXAN, the spatial relationships between planning units can be integrated into the analysis. These relationships typically quantify the geographic distance between adjacent planning units (i.e. shared physical boundaries), but they can also represent other types of measures expressing how favorable the connections are between two planning units (i.e. connectivity) that may be or not be adjacent to each other (Beger et al., 2010a; Game et al., 2011).

MARXAN outcomes used in this study included: (a) the ‘best solution’, which represented the network solution that met conservation targets with the lowest score (i.e. lowest summed penalty); (b) the ‘summed-solution’, which comprises the selection frequency of each planning unit accordingly with the number of run repetitions; and (c) the ‘summary information’, which contains information of each run repetition, such as the score, total cost, and penalties (Ball and Possingham, 2000). For description of terms used along this document see Table 2.1.

Data and Pre-processing

Cross-environmental connectivity. – Data on eleven different climatic and topographical variables were acquired through freely available global databases (Table 2.2) and used to characterize the study domain. Maps were rescaled to 30 m gridcell resolution, which was the smallest size in the original data, and clipped to be consistent across all variables (i.e. number of rows and columns).

Land facets. – 53 land facets were derived by performing an overlap of three categorical maps representing: (1) surface lithology, with nine classes (Costa Rica Geology Map, USGS et al., 1987); (2) elevation, with four classes (based on ASTER-GDEM2 validation team, 2011); and (3) the country division between Pacific and Atlantic slopes (Atlas of Costa Rica, 2014). We overlaid the total area of each land facet with the 2012 forest map (Programa REDD/CCAD-GIZ-SINAC, 2015), and summarized the land facet forest cover (in ha) contained within each planning unit.

Floristic regions. – We used a map of phytogeographic units (for now on referred to as floristic regions) that classified 33 terrestrial ecosystems for Costa Rica. These areas share particular floristic patterns, which were defined by the combination of field data, previous vegetation maps, and expert knowledge. Abiotic factors (i.e. patterns of precipitation, temperature variation, dry season length, topographic variation, altitudinal range, and edaphic factors) were also used in the delineation of these patterns. These floristic regions were used as the coarse-filter surrogate of biodiversity in the last national gap analysis in Costa Rica, known as GRUAS II (SINAC-MINAE, 2007). Of these 33 floristic regions, two of them belong to Coco Island; hence, 31 continental floristic regions are used in this analysis. We overlaid the total area for each floristic region with the 2012 forest map, and then we summarized the amount of floristic region forest cover (in ha) contained within each planning unit.

Aboveground biomass maps. – Three global, wall-to-wall aboveground biomass were used in the analysis for comparative purposes. Two of them were remote-sensing derived spatial datasets, Saatchi et al., (2011), at 1 km pixel size (subsequently termed RS1), and Baccini et al., (2012), at 500 m pixel size (subsequently termed RS2). The third map was published by Avitabile et al., (2016), at 1 km resolution. They fused the RS1 and RS2 maps with locally calibrated high-resolution maps and an independent field dataset to produce an integrated pan-tropical biomass map, subsequently termed the ‘fused map’ (see reference sources for details of the methods). All maps were rescaled to 30 m gridcell resolution and clipped to have the same extension (i.e. number of rows and columns) in order to match other maps used in this study. Then, following the procedure of Mitchard et al. (2014), carbon stock was calculated within each planning unit by multiplying the mean forest biomass within a planning unit by its forest area (in ha), and then converting biomass to carbon by multiplying the result by 0.5, assuming dry biomass is 50% carbon. For analyzing synergies with biodiversity, we used only the fused map (Avitabile et al., 2016).

Planning unit cost. – All planning units were set to have the same cost, a value of 1, hence the total cost of the conservation network will be expressed as the total number of planning units selected in the network.

Feature targets. – Targets for floristic regions and land facets were defined based on the Convention of Biological Diversity (CDB, 2010) agreement, which stated the protection of at least 17% of the original extent of each terrestrial ecosystem in the country. We calculated the contribution of Biological Reserves and National Parks towards meeting targets for each conservation feature. We then calculated the additional forest area needed for each floristic region and land facet to complete the CBD target. Biological Reserves and National Parks were excluded from the planning region, but other categories of protected areas, such as Forest Reserves and Wildlife Refuges, were not excluded because most of their lands are privately owned and, thus, they are subject to off-reserve conservation policies in Costa Rica, such as PES.

The carbon storage target was set to 25% of the total forest carbon stock of the country. In order to select the carbon target, we run assessments targeting simultaneously floristic regions, land facets, and carbon storage, different target values were tested, until having a network solution in which most of the targets were met without overrepresentation (i.e. exceeding target). Conservation Areas were included in one carbon storage scenario as a way of spreading out across the country the resulting conservation network. For each Conservation Area we set a target of 15% of forest cover outside Biological Reserves and National Parks. For calibrating the Conservation Area targets, we run assessments targeting both carbon storage and Conservation

Areas, testing different target values, following the same calibration approach for carbon target explained above.

Analyses

Spatial Pattern Comparison of Aboveground Biomass Maps.

We used correlation analysis (Pearson's *r*) to compare the fused map with both RS1 map and RS2 map at both the national scale and the scale of conservation areas. Then, conservation assessments were run with MARXAN and the solutions were compared using proportional overlap analysis between best networks and correlation analysis between planning unit irreplaceability values based on the selection frequency of planning units (methods described in following sections).

Cross-Environmental Connectivity.

Following Game et al., (2011), the mean value of a planning unit for each of the 11 environmental attributes (Table 2.2) were used to calculate the Euclidean distance in environmental space between all adjacent planning units. The environmental distance was used, as the boundary length variable in MARXAN, which represents a measure of the spatial relationship between two planning units. Typically, as boundary length is used the shared physical boundary between adjacent planning units; for now on, we will refer to it as the geographic distance. The boundary length variable is considered as the cost or penalty that must be paid if a pair of adjacent planning units are not considered in the final solution. Thus, a high boundary length value increases the probability that if one of the planning unit is selected the other will be selected too (Game and Grantham, 2008). Both the geographic and environmental distances were rescaled to a range of values from 1 to 100 and then a boundary file containing each of the distances were created. The boundary length along with the Boundary Length Modifier (BLM) parameter are used to control de level of compactness of a solution, higher BLM values reduced the overall boundary length and, thus, the level of fragmentation (Game and Grantham, 2008).

Because any change to the boundary file will change the influence of the boundary length on the MARXAN objective function (Game et al., 2011), the BLM value had to be calibrated in order to keep relatively constant the boundary penalty added to the objective function and make the outcomes comparable. The Zonae Cogito decision support software (Segan et al., 2011) was used to run MARXAN, testing 20 BLM values (with 20 repeated runs) for each assessment and, then, the boundary penalties between solutions were compared using analysis of variance and Tukey test. When necessary, the BLM were calibrated manually.

Conservation Assessments and Outcome Comparisons: Environmental Heterogeneity and Spatial Synergies.

To explore the implications of including carbon storage as well as biodiversity conservation and of integrating the two climate adaptation approaches into conservation assessments, three groups of comparisons were made: (a) between assessments using geographic distance and environmental distance, this type of comparison allowed to analyze changes on internal environmental heterogeneity, efficiency, and spatial patterns of conservation networks when incorporating the cross-environmental connectivity; (b) between assessments targeting either only floristic regions or land facets as conservation feature, allowing analysis of how specific land facets influence conservation network attributes; and finally, (c) between assessments targeting either only carbon storage or biodiversity (i.e. including both floristic regions and land facets), as well as with assessments targeting “All” (except of Conservation Areas) in order to analyze spatial synergies and trade-offs between conservation networks.

First, we calibrated the BLM values (following the method described above). Once the BLM values were selected, conservation assessments were run with 1000 repetitions. Total internal environmental heterogeneity was calculated as the sum of all environmental distances between planning units comprising the best solution (i.e. the network with the lowest score from a number of solutions), and then the average proportional increase of internal environmental heterogeneity was calculated for the best solutions. The efficiency was compared using the total cost incurred in best solutions for meeting targets, and the ratio between total forest area and total overall area in the network. The latter helped to explore the efficiency of networks in terms of area required for achieving targets. The level of fragmentation of a conservation network was interpreted with the overall external boundary length (i.e. perimeter), increases in values revealed more fragmentation.

The spatial congruency between two networks was measured in two ways: proportional overlap analysis of best solutions and with irreplaceability similarity (i.e. correlation of planning unit irreplaceability values) (Chan et al., 2006; Egoh et al., 2011). Proportional overlap analysis was measured as the number of planning units shared between two networks expressed as a percentage of the one with the smallest number. Irreplaceability similarity was measured with correlation analysis (Pearson’s *r*) between planning unit irreplaceability values. The irreplaceability value of a planning unit is a way to measure the importance of a planning unit in contributing to the achievement of feature targets (Carwardine et al., 2006) and it was measured as the number of solutions containing the planning unit divided by the total number of solutions (1000) in a scenario.

Statistical Procedures

Data preparation and Euclidean distance between environmental variables, as well as analysis of variance (ANOVA), Tukey test, and Pearson's correlation were performed using R statistical software 3.1.4 (The R Development Core Team, 2014) and InfoStat software (Di Rienzo et al., 2014).

RESULTS

Spatial Pattern Comparisons of Aboveground Biomass Maps

Major differences in spatial patterns were found between the fused map and RS1. Although the correlations between the two maps were positive in all of the conservation areas, in six of the conservation areas the fused map and RS1 showed Pearson's correlation values below $r=0.50$ (Table 2.3). In four conservation areas the correlations between the maps were very low ($r \leq 0.35$). Of these, two corresponded to the biggest forest mass of Costa Rica, a great part of this area is protected within a complex of National Parks, located in the South-center and South-eastern regions of the country (ACLAP and ACLAC). The other two in the North-eastern and North-western regions of the country (ACTO and ACT, respectively). The two latter regions also showed the lowest correlations between the fused map and RS2. Nonetheless, in general, the RS2 showed strong positive spatial correlations with fused map.

For the three maps, an important part of the forest aboveground biomass was comprised in protected areas (i.e. Biological Reserves and National Parks) with 32% for the fused map, 29%

for RS2, and 25% for RS1. Excluding protected areas did not change the results on the spatial correlation between the fused map with RS1 and RS2 maps at the national scale (0.56 and 0.85, respectively).

When solutions were compared between assessments run using either the fused map or RS1, as underlying data set to calculate carbon stock within planning units, the correlation between selection frequencies of planning units (i.e. irreplaceability similarity), was of 0.70. Also, there was a 69% of proportional overlap between the best network solutions. While differences in spatial patterns between networks were reduced as a secondary effect of summarizing the data into the planning units, there were still important spatial differences between using the fused map or RS1 that can be observed in Fig. 2.3 (A), particularly at the North-Center area of the country. In the other hand, adding Conservation Areas into carbon storage assessments improved the irreplaceability similarity between solutions, with Pearson's r = 0.83, but the proportional overlap between best solutions remained similar (68%). Nonetheless, when visualizing the maps of best solutions in Fig. 2.3 (B), we noticed better spatial agreement at the North-Center part of the country. But also, in both best solutions there were locations selected in the Tempisque Conservation Area, which did not appeared before in any of the best solutions from single carbon scenarios.

Using Conservation Areas as stratification units had two advantages. First, they were useful in understanding which areas harbored major differences in spatial pattern among the three AGB databases. Second, they helped to distribute the carbon priority areas across the country. Using the Conservation Areas resulted in an increase in the total number of planning units by 21.4% as well as in the external boundary length, total area, and total forest area (Table 2.4).

Increasing the Internal Environmental Heterogeneity and Other Conservation Network Attributes

In general, replacing the typical geographic distance with the environmental distance showed an improvement in the internal environmental heterogeneity of conservation networks, although such proportional increases were low (i.e. about 2%, Fig. 2.4, a). This result was regardless of the suite of conservation features targeted. On the other hand, conservation networks that targeted only the land facets showed about 6% more internal environmental heterogeneity than conservation networks that targeted only the floristic regions. When looking at the effect of targeting jointly floristic regions and land facets, compared with targeting only floristic regions, it was possible to increase over 26% the internal environmental heterogeneity of the conservation network. Targeting both biodiversity conservation (jointly floristic regions and land facets) and carbon storage produced an increase in internal environmental heterogeneity over 35% (Fig. 2.4, c).

Such increases in network environmental heterogeneity, mentioned above, were accompanied by increases in total external boundary length, total area, and total forest area (Fig. 2.4, c). Comparing between biodiversity conservation networks (networks 3 and 4, Fig. 2.4, b) with those including both biodiversity and carbon storage (networks 5 and 6, Fig. 2.4, b), the result was that adding carbon storage increased the network environmental heterogeneity and total forest area (8% in both attributes), but increases in total external boundary length and total area were very low (3% in both attributes). Furthermore, there was a slight increase in network efficiency in terms of reducing areas not required for achieving targets (Table 2.4, ratio between forest area and total area). This results were consistent using either geographic or environmental distance as a measure of connectivity between planning units. Conservation networks (i.e. best solutions) from the eight conservation assessments are presented in Fig. 2.5.

Spatial Synergies

Looking at the spatial congruency between carbon storage and biodiversity, our results revealed spatial tradeoffs (Table 2.5 and 2.5, Fig. 2.6). There was no spatial relationship (Pearson's r = 0) between the planning selection frequency patterns of the single carbon network with none of the three networks that included biodiversity features (FR, FRLF or All). In the same fashion, the overlap between the best network solutions were low, even when targeting carbon jointly with biodiversity features the overlap was of 24% (Carbon versus All). However, when we included the Conservation Areas as features within carbon assessment (Carbon-CA), the spatial congruency increased. The correlation between the selection frequency patterns of planning units showed a low positive relationship, with Pearson' r value = 0.25, and the overlap between the best networks went up to 39%. Our results showed that the spatial congruency between FR and Carbon-CA solutions were higher than FRLF and Carbon-CA. This result is consistent when comparing Carbon-CA with LF, irreplaceability similarity patterns presented a very low positive correlation (Pearson's r = 0.16) and network overlap of 28% (results not presented).

However, we did not include Biological Reserves and National Parks in the planning region, and when looking at what they enclose, we found that 7 floristic regions and 16 land facets were

100% represented within them, and that approximately 32% of carbon stock was protected within the protected areas.

DISCUSSION

We compared the spatial patterns of the AGB fused map, presented by Avitabile et al., (2016), with the AGB maps from Saatchi et al., (2011) (RS1) and Baccini et al., (2012) (RS2). For Costa Rica, important spatial pattern differences were found between the fused map and RS1. These spatial differences were reduced somewhat when summarizing the data within planning units. But still, the selection of the AGB spatial dataset, for the quantification of carbon stock within each planning unit, affected the selection of priority areas.

For countries depending on these type of data sources, these spatial discrepancies would affect the identification of priority areas for protecting carbon stock as well as the identification of spatial synergies with biodiversity and other ecosystem services. For instance, Mitchard et al., (2014) reported striking differences in spatial patterns of AGB distribution between RS1 and RS2 and field data across the Amazonia. The fused map presented by Avitabile et al., (2016) addressed this issue by combining RS1 and RS2 datasets and developing an integrated map, with lower error and biased estimates. But most importantly, their fusion method, largely driven by local reference dataset, could be applied at any scale, representing an opportunity for future map improvement and studies.

In our study, adding the Conservation Areas into carbon storage assessment increased the irreplaceability similarity between conservation networks that used the fused map and RS1 by spreading across the country the selection of areas. In this way, it was possible to identify areas of spatial agreement between the two networks in the North-Central and North-West part of the country. Particularly, in the North-West, both networks identified new priority areas for carbon storage in the Nicoya Peninsula, which belong to the Tempisque Conservation Area (ACT, by its acronym in Spanish).

The North-West part of Costa Rica corresponds to the ecological range of the seasonally dry tropical forest, which is one of the most threatened tropical ecosystems in the world (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010; Quesada et al., 2009). Particularly in Mesoamerica, dry tropical forest is highly fragmented and under-protected, and at high risk of severe climate change (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). Defining how to target carbon storage in national assessments will have implications on how to link carbon-related conservation strategies (e.g. PES, REDD) with biodiversity conservation and find spatial synergies between them. In other words, the extent of gains for tropical forest and biodiversity conservation will depend on the design and implementation of these strategies and will determine where and how much tropical forest is conserved (Harvey et al., 2010).

We added the Conservation Areas in carbon storage conservation assessment as features, for which targets were assigned, in order to stratify and spread out across the country the selection of sites. The Conservation Areas are the administrative units of the National System of Conservation Areas in Costa Rica, the national authority in conservation matters. However, in some instances, other stratification units with ecological meaning might be more appropriate for climate adaptation purposes. Chan et al., (2006) also introduced stratification units into ecosystem services conservation assessments, but not for the specific case of carbon storage, in order to capture ecosystem services across their range of environmental variation and provide sufficient replication for persistence in the face of environmental change. In their case, they used different strata accordingly with the nature of the ES of interest. For instance, for biodiversity, water provision, and forage production, they used the same stratification units based on coarse patterns of vegetation, climate, and physiography. In the other hand, for recreation they used five areas around major urban centers.

Integrating climate adaptation approaches based on environmental heterogeneity into biodiversity assessments helped to identify conservation networks that captured more internal environmental heterogeneity. But in the case of promoting cross-environmental connectivity, the results were not as expected. Our results were modest, with barely 2% of increase in network internal environmental heterogeneity. Game et al., (2011) obtained an increase of over 40% in Papua New Guinea. This result is an indication that the level of success of integrating these approaches will depend on the environmental characteristics of the planning region, its extent, and resolution of the data. Costa Rica territory is ten times smaller than Papua New Guinea, and using the same resolution of underlying climate data (1 km), it would not be possible to capture similar level of heterogeneity of coarse patterns of climate conditions. Furthermore, in Costa Rica, changes in topographic conditions occur at very short distances, due mainly to rapid changes in elevation, which are related to the volcanic mountain ranges characteristics of the country. Hence, similar levels of topographic-related environmental heterogeneity would be captured by both geographic and environmental distances, because the boundary relationship used was between adjacent planning units.

For Costa Rica, improving the possibilities of capturing more environmental heterogeneity with cross-environmental connectivity approach could be done by either or both getting data at finer resolution, thus subtle changes in environmental conditions could be detected, or/and integrating other patterns of ecological connectivity. For instance, incorporating asymmetric connectivity, which recognized that the degree of connectivity is not equal in all directions

(Beger et al., 2010b) and, furthermore, connectivity measure could express not only the relationship between adjacent planning units, but also between pairs of distant sites with a functional connectivity (e.g. migration routes, dispersal, seasonal or daily movements). Other types of connectivity through particular habitat conditions could be also considered (e.g. across-realms, Beger et al., 2010a).

When looking at the effect of integrating the geophysical diversity, by adding as conservation features the land facets, showed that was possible to increase even more the internal environmental heterogeneity of conservation networks. The synergetic effect of targeting both floristic regions and land facets resulted in networks with over more 25% of internal environmental heterogeneity, because solutions were more spread across the full range of environmental gradients.

Resultant conservation networks from assessments integrating land facets and cross-environmental heterogeneity were more fragmented (i.e. larger external boundary length). Although, in general, it is desirable to reduce the level of fragmentation of conservation networks, integrating these approaches faced practitioners with trade-offs between capturing more environmental heterogeneity and the level of compactness of the conservation network. Conservation networks of highly connected sites across a wide range of environmental gradients will be more robust in the face of climate change (Game et al., 2011) and the unpredictability of the response of species populations, communities, and ecological processes to altered, disappearing and/or novel climate conditions (see Williams et al., 2007). Therefore, it would be necessary to look for a balance between these two conservation design objectives. We considered that it could be achieved by integrating jointly the two approaches of conserving the geophysical diversity and promoting cross-environmental connectivity.

When looking at synergies between biodiversity conservation and carbon storage priorities, we did not find a spatial relationship between conservation networks targeting only carbon storage with conservation networks targeting only biodiversity conservation. This results responded to differences in the ways that the two conservation objectives are targeted. For biodiversity, we were looking for the representation of the regional diversity, which spanned the selection of priority areas across the country. In the other hand, for carbon storage the emphasis was on high concentration areas of carbon stock, which produced more compacted conservation networks. However, adding the Conservation Areas, as stratification element for selecting carbon storage priority areas, improved the spatial synergies with biodiversity priorities. In this study, we excluded protected areas corresponding to the categories of Biological Reserves and National Parks from the planning region, which already hold approximately the 32% of the country forest carbon stock, and therefore we did not report on synergies provided by this areas.

Locatelli et al., (2013) analyzed spatial synergies and tradeoffs between ES in Costa Rica, including protected areas. They used RS1 for carbon in vegetation, and produced a map of provision level. They found a positive relationship between carbon and biodiversity (+0.33 Spearman correlation), but they used species richness and endemic species richness as indicator of biodiversity and where focus on high carbon concentration areas at national scale. For instance, we identified locations for protection of carbon storage in the Tempisque

Conservation Area (TCA) and Locatelli et al., (2013) identified this area as a coldspots for carbon storage.

A focus on areas of high carbon concentrations at national scale will tend to captured areas that have similar biodiversity, reducing opportunities for biodiversity conservation gains. Integration of ecosystem services into systematic conservation planning should go beyond to focus only on local objectives (e.g. species richness and high carbon stock) towards a more comprehensive approach for conservation of the regional representation (Faith, 2014) of biotic and abiotic diversity (Bonn and Gaston, 2005). In the face of climate change, changes in precipitation patterns will affect future AGB patterns (Poorter et al., 2015) as well as biodiversity patterns (Williams et al., 2007). Hence, conservation networks robust to these uncertainties are urgently needed, requiring approaches that could be readily implemented, such as the ones presented here.

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Table 2-1: Definition of some terms related to Systematic Conservation Planning and Marxan analysis.

Systematic Conservation Planning (SCP)	A multidisciplinary science; a discipline of decisions supported by spatial analyses; and a stage-wise operational model concerning "the prioritisation of sites for their biodiversity value and the participatory planning and collaborative implementation of strategies, decisions and actions that secure the long-term survival and favorable conservation status of biodiversity in general" (Kukkala et al., 2013; first described by Margules and Pressey, 2000).
Conservation assessment	A quantitative assessment for the identification of spatial priorities for conservation action, i.e., site selection (Egoh et al., 2007; Kukkala et al., 2013).
Conservation feature	A measurable, spatially definable component of biodiversity that is to be conserved within a reserve network (Ardron et al., 2010)
Conservation feature target	The amount of the conservation feature to be included within the reserve network (Ardron et al., 2010)
MARXAN	A software that delivers decision support for reserve system design, aiming to identify a combination of planning units or reserve network that will meet user-defined biodiversity targets for the minimum cost (Game and Gratham, 2008).
Planning Units	The unit of analysis where input data is summarized or compiled, principally the amount of a conservation feature in a planning region. The planning region is subdivided into a number of planning unit polygons, which can be of regular or irregular shape (Nhancale and Smith, 2011).
Cost (of a planning unit)	A measure of the cost (or suitability) of including each planning unit in the reserve system (Game and Gratham, 2008).
Conservation network	Also can be found as reserve system, reserve network, or conservation portfolio. It is a set of sites that collectively contribute to the achievement of conservation objectives.
Best solution	The reserve network with the lowest Marxan objective function value (i.e., the most efficient solution) from a series of Marxan solutions (Ardron et al., 2010)

Species Penalty Factor (SPF)	A multiplier that represents the penalty that must be paid for not meeting a conservation feature target in the current reserve scenario. The higher the value, the greater the relative penalty (Game and Grantham, 2008).
Irreplaceability value	A measure of how important is each planning unit in its contribution for efficiently meeting biodiversity conservation targets. Using MARXAN, the irreplaceability value of a planning unit is measured as the proportion of solutions containing it; how often a planning unit is selected over the total number of solutions per scenario (Ardron et al., 2010; Carwardine et al., 2006).
Boundary length	A variable used in MARXAN that represents a measure of the spatial relationship or connectivity between two planning units, which may or may not be adjacent to each other. Typically, the boundary length is the geographic length of the shared boundary between adjacent planning units, and it is considered as the cost that must be paid if a pair of adjacent planning units are not included together in the reserve network solution. (Game and Grantham, 2008; Possingham et al., in Lovett et al., 2005).
Boundary Length Modifier (BLM)	A multiplier used to determine how much emphasis should be place on minimizing the overall reserve network boundary length (Game and Grantham, 2008).

Table 2-2: Environmental data and sources.

No.	Environmental attributes	Source
	Climate attributes	
1	Precipitation of the coldest quarter	Climate attributes from Hijmans et al., 2005; available on-line htpp://worldclim.org/download. Potential annual evapotranspiration from Trabucco et al., 2009; available on-line http://csi.cgiar.org/Aridity/
2	Precipitation of the warmest quarter	
3	Precipitation seasonality	
4	Potential evapotranspiration	
5	Precipitation/Potential evapotranspiration	
6	Minimum temperature of the coldest month	
7	Temperature annual range	
8	Temperature seasonality	
	Topographic attributes	
9	Elevation	Aster-GDEM2 validation team (2011). Slope tool of spatial analyst ArcMap 10.3 (©2009-2014 ESRI Inc.). CTI ArcGIS tool Evans et al., (2014)
10	Slope in degrees	
11	Compound topographic index (CTI)	

Table 2-3: Correlations (Pearson's r) between forest above-ground biomass maps for each Conservation Area and at the national scale. The "fused" map from Avitabile et al., (2016); "RS1" map from Saatchi et al., (2011); and "RS2" map from Baccini et al., (2012).

	Fused										
	ACTO	ACT	ACOPAC	ACOSA	ACLAP	ACLAC	ACG	ACCVC	ACAHN	ACAT	National
RS1	0.35	0.34	0.42	0.55	0.30	0.34	0.73	0.40	0.53	0.72	0.56
RS2	0.68	0.67	0.85	0.70	0.88	0.73	0.84	0.77	0.80	0.87	0.87

ACTO: Tortuguero Conservation Area; ACT: Tempisque Conservation Area; ACOPAC: Central Pacific Conservation Area; ACOSA: Osa Conservation Area; ACLAP: Pacific La Amistad Conservation Area; Caribbean La Amistad Conservation Area; ACG: Guanacaste Conservation Area; ACCVC: Central Volcanic Conservation Area; ACAHN: Arenal Huetar Norte Conservation Area; ACAT: Arenal Tilaran Conservation Area.

Table 2-4: Summary of main attributes of best network solutions from the eight different conservation assessments run in this study.

No.	Network	Boundary distance	BLM	Average boundary penalty (over 1000 repeated runs)	Boundary penalty of best network solution	Summed EH	Total number of PU	External boundary length (km)	Total area (ha)	Forest area (ha)	Forest area / Total area
1	C stock	Geographic	0.001724				588	1287	283510	267883	0.94
2	C stock CA	Geographic	0.001724				714	1750	348929	319737	0.92
3	FRLF geo.	Geographic	0.001381	496	463	4458513	1588	4983	782755	491497	0.63
4	FRLF env.	Environmental	0.010345	498	463	4554587	1615	5367	797753	496060	0.62
5	All geo.	Geographic	0.001379	498	470	4796372	1635	5046	806318	531388	0.66
6	All env.	Environmental	0.010345	497	463	4901524	1666	5342	822781	533560	0.65
7	**FR**	**Geographic**	**0.002319**	**497**	**446**	**3540175**	**1424**	**3035**	**698024**	**465732**	**0.67**
8	LF	Geographic	0.001724	496	446	3770011	1424	3969	696574	465897	0.67

FR: floristic regions; LF: land facets; C: carbon; geo: geographic distance; env.: environmental distance; bold: conservation network used as reference for comparisons.

Table 2-5: Correlation (Pearson's r) between planning unit irreplaceability values based on their selection frequencies (i.e. Irreplaceability Similarity). Values range from -1 to 1, values towards 1 indicate positive correlation, values close or equal 0 indicate there is no correlation, and values towards -1 indicate negative correlation.

	Carbon	Carbon-CA	FR (geo.)	FRLF (env.)	All (env.)
Carbon	1				
Carbon-CA	0.69	1			
FR	-0.05	0.22	1		
FRLF	-0.05	0.14	0.74	1	
All	0.05	0.25	0.76	0.97	1

Table 2-6: Proportional overlap between conservation networks (i.e. proportion of planning units that are shared between best solutions), values presented in range from 0 to 1.

	Carbon	Carbon-CA	FR (geo.)	FRLF (env.)	All (env.)
Carbon	1				
Carbon-CA	0.60	1			
FR	0.11	0.34	1		
FRLF	0.14	0.28	0.57	1	
All	0.24	0.39	0.62	0.66	1

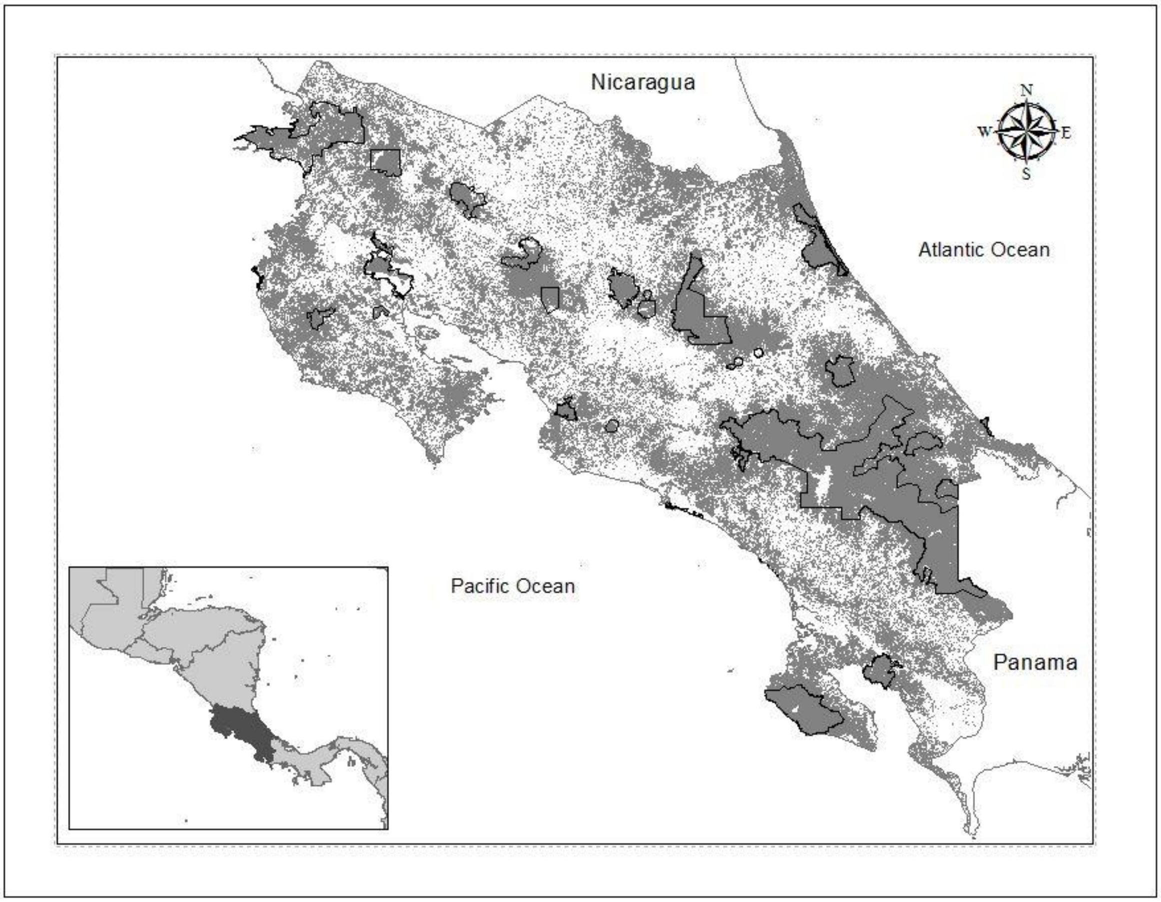

Figure 2-1: Map of the study area, Costa Rica, and its location in Central America (small box at left lower corner). Current forest cover presented in gray and strict protected areas (terrestrial Biological Reserves and National Parks) in black lines.

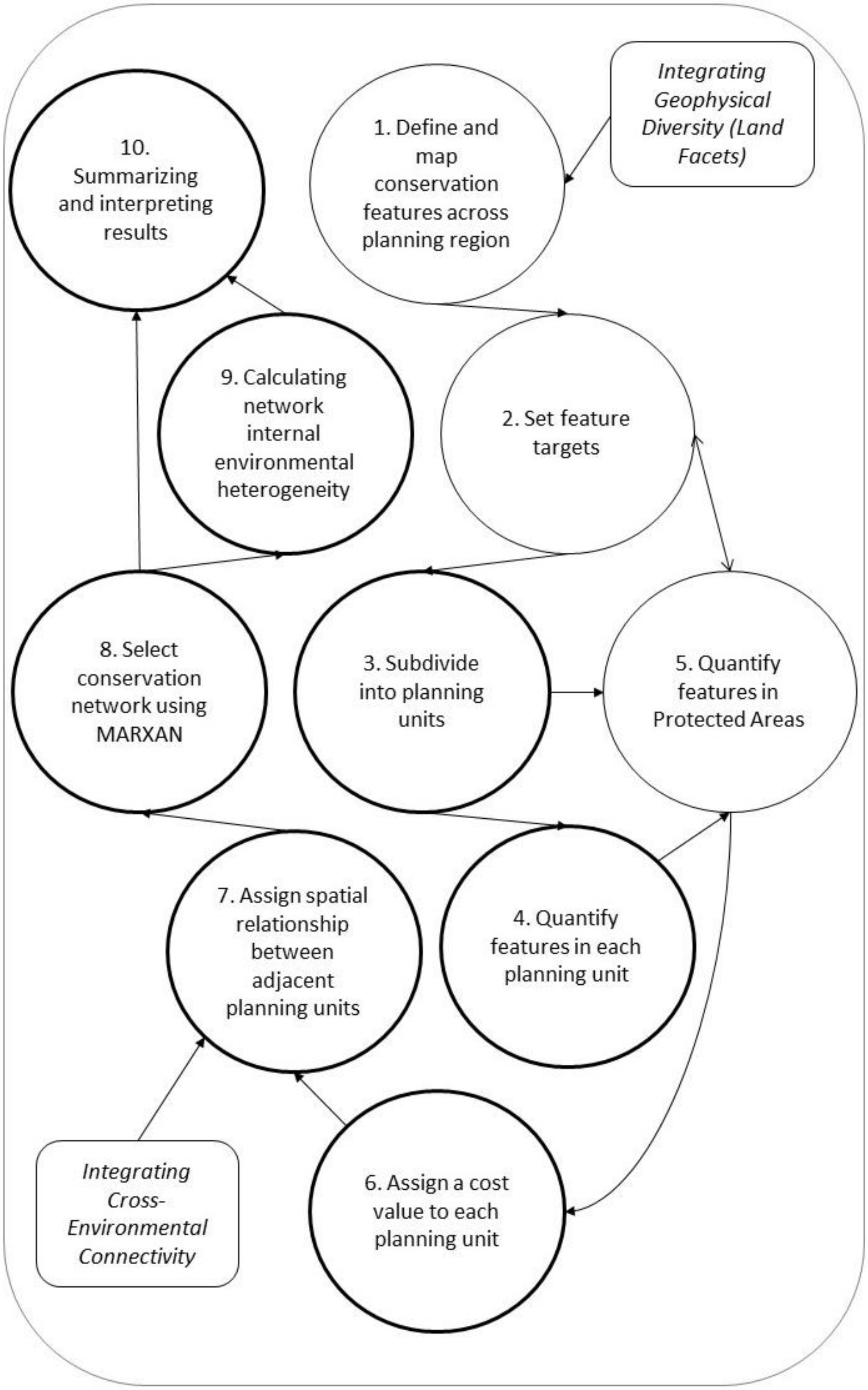

Figure 2-2: Steps followed for conservation assessments in this study based on Systematic Conservation Planning framework. Steps were climate adaptation approaches were integrated are shown (approach name in italic).

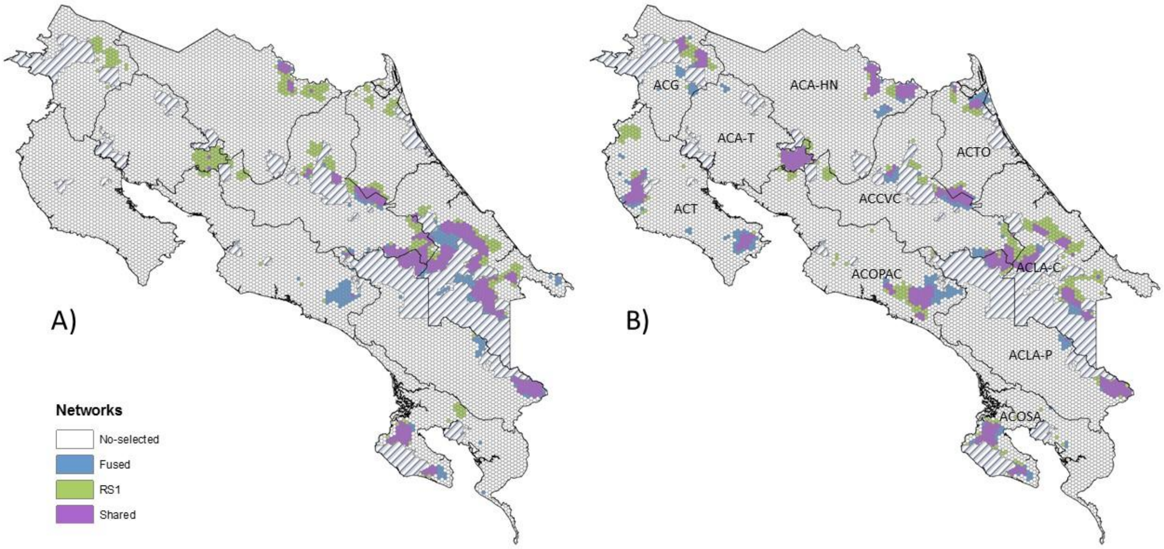

Figure 2-3: Map comparing network solutions from assessment targeting carbon storage using two different datasets: Fused (Avitabile et al., 2016) and RS1 (Saatchi et al., 2011). A) Single carbon networks (without strata), B) Carbon-CA (with strata) networks. Planning units that were selected in both analysis are indicated as shared. Strict protected areas are presented in diagonal gray lines. The names of Conservation Areas are indicated in B.

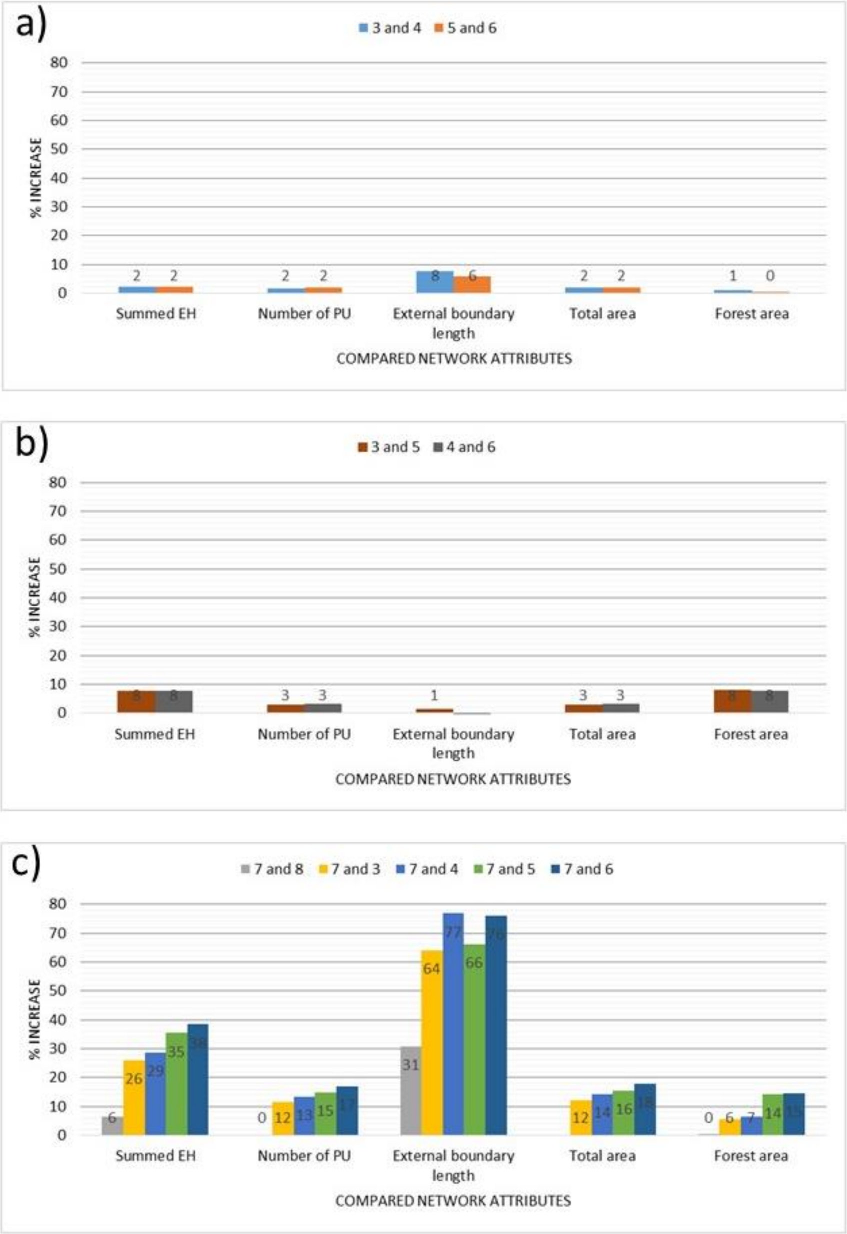

Figure 2-4: Proportional increase in networks attributes between comparing network solutions from: A) Assessments using geographic and environmental distance; B) Assessments targeting only biodiversity (FRLF) and both biodiversity and carbon storage; C) Assessment targeting only FR (geographic distance), used as reference, with different assessments. Compared networks: 7. FR (geo.) and 8. LF (geo.), 3. FRLF geo., 4. FRLF env., 5. All geo., 6. All env.

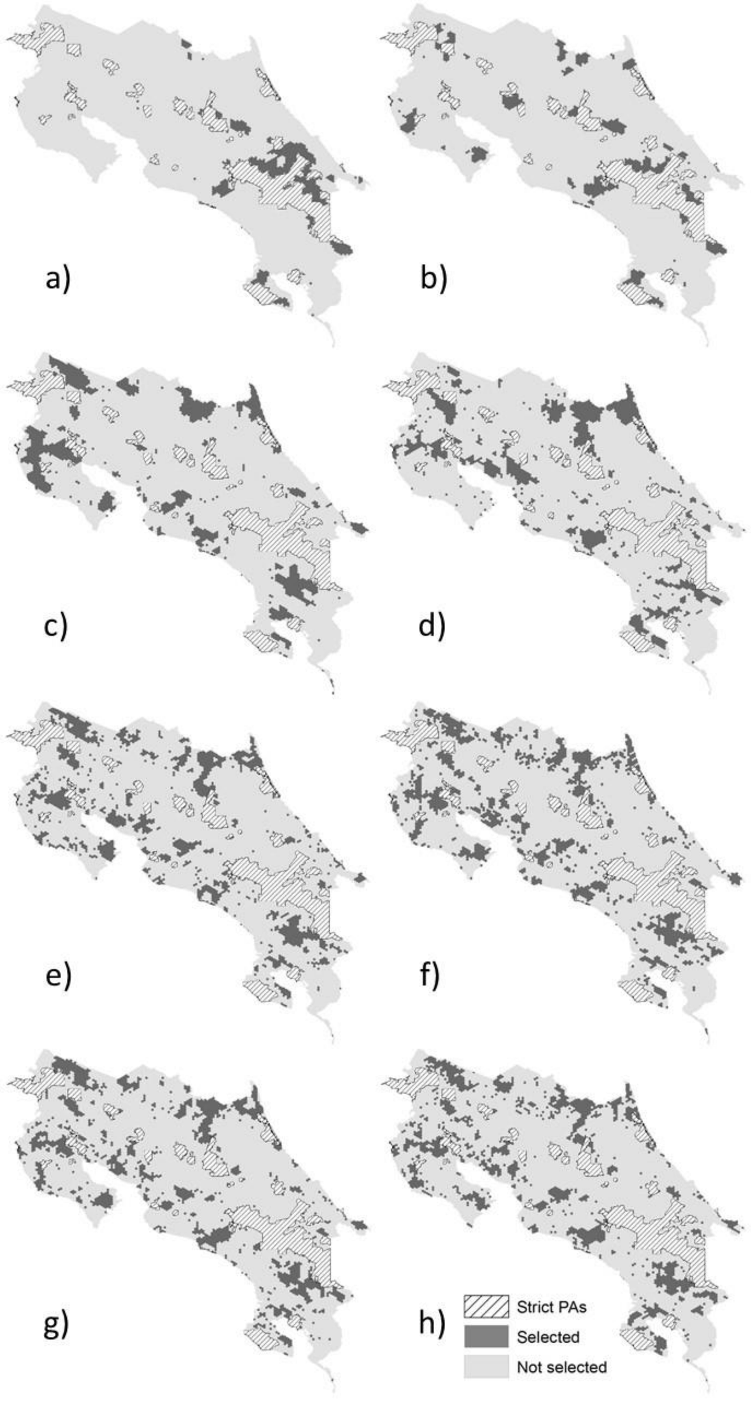

Figure 2-5: Selected locations in best network solutions from the 8 different conservation assessments: a) Only Carbon; b) Carbon and Conservation Areas; c) Only Floristic Regions, using geographic distance; d) Only Land Facets, using geographic distance; e) Floristic Regions and Land Facets, using geographic distance; f) Floristic Region and Land Facets, using environmental distance; g) All, using geographic distance; h) All, using environmental distance. “Strict PAs” refers to Biological Reserves and National Parks

CHAPTER 3. INTEGRATING MULTI-DATE IMAGERY AND TERRAIN VARIABLES FOR DETECTING SECONDARY FOREST TYPES AND DECIDUOUSNESS PATTERNS IN A SEASONALLY DRY TROPICAL LANDSCAPE

ABSTRACT

Tropical dry forests are among the world's most threatened ecosystems, and occur in heterogeneous matrices of land cover types that can be difficult to discriminate using remote sensing imagery. We therefore explored whether using multi-date imagery instead of single-date imagery from Landsat 8 surface reflectance product could improve the accuracy of detecting three different types of tropical dry secondary forests, as well as other land cover types. We tested and compared classification accuracy for each land cover type using two separate classifiers, Random Forest and Support Vector Machine. Our results suggested that: (1) in general, the Random Forest classifier outperformed the Support Vector Machine classifier; and (2) using multi-date spectral data directly in the classification scheme improved the classification accuracy, and in particular reduced the error in discriminating crops and forest plantations. Based on our findings, we suggest further work to: (1) test the use of vegetation indices and other phenological variables that could highlight spectral differences between classes; and (2) based on results presented here, revise land cover classes and improve spectral signatures.

INTRODUCTION

Tropical dry forests are among the most threatened ecosystems worldwide (Janzen, 1988; Miles et al., 2006). They are located in regions that are highly preferred for human settlement and development of economic activities for their fertile soils and climate conditions (Janzen, 1988).

In Mesoamerica, tropical dry forests are highly fragmented, exposed to human disturbance and deforestation, susceptible to fire, and at risk of climate change (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). However, in terms of research and conservation, tropical dry forests have received far less attention than tropical moist forests (Murphy and Lugo, 1986; Sánchez-Azofeifa et al., 2005). Monitoring and managing these biodiverse ecosystems warrant greater attention.

Despite the importance of monitoring and managing these biodiverse ecosystems, remote sensing research of tropical dry forests is challenging due to the interplay between phenology and annual climate patterns. Most dry forest species drop their leaves, totally or partially, during the dry season. Cloud-free remote sensing imagery is acquired during the dry season, but leafless forests are difficult to detect as they are often confounded with pasture lands and other land cover types (Sánchez-azofeifa et al., 2003). Furthermore, most tropical dry forests exist today as fragments, and future conservation will depend largely on secondary forests (Portillo-Quintero and Sánchez-Azofeifa, 2010; Quesada et al., 2009). The occurrence of different stages of tropical dry forest succession brings more complexity to remotely detecting forest patterns, because the rate of senescence, leaf drop, and level of deciduousness can depend on the successional stage, topography, and tree species composition. Due to these factors, differences in phenology could potentially be used to discriminate different types of forests in this ecosystem (Arroyo-Mora et al., 2005a).

In this study, we aimed to detect and map secondary forest types in a seasonally dry tropical landscape in the Nicoya Peninsula of northwest Costa Rica. To our knowledge no previous work has been attempted to map these seasonally dynamic tropical dry forests. We hypothesized that multi-date imagery, rather than a single image date, and terrain variables, would enhance the spectral separability of secondary forest types by exploiting differences in their seasonal patterns of deciduousness.

Vegetation phenology, captured in time-series remote sensing data, offers opportunities for discriminating and mapping vegetation (Simonetti et al., 2014). We used field data from a recent study (Granda Moser et al., 2015) that characterized three types of secondary forests in the study area, based on composition and structure. For classification purposes, we used these data in conjunction with reference data for other land covers and moderate spatial and temporal resolution imagery from Landsat 8 (Roy et al., 2014), specifically surface reflectance products (USGS, 2015a), from which we were able to acquire imagery from the end of the rainy season to nearly the end of the dry season (December 2013 to March 2014). We tested and compared two different classifiers, Random Forest and Support Vector Machine, that have been used for the detection of tropical forests, including TDF (Sesnie et al., 2010, 2008).

METHODS

Study Area

The study region is located in the Nicoya Peninsula, covering approximately 200,000 hectares (Figure 1), comprising the Nicoya, Hojancha, and Nandayure counties. This landscape is dominated by secondary forest, containing a mixture of moist and seasonally dry tropical forests in different successional stages, which is the result of more than 30 years of forest recovery on abandoned pastures (Arroyo-Mora et al., 2005b; Calvo-Alvarado et al., 2009). This region has experienced a distinct land use history defined by: (1) a large deforestation process, mainly occurring between 1960 and 1980, and (2) a reforestation process, beginning in the 1980s (Arroyo-Mora et al., 2005b) and extending to the present. The mean annual temperatures and the mean annual precipitation ranges between 24°C to 27°C and 1500 mm to 4000 mm, respectively. Normally, the dry season extents from the middle of December to April, and the remaining months correspond to the rainy season.

Secondary Forest Types

Three types of secondary forests were described in our study region by Granda Moser et al. (2015) based on the tree composition and structure of 53 plots of 0.12 ha (60 m x 20 m) distributed in 25 farms. These forest types were termed based on their characteristic species as: (1) *Schizolobium parahyba – Miconia argentea*, (2) *Semialarium mexicanum – Lonchocarpus spp.*, and (3) *Guazuma ulmifolia*. These forests were dominated by tree species of low to medium height as adults; except for *S. parahyba*, a canopy forest species, which as adults can reach heights of 30 m or more. Granda Moser et al. (2015) showed that these forests were characterized by tree species adapted to agricultural landscapes and similar to that found by studies in secondary dry forests; while the main life zone in the study region is tropical moist forest.

Remote Sensing Data

For this exploratory study, using moderate spatial resolution (30 meters) of Landsat 8 surface reflectance products (L8-SR products, from now on), we acquired a time series of imagery corresponding from December 2013 to March 2014, with a total of five different image dates. These dates covered the end of the rainy season to the late dry season. During the rainy season it is not possible to acquire cloud-free imagery for this region. For each date, we used 5 out of the 7 spectral bands in L8-SR products. We excluded bands 1 and 2, which corresponded to the blue bands, in order to avoid as much as possible problems related to atmospheric effects. To enhance separability among land covers, particularly among forest types, we included the

Normalized Difference Vegetation Index (NDVI) from USGS (2015b), which combines the red (band 4) and the NIR (band 5) wavelengths.

We included three terrain variables: elevation, slope, and compound topographic index; which have been used in mapping TDF close to our study region (Sesnie et al., 2008). The topographic attributes were extracted using the ASTER-GDEM2 at 30 m resolution (ASTER-GDEM validation team, 2011). Slope was calculated using the slope tool of Spatial Analyst in ArcMap 10.3 (©2009-2014 ESRI Inc.). The compound topographic index was calculated using the ArcGIS tool of Evans et al. (2014).

Data Analysis

Classification accuracy was evaluated for each land cover type from two separate classifiers, Random Forest (RF) and Support Vector Machine (SVM), with and without the use of multi-date imagery for comparison. The two classifiers were run in R statistical software version 3.3.1 (The R Foundation for Statistical Computing, 2016) and associated packages. The R script for the analysis is part of a land cover classification tool that is under development at CATIE, by the statistical group and environmental modeling laboratory. For this analysis, two types of results were explored, the classification maps and error matrices, which were used to evaluate and compare classification accuracy. We also explored the importance of each variable as a predictor for land cover classification from random forest procedure, using the mean decrease Gini (i.e. measure of variable importance based on the Gini impurity index; Breiman and Cutler, 2012).Then, we made recommendations to the classification procedure and data preparation in order to improve the classification accuracy.

RESULTS

In general, the Random Forest (RF) classifier performed better than the Support Vector Machine (SVM) classifier. Using single-date imagery, overall classification accuracy for RF was 85%, while for SVM was 69%. When using multi-date imagery, RF had an overall accuracy of 89%, while SVM 68%.

Using spectral data from multi-date imagery directly in the classification scheme improved the classification accuracy when using RF classifier (Table 1a, b). In general, RF performed very well in both at the level of the land cover and at the level of the overall classification. Particularly, performed better than SVM for separating between the three types of forests, forest plantation, and orchards. Inspecting visually the classification maps, we observed that when using single-date imagery coffee and mangroves were slightly over-predicted (Fig. 2a). When using multi-date imagery, coffee classification improved, but in the case of mangroves still we observed misclassified pixels as mangroves in areas where it is not possible for this land cover exist (i.e. mountain ranges) (Fig. 2b).

Using single-date imagery, SVM had large errors for the three types of secondary forests, which were mainly predicted as forest plantation (Table 2a). With an inspection of the classification map, we observed that forest plantation was over-predicted by SVM (Fig. 3a). Using multi-date imagery, classification errors of the three type of forests were reduced, but it increased for forest plantation (Table 2b). Forest 2 was over-predicted, particularly over forest plantation, orchards, and forest 3 (Table 2b, Fig. 3b). Lower classification errors were obtained for coffee, crops, mangroves, and urban areas. For these classes SVM performed very well with both single-date and multi-date imagery, improving in general the classification with the later. In the case of orchards, the errors were significant, and the classification was not improved by using multi-date imagery.

Looking at the importance of predictor variables from classifications with RF, the most important variable was elevation. Then, we observed that spectral information from the early (December) and late dry season (March) were more important for separating among land cover classes. Finally, we observed that in general SWIR bands were more important for classification than NIR bands from the different dates along the dry season.

DISCUSSION

We had a good level of accuracy using the multi-date spectral data. L8-SR products are relatively new; Landsat 8 was launched on 2013, with improved instrumentation, and better image radiometric quality relative to previous Landsat platforms (Roy et al., 2014; Simonetti et al., 2014). We explored whether the classification accuracy could be improved by exploring the potential advantages of vegetation indices and other phenological variables to separate vegetation classes by their seasonal patterns (Dymond et al., 2002; Simonetti et al., 2014).

Here, we obtained better classification accuracy using RF classifier compared with SVM classifier. This is slightly different from the results of Sesnie et al., (2010), who had similar results with both classifiers. Multi-date imagery improved the classification accuracy and reduced errors. For SVM these results were at the level of particular land covers, but for RF these results were at both the level of land covers and of the overall classification. SVM classifier did not performed well for separating among secondary forest types, forest plantations, and orchards. However, it had a very good performance classifying the other land covers, particularly mangrove areas. In the other hand, RF produced satisfactory results in separating among the three secondary forest types, forest plantations, and orchards.

For further analysis, we suggest to: (1) test the use of different vegetation indices and phenological variables (e.g. phenological difference or change) that could highlight spectral differences between classes; (2) based on results presented here, review classes and improve their spectral signatures, and (3) explore procedures that incorporate different stages of classification.

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Table 3-1: Error matrices from two classifications using Random Forest (RF) classifier with: a) single-date imagery (December 2013), and b) multi-date imagery (from December 2013 to March 2014). Abbreviations: cffe (coffee), crps (crops), for1 (forest type 1), for2 (forest type 2), for3 (forest type 3), fplt (forest plantation), mgrv (mangrove), orch (orchards), otrs (others), ptrs (pastures), urbn (urban).

a)

		Reference											Error (%)	
	Class	cffe	crps	for1	for2	for3	fplt	mgrv	orch	otrs	ptrs	urbn	Commission	Omission
Predicted	cffe	43	0	0	1	0	0	0	0	0	0	0	2.27	15.69
	crps	0	70	0	0	0	0	0	0	1	12	10	24.73	15.66
	for1	0	0	19	0	0	0	0	0	0	0	0	0.00	9.52
	for2	0	0	0	18	0	0	0	0	0	0	0	0.00	28.00
	for3	0	0	0	0	16	0	0	0	0	0	0	0.00	23.81
	fplt	0	0	1	6	5	81	1	10	0	4	0	25.00	10.99
	mgrv	0	0	0	0	0	0	19	0	0	0	0	0.00	5.00
	orch	8	2	1	0	0	4	0	59	0	0	0	20.27	15.71
	otrs	0	0	0	0	0	0	0	0	9	0	0	0.00	10.00
	ptrs	0	2	0	0	0	4	0	0	0	81	0	6.90	17.35
	urbn	0	9	0	0	0	2	0	1	0	1	70	15.66	12.50

b)

		Reference											Error (%)	
	Class	cffe	crps	for1	for2	for3	fplt	mgrv	orch	otrs	ptrs	urbn	Commission	Omission
Predicted	cffe	44	0	0	0	0	0	0	0	0	0	0	0.00	12.00
	crps	0	82	0	0	0	0	0	0	0	8	3	11.83	18.00
	for1	0	0	19	0	0	0	0	0	0	0	0	0.00	5.00
	for2	0	0	0	18	0	0	0	0	0	0	0	0.00	28.00
	for3	0	0	0	0	16	0	0	0	0	0	0	0.00	11.11
	fplt	2	2	1	6	0	89	0	2	0	6	0	17.59	3.26
	mgrv	0	0	0	0	0	0	19	0	0	0	0	0.00	0.00
	orch	4	0	0	1	2	1	0	64	0	2	0	13.51	5.88
	otrs	0	0	0	0	0	0	0	0	9	0	0	0.00	0.00
	ptrs	0	6	0	0	0	2	0	0	0	79	0	9.20	19.39
	urbn	0	10	0	0	0	0	0	2	0	3	68	18.07	4.23

Table 3-2: Error matrices from two classifications using Support Vector Machine (SVM) classifier with: a) single-date imagery (December 2013), and b) multi-date imagery (from December 2013 to March 2014). Abbreviations: cffe (coffee), crps (crops), for1 (forest type 1), for2 (forest type 2), for3 (forest type 3), fplt (forest plantation), mgrv (mangrove), orch (orchards), otrs (others), ptrs (pastures), urbn (urban).

a)

		Reference											Error (%)	
	Class	cffe	crps	for1	for2	for3	fplt	mgrv	orch	otrs	ptrs	urbn	Commission	Omission
Predicted	cffe	35	0	3	1	0	5	0	0	0	0	0	20.45	20.45
	crps	0	63	0	0	0	7	0	1	1	11	10	32.26	14.86
	for1	0	0	6	0	0	10	1	2	0	0	0	68.42	57.14
	for2	1	0	3	1	0	11	0	2	0	0	0	94.44	50.00
	for3	0	0	0	0	0	12	0	4	0	0	0	100.00	100.00
	fplt	0	2	0	0	1	93	0	4	0	8	0	13.89	52.06
	mgrv	0	0	0	0	0	0	19	0	0	0	0	0.00	9.52
	orch	8	0	2	0	0	26	1	37	0	0	0	50.00	26.00
	otrs	0	0	0	0	0	0	0	0	8	0	1	11.11	20.00
	ptrs	0	3	0	0	0	25	0	0	0	59	0	32.18	25.32
	urbn	0	6	0	0	0	5	0	0	1	1	70	15.66	13.58

b)

		Reference											Error (%)	
	Class	cffe	crps	for1	for2	for3	fplt	mgrv	orch	otrs	ptrs	urbn	Commission	Omission
Predicted	cffe	39	0	0	5	0	0	0	0	0	0	0	11.36	27.78
	crps	1	66	0	6	0	2	0	0	1	7	10	29.03	9.59
	for1	0	0	11	5	3	0	0	0	0	0	0	42.11	21.43
	for2	0	0	1	15	2	0	0	0	0	0	0	16.67	88.46
	for3	0	0	1	11	4	0	0	0	0	0	0	75.00	60.00
	fplt	4	3	0	40	1	54	0	0	0	6	0	50.00	10.00
	mgrv	0	0	0	0	0	0	19	0	0	0	0	0.00	0.00
	orch	8	0	1	34	0	0	0	31	0	0	0	58.11	0.00
	otrs	0	0	0	0	0	0	0	0	9	0	0	0.00	43.75
	ptrs	2	2	0	6	0	4	0	0	0	73	0	16.09	15.12
	urbn	0	2	0	8	0	0	0	0	6	0	67	19.28	12.99

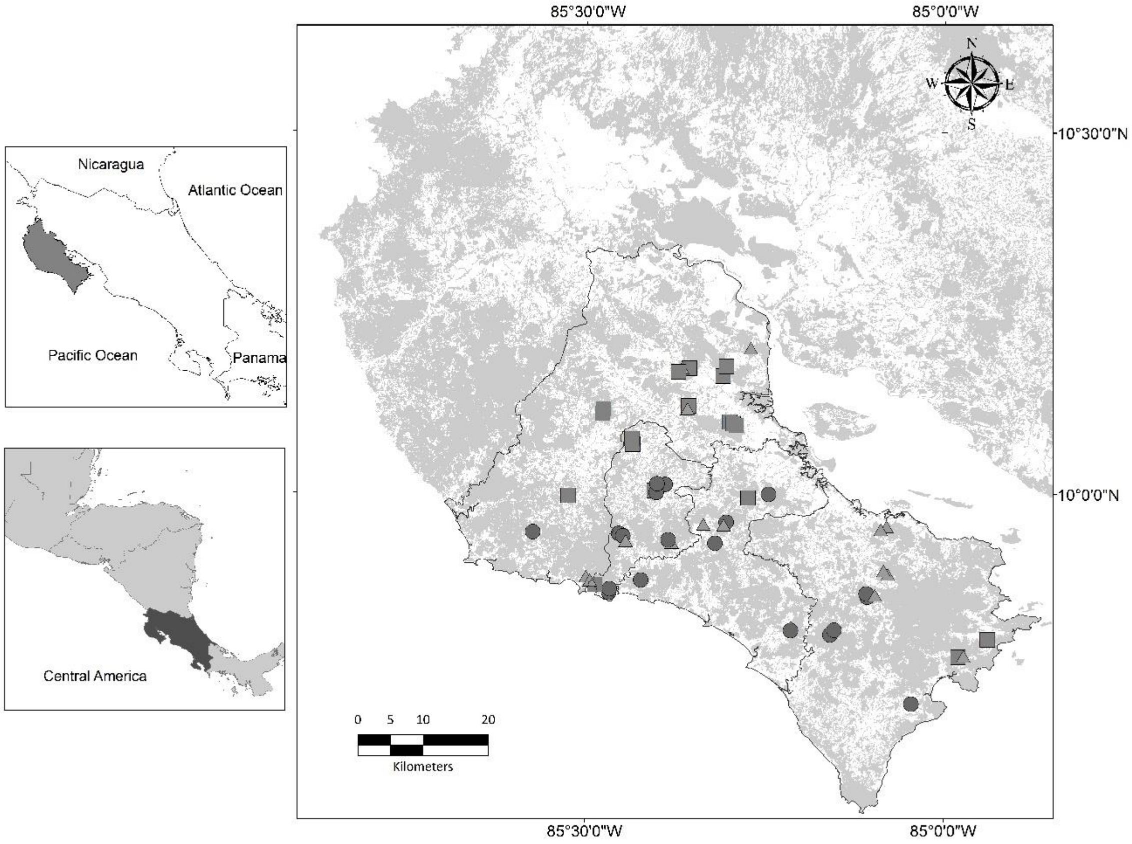


Figure 3-1: Study area in the Peninsula of Nicoya. Symbols represent three types of secondary forests characterized by Granda Moser et al., (2015): (1) Schizolobium – Miconia (circles), (2) Semialarium – Lonchocarpus (squares), and (3) Guazuma (triangles). Forest were named using the genera of species characteristic for each of them.

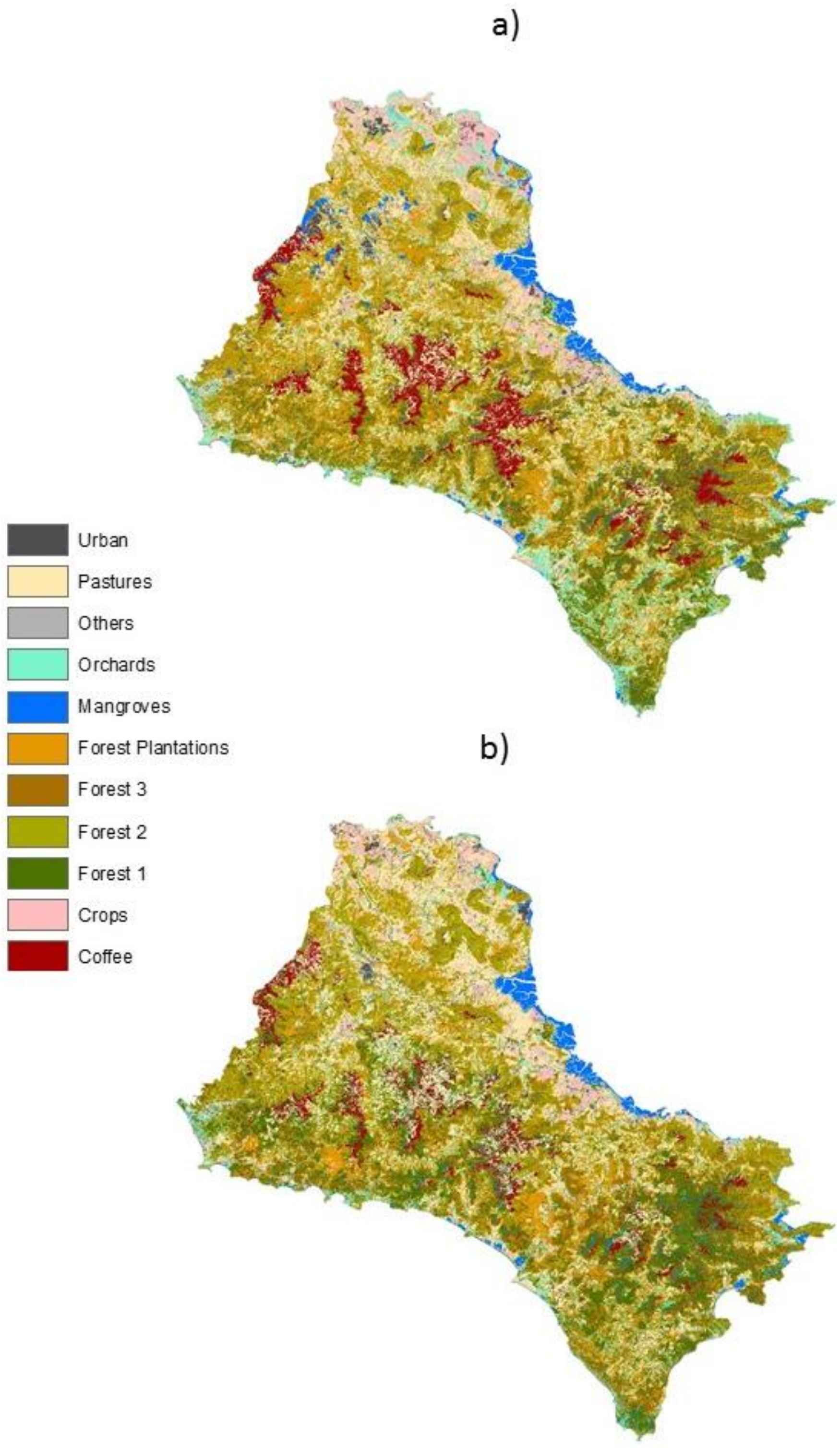


Figure 3-2: Classification maps using Random Forest classifier with: a) Single-data imagery (December 2013); and b) Multi-date imagery (from December 2013 to March 2014).

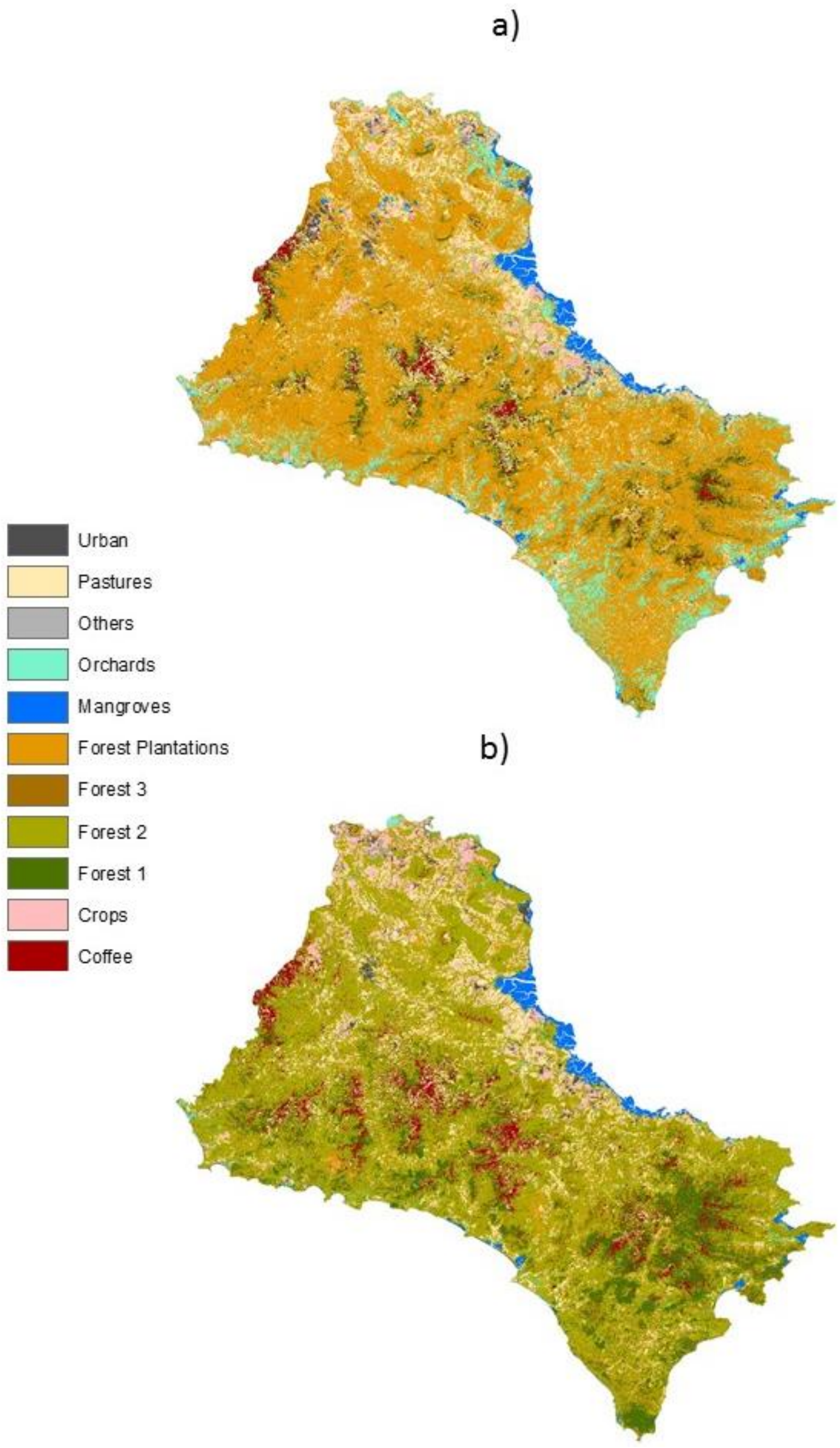
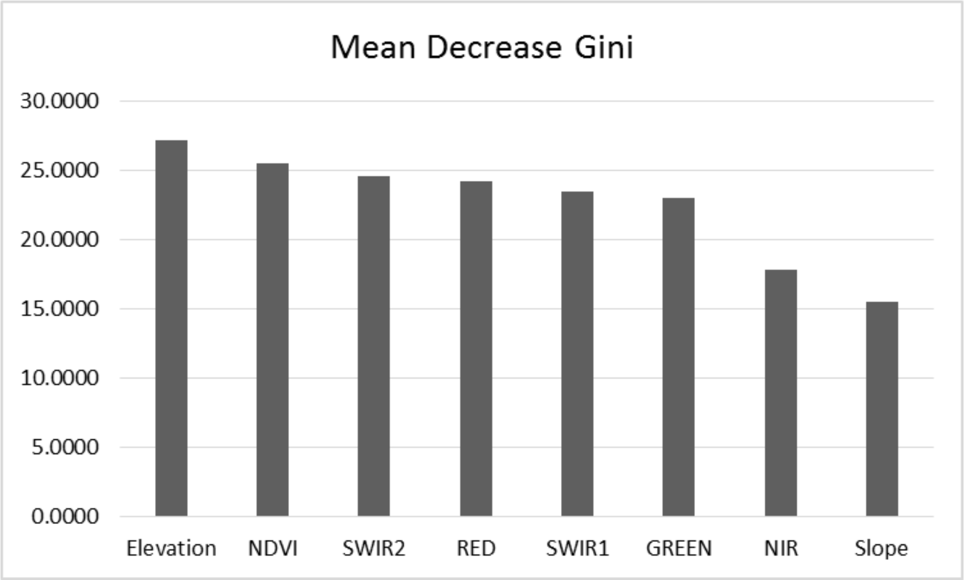


Figure 3-3: Classification maps using Support Vector Machine classifier with: a) Single-data imagery (December 2013); and b) Multi-date imagery (from December 2013 to March 2014).

a)



b)

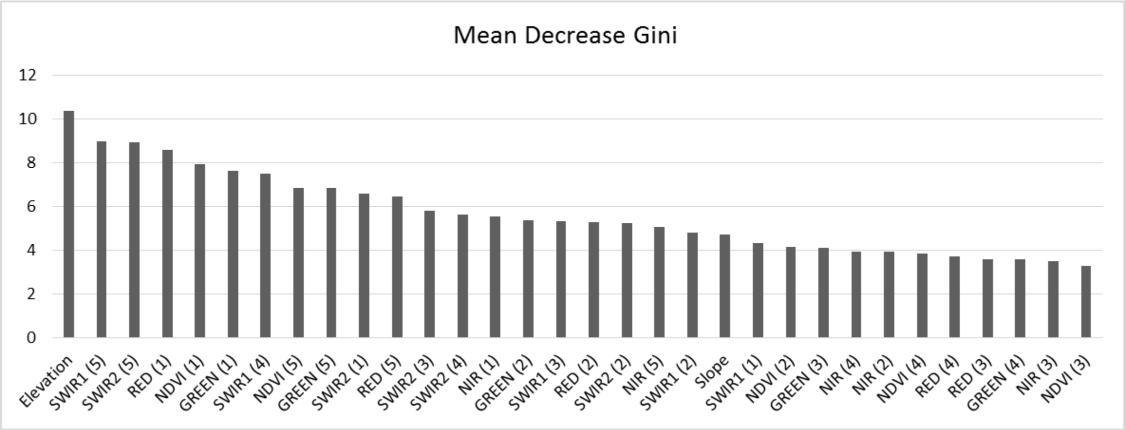


Figure 3-4: Importance of predictor variables from Random Forest classification based on the Gini impurity index (Breiman and Cutler, 2012) using: a) Single-date imagery (December 2013); and b) Multi-date imagery (from December to March 2014).

CHAPTER 4: SCALING-UP FUNCTIONAL TRAITS FOR ECOSYSTEM SERVICES WITH REMOTE SENSING: CONCEPTS AND METHODS[1]

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SUMMARY

1. Ecosystem service-based management requires an accurate understanding of how human modification influences ecosystem processes and these relationships are most accurate when based on functional traits. Although trait variation is typically sampled at

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local scales, remote sensing methods can facilitate scaling-up trait variation to regional scales needed for ecosystem service management.

2. We review concepts and methods for scaling-up plant and animal functional traits from local to regional spatial scales with the goal of assessing impacts of human modification on ecosystem processes and services. We focus our objectives on considerations and approaches for (1) conducting local plot-level sampling of trait variation and (2) scaling-up trait variation to regional spatial scales using remotely-sensed data.
3. We show that sampling methods for scaling-up traits need to account for the modification of trait variation due to land cover change and species introductions. Sampling intra-specific variation, stratification by land cover type or landscape context, or inference of traits from published sources may be necessary depending on the traits of interest.
4. Passive and active remote sensing are useful for mapping plant phenological, chemical and structural traits. Combining these methods can significantly improve their capacity for mapping plant trait variation. These methods can also be used to map landscape and vegetation structure in order to infer animal trait variation. Due to high context-dependency, relationships of trait variation and remotely sensed data are not directly transferable across regions.
5. We end our review with a brief synthesis of issues to consider and outlook for the development of these approaches. Research that relates typical functional trait metrics, such as the community weighted-mean, with remote sensing data and that relates variation in traits that cannot be remotely sensed to other proxies is needed. Our review

narrows the gap between functional trait and remote sensing methods for ecosystem service management.

Key-words Ecosystem function, effect traits, functional homogenization, human modification, land cover and climate change, LiDAR, landscape management and policy, regional spatial scale.

INTRODUCTION

Evaluation of ecosystem service policy and management requires understanding the consequences of human modification on ecosystem processes and dependent ecosystem services at regional scales (sensu Forman & Godron 1986; Chazdon 2008; Daily et al. 2009). To this end, functional trait approaches have the potential to be more accurate than species based approaches due to the continuous nature of functional traits and the direct link between traits and ecosystem processes (McGill et al. 2006; Westoby & Wright 2006). The use of functional traits to inform ecosystem service policy and management requires the scaling-up of plot-scale data from local to regional scales (Lavorel et al. 2011). Nevertheless, we currently lack consensus on how to estimate functional trait variation at regional spatial scales relevant to land use planning and policymaking. In this paper, our main goal is to review concepts and methods for scaling local plot-scale functional trait composition to regional scales relevant to ecosystem service policy and management. In particular, we review and synthesize the knowledge necessary for sampling local plot-level functional trait variation and the available remote sensing methods that can be used to scale-up this local trait variation to regional scales (Fig. 1).

Methods for assessing the effects of human modification on ecosystem services typically rely on correlating vegetation type with ecosystem processes (Daily et al. 2009). For example, change from forest to pasture vegetation affects local water fluxes by modifying interception and transpiration (Foley et al. 2003). These local changes can be scaled-up to regional scales vis-à-vis vegetation type to assess effects on ecosystem services such as the regulation of peak flood and low flow events (Foley et al. 2007). However, this approach is limited because it does not incorporate the fine-scale functional trait variation within vegetation types, which can constitute up to 75% of the variation in trait values (Kattge et al. 2011). Traits such as tree biomass, crown diameter, and leaf area affect water fluxes and can vary significantly across and within vegetation types (Meinzer et al. 2005; Park & Cameron 2008; Abelleira 2015). In addition, tree species composition may change but trait composition may not, or vice-versa, within a given vegetation type due to trait variation at the individual, species, and community levels (Albert et al. 2010; Messier, McGill & Lechowicz 2010). Vegetation classifications are also insufficient for determining changes in ecosystem services that depend on the effect traits of highly mobile organisms, whose movement is influenced by habitat heterogeneity and landscape structure (Leyequien et al. 2007; Keitt 2009). For example, traits such as body size affect the foraging range and dispersal capacity of bees, and dependent ecosystem services such as crop pollination (Wray, Naeme & Elle 2014; Martins, González & Lechowicz 2015).

Current research in ecosystem services aims to resolve these issues by focusing on metrics of effect functional traits, such as the community-weighted mean (CWM) or functional diversity indices, rather than vegetation types (Grime 1998; Lavorel & Garnier 2002; Lavorel et al. 2013). These metrics can be related to the ecosystem processes of interest based on experimental data gathered at local plot scale, and subsequently to dependent ecosystem services according to the values placed on ecosystem properties or fluxes by stakeholders (Díaz et al. 2007; Lavorel et al. 2011; Finegan et al. 2015). Nevertheless, it is unclear how sampling should be conducted to capture the necessary functional trait variation in highly heterogeneous human-modified regions and whether it is even possible to model the corresponding fine-resolution trait data at the regional scale with currently available methods (Garnier et al. 2007; Van Bodegom et al.

2012). These concerns limit the adoption of functional trait approaches to quantify ecosystem processes at regional scales relevant for ecosystem service management and policy design (Daily et al. 2009; Fremier et al. 2013; Rollin et al. 2015).

A promising alternative approach is the fine-resolution regional mapping of functional traits using remote sensing (Fig. 1). Currently available remote sensing methods can provide a direct link between local plot-scale functional trait variation and regional scale ecosystem service management because they are repeatable across time and space, and capable of producing fine-resolution data across broad areas (Asner et al. 2011a; Ustin & Gamon 2011; Homolová et al. 2013). In particular, remote sensing can facilitate scaling-up functional trait variation in highly heterogeneous human-modified regions where land cover and climate change are disrupting original patterns in trait variation and where ecosystem service assessments are most needed (Daily et al. 2009; Hobbs, Higgs & Harris 2009; Keitt 2009). Although technological advances have improved the available array and capabilities of remote sensing methods, their application to functional trait mapping for assessing ecosystem services at regional scales has not become widespread (Ustin & Gamon 2010; Galbraith, Vierling & Bosque-Pérez 2015).

To better understand the application of functional traits to ecosystem service assessments in human-modified regions, our objectives are to review (1) the current conceptual understanding of trait-based approaches for sampling trait variation across spatial scales and (2) existing remote sensing-based methods that can be used to scale-up trait variation from plot to regional scales. We begin our first objective by reviewing the sources of functional trait variation found across ecological levels of organization that span individuals, species, communities and landscapes. We then synthetize how these sources combine to structure functional trait variation across space in light of human-modification, and the implications that the resulting spatial trait variation has for the design of local plot-scale sampling methods. We structure our second objective around groups of remotely sensible traits that correspond to different sets of available remote sensing methods. In general, phenological and chemical plant traits can be sampled by optical-based remote sensing while plant structural traits can be sampled by active laser-based remote sensing. Animal traits may be inferred by combining remote sensing of plant and vegetation structural traits with landscape structure. We illustrate the applicability of some of these methods by citing examples of how variation in plant and animal traits has been sampled and scaled-up to regional scales. We end our review by providing a brief synthesis of results, identified knowledge gaps, and outlook for further development of these methods to improve ecosystem service assessments.

SAMPLING TRAIT VARIATION

Sources of Trait Variation

Functional traits can vary across individuals, species, communities, and landscapes. A better understanding of the sources and spatial scales in which most of the effect trait variation is found will allow for better allocation of sampling effort in trait-based approaches. Although we cannot logistically measure all trait values across all ecological levels, understanding the magnitude of trait variation sources will reduce uncertainty when scaling from local plot-scale estimates of trait values to broader spatial scales.

Individuals and Species

Intraspecific variation in functional traits arises from microsite environmental variability and gradients occurring across the geographical range of plant and animal populations (Peat et al. 2005; Bolnick et al. 2011; Violle et al. 2012). Intraspecific trait variation can rival interspecific variation (Hulshoff & Swenson 2010; Ruiz & Potvin 2011). The plant trait variation attributable to intra- versus interspecific sources can vary by species, trait, or community type (Albert et al.

2010; Kattge et al. 2011; Kazakou et al. 2014). Determining the variation attributable to intra- vs. interspecific sources in mobile animals is hampered by the challenge of obtaining a fully random sample (de Bello et al. 2011).

Communities and Landscapes

Environmental gradients produced by soil properties, topography and climate drive functional trait variation across and within natural plant communities (Cornwell & Ackerly 2009; Ordoñez et al. 2009; Baraloto et al. 2012). This structuring is less evident at fine spatial scales within communities (≤100 m2) due to founder effects and successional processes (Swenson et al. 2007; Yang et al. 2014). Land cover change can disrupt the natural trait variation found within and across plant communities by altering site conditions, successional status, landscape structure, and by species introductions (Fig. 2; Leishman et al. 2007; Giraõ et al. 2007; Lebrija-Trejos et al. 2010; Lasky et al. 2014). If previous land use intensity and successional stage are accounted for, patterns in trait composition and diversity still emerge across environmental gradients (Mayfield et al. 2005; Mayfield, Ackerly & Daily 2006; Lohbeck et al. 2013). However, there are no consistent patterns in the plant trait composition of successional vegetation across landscapes of varying environmental conditions and land use history (Mayfield et al. 2013).

Overlaying environmental gradients and land use history is the confounding effect of animals on plant trait composition, and vice versa. The functional trait composition of plants can be mediated by the functional diversity of organisms at higher trophic levels, and in turn, have feedback effects on the trait composition of animal communities across the landscape (Giraõ et al. 2007; Cardinale et al. 2012). Pollinators and seed dispersers, which include a wide array of animal groups, affect the trait composition of plant communities in ways that are beginning to be understood (Suding et al. 2008; Lavorel et al. 2013). The trait composition of pollinators and seed dispersers is determined by habitat suitability and landscape structure variables such as patch size and isolation (Tscharntke et al. 2008; Barbaro & van Halder 2009; Bommarco et al. 2010; Jauker et al. 2013). Although the effects of landscape structure on plant trait composition are not as evident as those of environmental gradients and land use history, the loss of pollinator or disperser functional groups due to fragmentation can eventually modify the trait composition of plant communities (Fig. 2; Giraõ et al. 2007; Sutton & Morgan 2009).

Trait Variation across Space: Impact of Human Modification

Trait variation is partitioned similarly across intraspecific, interspecific, and community sources, and higher trait variation exists within than across communities due to redundancy across communities (de Bello et al. 2009; Messier et al. 2010; Kattge et al. 2011; Freschet et al. 2012). Less is known about how trait variation is partitioned across spatial scales yet the steepness of environmental gradients within the spatial extent of interest, rather than the spatial scale itself, appears to drive trait variation (Willis et al. 2010; Freschet et al. 2012). Thus, environmental gradients drive functional trait variation across all ecological levels and spatial scales, and natural or anthropogenic disturbances act across levels and scales to counteract trait convergence due to these gradients.

Human modification can alter the trait variation found across ecological levels at the regional scale (Fig. 2). Land cover and climate change can result in the dominance of introduced species possessing traits for which there is no native analog and lead to the emergence of novel community types (Leishman et al. 2007; Hobbs, Higgs & Harris 2009; Abelleira 2011; Drenovsky et al. 2012). Within novel communities, dominant introduced species may increase the magnitude of intra- vs. interspecific trait variation (Fig. 2; Hillebrand, Bennet & Cadotte 2008). Managed systems, such as plantations and agriculture, may perpetuate the dominance of introduced species, which can also lead to higher trait variation across community types within a region. The functional traits of novel and managed communities can thus differ from the original communities they replaced and increase the magnitude of trait variation across communities relative to other sources (Fig. 2). Concurrently, functional trait homogenization may occur in regions that have suffered extensive land conversion and high rates of species extinctions and introductions (Olden et al. 2004; Grass, Berens & Farwig 2014). Homogenization may result in trait values closer to the global mean and increase trait divergence between relatively undisturbed and highly human-modified regions (Fig. 2).

Implications for Trait Sampling

Quantifying intraspecific variation may be unnecessary for capturing trait effects on ecosystem processes. However, this variation can be important when one or few species dominate certain community types across environmental gradients (Hillebrand, Bennet & Cadotte 2008). In such cases, metrics derived from in-situ sampling can capture intraspecific trait variation appropriately (Albert et al. 2011). The use of database values for dominant species may miss important intraspecific trait variation effects on ecosystem processes in regions where environmental gradients are steep and few species dominate common community or land cover types (Hillebrand, Bennet & Cadotte 2008). Since species that become dominants are frequently introduced, database values from regions with different environmental conditions may be inaccurate (Drenovsky et al. 2012).

Sampling stratification by community types of varying successional status, novelty, land use history, and management intensity is necessary to capture the effect trait variation in human-modified regions (Fig. 2; Garnier et al. 2007). Sampling needs to be efficient at capturing cross-community variation without compromising other trait variation sources. One plot (e.g., ~500m2 for forest tree communities) per site per community type (≥3 sites per community type) at selected points across the prevailing environmental gradients can be enough to capture the necessary effect trait variation into CWM or trait diversity indices (Ackerly & Cornwell 2007;

Lavorel et al. 2008; Messier et al. 2010). Dominant species (those contributing >80% of the CWM) should be adequately sampled as outlined by protocols (Cornelissen et al. 2003; Pakeman & Quested 2007). For subordinate species (those contributing <20% of the CWM; Grime 1998) in species-rich communities, such as old-growth or mature tropical secondary forests, sampling of one individual per species per plot per site is enough to capture the necessary effect trait variation (Baraloto et al. 2010). In plant communities exhibiting high species dominance and low species richness, database values may be appropriate to estimate effect traits of subordinate species but not of dominant ones (Pakeman & Quested 2007; Lavorel et al. 2008).

At higher trophic levels, landscape structure has greater influence on effect traits by affecting dispersal capacity of highly mobile organisms (Bommarco et al. 2010; Jauker et al. 2013). In the case of mobile animals, CWM and trait diversity indices are typically based on in-situ species abundance estimates across community types accounting for variation in landscape structure (Vandewalle et al. 2010). Measuring traits directly among the communities being studied is often not possible due to logistical constraints (e.g., behavioral traits within diverse insect communities). In such cases, traits can be inferred from phylogeny or published keys (Moretti et al. 2009; Vandewalle et al. 2010; Wray, Naeme & Elle 2014). This is more acceptable when trait diversity indices rather than a CWM are used to infer ecosystem services, as the mean trait values in a community may differ from database values depending on variables such as climate and resource availability (Peat et al. 2005; Gagic et al. 2015).

SCALING-UP TRAITS VIA REMOTE SENSING

Remote sensing facilitates the scaling-up of functional trait variation by fine-resolution mapping of trait-related data across broad spatial extents. The traits that can be mapped directly with remote sensing are currently limited to plant canopy phenological and chemical traits, and structural traits of plants and vegetation. In general, phenological and chemical traits can be mapped with optical-based passive remote sensing while structural traits can be mapped with laser-based active remote sensing. Along with the mapping of land cover and landscape structure, plant phenological, chemical and structural traits can be related to resource availability for animals in order to infer animal trait variation.

Canopy Phenological and Chemical Traits

Plant canopy traits related to phenology and chemistry, such as leafing and flowering periodicity, leaf mass per area, leaf water, carbon and nutrient content, and leaf area index (LAI) can be mapped using satellite-based passive multi- to hyperspectral remote sensing (Fig. 3; Ustin & Gamon 2010; Homolová et al. 2013). Passive sensors such as AVHRR and MODIS have high temporal resolution capable of quantifying the periodicity of leafing and flowering phenology (Fig. 3; Vieira et al. 2003; Kalacksa et al. 2007; White et al. 2009). Landsat can also be used for resolving phenological periodicity due to its spatial and temporal resolution (Kennedy et al. 2012; Melaas, Friedl & Zhu 2013). However, most plant canopy phenological and chemical traits cannot be directly retrieved from passive remotely sensed data but inferred by their relationship to canopy spectral properties using empirical or physical models based on statistical relationships or spectral processes, respectively (Gray & Song 2012; Homolová et al. 2013). Empirical and physical models may be used to estimate the spatial variation of similar phenological and chemical traits including leaf mass per area, leaf carbon, cellulose, lignin, nitrogen, phosphorous, photosynthetic pigment, and water content, and LAI, and may be used in tandem to facilitate or improve the estimation of other traits (Fig. 3; Colombo et al. 2008; Asner & Martin 2009; Asner et al. 2011b & c).

Empirical Models

Empirical models use regression analysis to establish statistical relationships between field measurements of traits and passive remote sensing data. A limitation of empirical models has been that most multispectral sensors sample few portions of the electromagnetic spectrum at bandwidths too wide to capture important features for the discrimination of canopy traits (Ollinger 2011). This limitation is addressed by hyperspectral sensors, which sample a high number of contiguous, narrow spectral bands and can be used to derive phenological and chemical traits such as leaf chlorophyll, nitrogen, phosphorous, and water content (Fig. 3; Townsend et al. 2003; Malenovský et al. 2007). With hyperspectral data, the effects of soil background, illumination, or albedo may be reduced with spectral transformations to enhance absorption features of interest (Schlerf et al. 2010). The most important limitation of empirical models is that the relationships between remotely sensed data and field observations of traits can be time, site, and species specific, and lack causality, robustness and transferability across regions (Homolová et al. 2013). Combining data from multi- to hyperspectral sensors that capture information at different spatial resolutions and extents (e.g., IKONOS and Landsat) with concurrent ground-based measurements can help solve this problem (Fig. 3; Anderson et al. 2004; Williams et al. 2008; Gray & Song 2012). The effects of canopy structure on leaf chemical traits are difficult to correct in empirical models yet a solution is to combine empirical with physical models (Asner & Martin 2008 & 2009).

Physical Models

Physical models of radiative transfer account for light absorption and scattering processes to simulate leaf to canopy reflected or emitted optical spectral properties based on multi- or hyperspectral data (Malenovský et al. 2007; Baret & Buis 2008; Jacquemoud et al. 2009; Ollinger 2011). The coupling of leaf and canopy radiative transfer models allows the spectral and directional variation of canopy reflectance to be described as a function of leaf chemistry and canopy structure. This inverse modeling allows for the retrieval of fine-resolution plant canopy functional traits from plot-scale to broader spatial extents (Colombo et al. 2008; Croft et al. 2013; Homolová et al. 2013). Incorporating soil radiative transfer models imposes a strong spectral constraint on the inversion process, decreasing the number of unknown variables and enhancing spectral consistency (Baret & Buis 2008; Jacquemoud et al. 2009). The main drawback of inverse modeling is high uncertainty because several combinations of canopy traits could lead to similar remotely sensed signals (Koetz et al. 2005). Using field data to constrain the distribution and limits of variables can improve the stability and reliability of solutions (Baret & Buis 2008). Since radiative transfer models do not incorporate all sources of variability in leaf spectra, the retrieval by inversion is limited to those traits that are directly involved in the modeled process, such as leaf mass per area, chlorophyll and water content (Fig. 3; Asner et al. 2011b & c; Homolová et al. 2013).

Plant Structural Traits

Individual plant structural traits such as height and crown diameter can be mapped with active remote sensing methods, particularly with LiDAR (Fig. 3; Popescu, Wynne & Nelson 2003; Popescu & Wynne 2004; Koch, Hyder & Weinacker 2006; Falkowski et al. 2006; Popescu & Zhao 2008), LiDAR typically underestimates plant height due to laser returns missing the highest point of tree crowns although the error remains constant (~0.15 m) and is mostly negligible for tall forest canopies (Asner et al. 2012). The sensing of tree and shrub crown diameter with LiDAR remains limited in closed canopy conditions (>50% cover), yet finer post-spacing of LiDAR returns (<1 m) may improve the sensing of this trait (Falkowski et al. 2008). Conducting sampling campaigns during the leaf-off period could also improve tree crown diameter detection with LiDAR in deciduous forests (Brandtberg et al. 2003). Tree crown diameter has been mapped with some success using multispectral aerial photography albeit with the same problems as LiDAR (Strand et al. 2006; Garrity et al. 2008).

Vegetation structural traits such as LAI, tree density and biomass, can also be mapped with LiDAR (Riaño et al. 2004; Martinuzzi et al. 2009; Zhao & Popescu 2009). LiDAR has been used in conjunction with passive remote sensing to scale aboveground carbon stocks in forests from plot to regional and global scales with high accuracy (Asner et al. 2011a; Baccini et al. 2012). Due to its accuracy in sensing forest structure across heterogeneous terrain, LiDAR can be used to map forest type, successional status, and potentially tree species diversity (Asner & Martin 2009; Castillo et al. 2012; Martinuzzi et al. 2013; Hernández et al. 2014). Links between plant structure and function can be derived directly from combining the 3-dimensional location data of returned LiDAR pulses with return intensity, which can open new opportunities for fine-resolution mapping of leaf chlorophyll and N content, and photosynthetic performance (Eitel, Vierling & Long 2010, Eitel et al. 2011; Magney et al. 2014). Improvements in airborne and terrestrial LiDAR technology have increased their utility in characterizing structural traits of low-stature vegetation such as shrublands and tundra (Streutker & Glenn 2006; Vierling et al. 2012; Greaves et al. 2015). Other active remote sensing methods, such as satellite-based LiDAR (Lefsky et al. 2005), high-density laser scanning (Maltamo et al. 2004), and synthetic aperture radar (Santos et al. 2003) can be used to map traits such as canopy height yet their development lags behind compared to airborne LiDAR (Fig. 3).

Animal Traits

Mapping plant phenological, chemical and structural traits along with land cover variables, such as successional status and landscape structure, can be useful for predicting the functional traits of animals because they move across landscapes depending on resource availability, and on traits such as foraging range and dispersal abilities (Fig. 3; Leyequien et al. 2007; Jarnevich et al. 2014; Pettorelli et al. 2014). Some optical satellite sensors such as Landsat, IKONOS and Worldview-2, which have been typically used for mapping discrete land cover classes and landscape structure, have high enough spatial resolution to resolve the successional status of vegetation (Kenendy et al. 2012).

Vegetation structure variables derived from airborne LiDAR can be used for mapping animal trait diversity by describing horizontal and vertical (3-dimensional) habitat structure across landscapes. Some useful LiDAR-derived structural variables include understory vegetation density, LAI, canopy architecture, snag size and density, and tree biomass and basal area (Fig. 3; Turner et al. 2003; Vierling et al. 2008; Bergen et al. 2009; Galbraith, Vierling & Bosque-Pérez 2015). In-situ field data on the abundance of animal functional groups can be combined with structural variables to scale-up animal trait diversity based on field-validated models (Hinsley et al. 2002; Martinuzzi et al. 2009; Müller & Brandl 2009; Newton et al. 2009). Coupled with passive sensors that can map leaf phenology and chemistry, the potential for LiDAR to relate plot-scale structural properties, such as plant canopy height, crown diameter, and aboveground biomass, can facilitate the spatial scaling-up of multiple plant and animal traits (Fig. 3; Zhao & Popescu 2009; Asner et al. 2011a; Gray & Song 2012; Müller et al. 2014).

CONCLUSION

Our review found and synthetized various issues to consider and corresponding viable approaches for scaling-up plant and animal traits from plot to regional scales using remote sensing (Table 1). Deciding which of these approaches is more suitable will depend on the traits needed and selected for the ecosystem service assessment. A key issue is the regional context dependency of the relationships between functional trait variation, degree of human modification, and remotely sensed data. Our review shows that functional trait sampling needs to account for the regional modification of trait variation due to dominant introduced species, managed and novel community types, diverse land use history and heterogeneous landscape structure. Statistical relationships that link local trait variation to regional environmental gradients can fail to capture these anthropogenic effects on trait variation and be of limited use in human-modified regions. Methods that rely on environmental gradients to integrate field-sampled functional trait variation into land cover types have been used in ecosystem service assessments (Lavorel et al. 2011). These methods may be significantly improved by applying developments in remote sensing that allow for fine-resolution regional mapping of trait variation and that directly account for the effects of human modification. Eventually, dynamic vegetation models may reproduce the spatial variation in functional traits after their response to environmental gradients, land cover and climate change (Suding et al. 2008; Van Bodegom et al. 2012). However, the science is not there yet. In-situ sampling of trait variation is still needed and more so in highly human-modified regions for which ecosystem service assessments are most relevant.

Our review focused on the objectives of conducting field sampling of trait variation and scaling-up trait variation using remotely-sensed data with the ultimate goal of improving ecosystem service assessments. An important knowledge gap implicitly found by our review is the lack of research directed towards linking the functional trait metrics that are typically related to ecosystem processes and services, the CWM and functional diversity indices, with remotely sensed data. We could not find any papers on this topic and this remains a next step to improve the utility of functional traits for ecosystem service management. In addition, most of our review of methods for scaling-up traits applied to traits that can be remotely sensed. Other plant traits that may be useful for ecosystem service assessments, such as wood density or belowground biomass, still would need to be inferred based on their relationship to environmental variables or to other traits via modeling approaches akin to the inference of animal traits as illustrated by our review. Nevertheless, fusion of passive and active remote sensing along with technological developments that increase sensor spectral, spatial and temporal resolutions can improve the mapping of sensible plant functional traits and animal traits related to landscape and vegetation structure. At present, remote sensing is a powerful tool for capturing variation in functional traits at multiple spatial scales and, to improve their accuracy, ecosystem service assessments should take advantage of traits that can be remotely sensed.

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Data Accessibility

All data are included in the manuscript.

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Table 4-1: Summary of issues to consider and approaches for scaling-up functional traits that resulted from the objectives of this review.

Objective	Issues to consider	Approach
1. Field sampling of functional trait variation.	Natural sources of plant trait variation are compounded by human-modification that results in dominance of introduced species and heterogeneous landscapes.	Quantification of intraspecific variation and sampling stratification by successional status, land use history and management intensity may be required.
	Land cover change can affect animal traits by modifying the dispersal capacity of mobile organisms.	Account for landscape variables related to animal traits, which may be inferred from phylogeny or published keys if necessary.
2. Scaling-up trait variation via remote sensing.	The relationships between plant trait variation and remotely sensed data depend on regional context and more so due to human modification.	Remote sensing and ground-truthing by in-situ sampling of trait variation needs to occur independently for regions with different levels of human modification.
	Remotely sensed data cannot be directly related to animal trait variation.	Animal trait variation may be inferred from the combination of different types of remotely sensed data on vegetation and landscape structure.

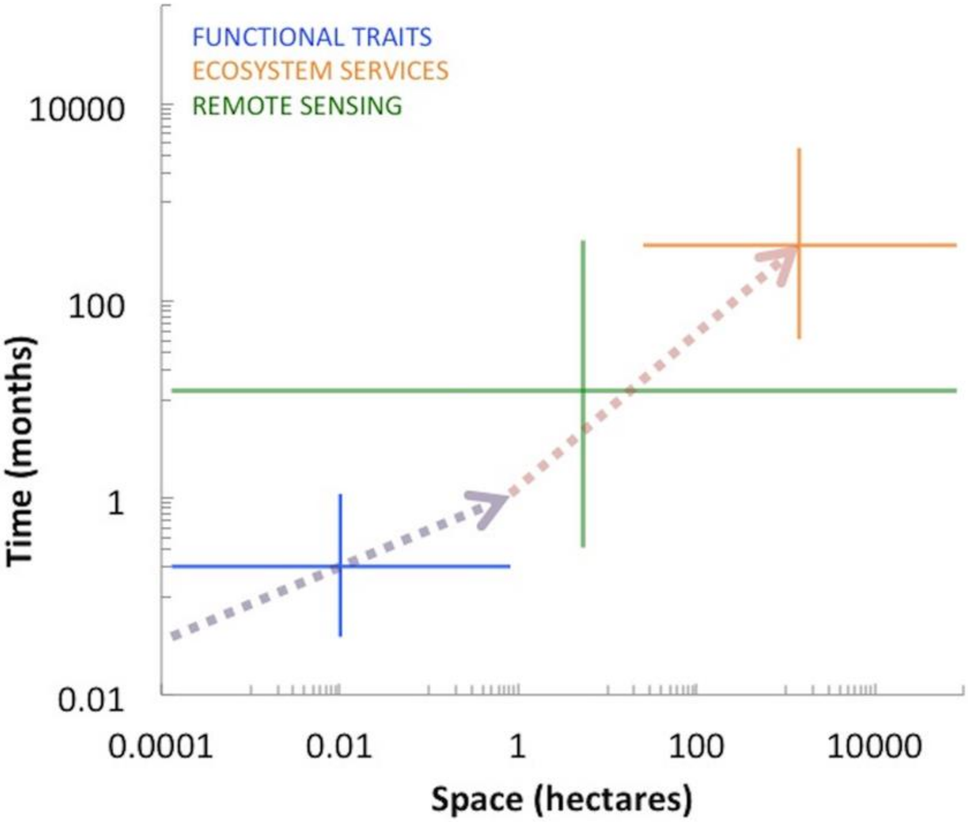

Figure 4-1: The use of functional traits to inform ecosystem service policy and management requires the scaling-up of plot-scale data from local to regional scales. In this review, we outline (1; purple dashed arrow) the sampling considerations for capturing the necessary variation in functional trait composition across space so that these proxies can be used for (2; brown dashed arrow) the fine-resolution scaling-up of trait composition from local to regional scales via remote sensing methods.

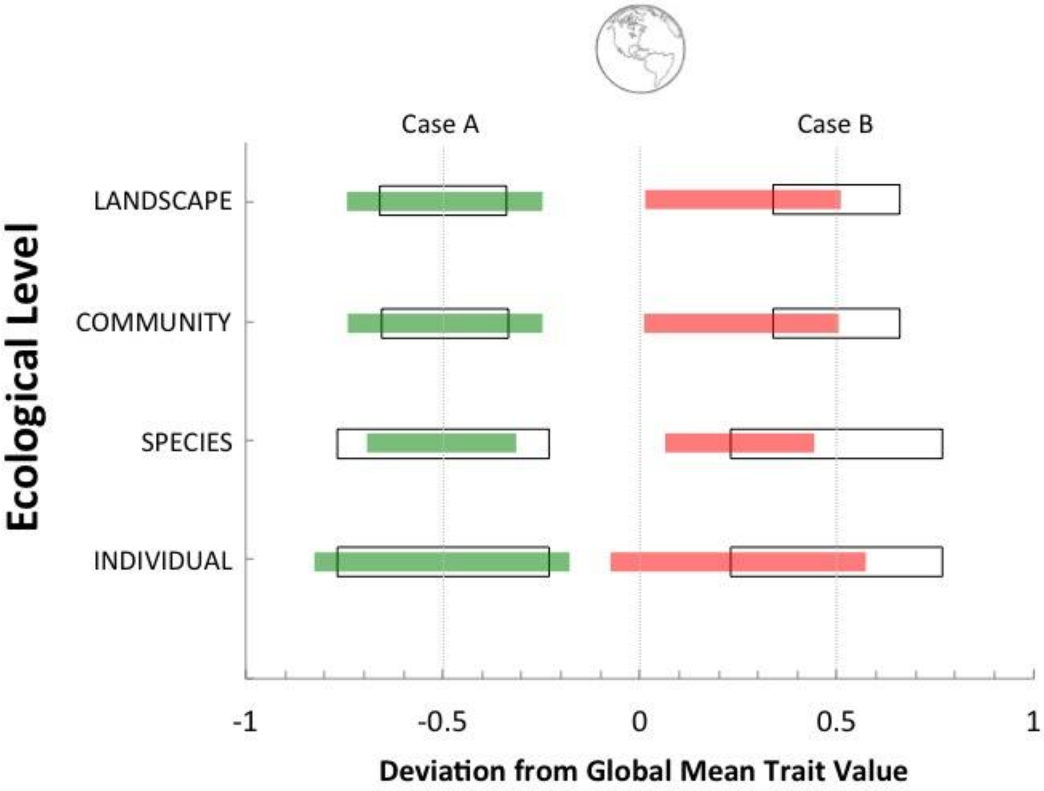

Figure 4-2: Range of functional trait variation and deviation from a global mean value corresponding to individual, species, community, and landscape ecological levels of a given biome under natural and human-modified conditions. Black empty bars represent the proportional range of trait variation found across ecological levels under natural undisturbed conditions for two given regions within a biome (hypothetical estimates based on Freschet et al. 2012). Green colored bars represent a region (case A) where land cover change and species introductions have resulted in a relative decrease of trait variation found across the species level due to localized extinctions of species coupled with a relative increase in trait variation found across the individual, community, and landscape levels due to the dominance of introduced species, novel and managed community types, and landscape fragmentation, respectively. Red colored bars represent another region (case B) where land cover change, and species extinctions and introductions have acted to homogenize trait variation by increasing trait values that deviate less from the global mean trait value for the biome at each ecological level. Divergence in trait values between natural and human-modified regions is higher in case B.

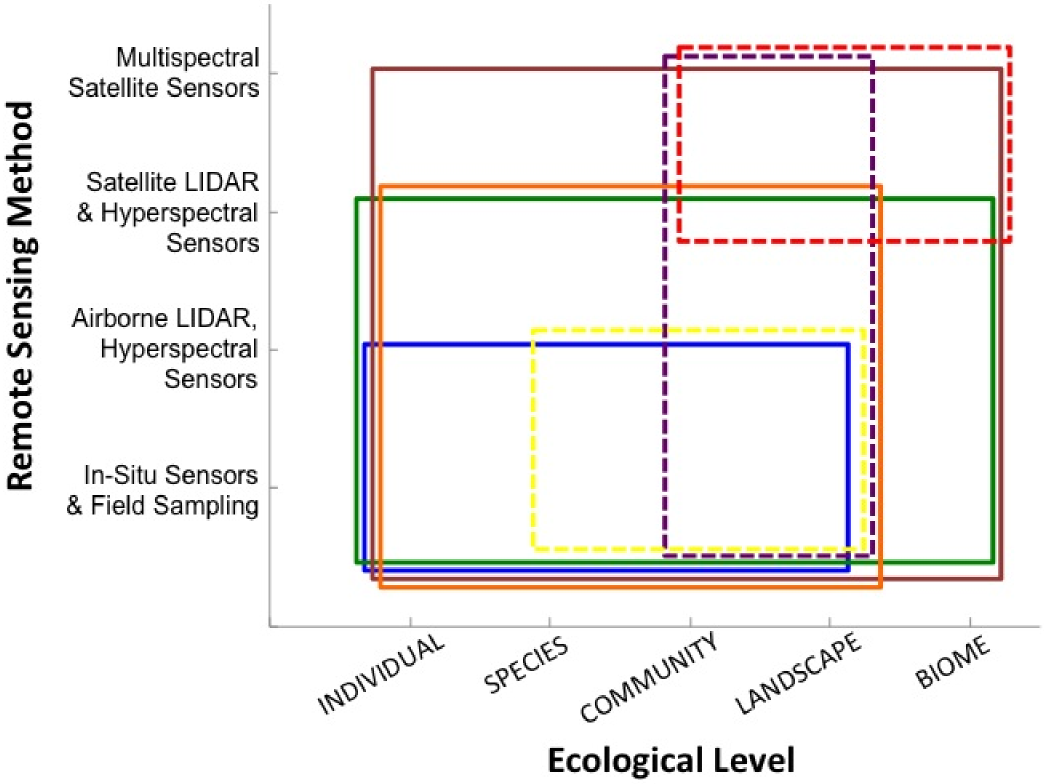

Figure 4-3: Remote sensing methods for mapping plant and animal functional traits at different ecological levels. The area of the solid boxes cover the ecological levels where remote sensing methods coupled with field sampling and validation allow for the mapping of the following plant functional traits: leaf phenology (brown), leaf chemical content and mass per area (green), and plant height (orange) and crown diameter (blue). Dashed boxes cover the ecological levels where remote sensing methods allow for the mapping of the following proxies that relate to animal functional trait diversity: habitat and vegetation structure (e.g., tree density and biomass; yellow), leaf area index (purple), and landscape structure (e.g., patch size, isolation, and perimeter to area ratio; red).