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Synergies and trade-offs between ecosystem services in Costa Rica

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SUMMARY

Ecosystems services have become a key concept in understanding the way humans benefit from ecosystems. In Costa Rica, a pioneer national scheme of payment provides compensation for forest conservation that is assumed to jointly produce services related to biodiversity conservation, carbon storage, water and scenic beauty, but little is known about the spatial correlations among these services. A spatial assessment, at national scale and with fine resolution, identified the spatial congruence between these services, by considering the biophysical potential of service provision and socioeconomic demand. Services have different spatial distributions but are positively correlated. Spatial synergies exist between current policies (national parks and the payment scheme) and the conservation of ecosystem services: national parks and areas receiving payments provide more services than other areas. Biodiversity hotspots have the highest co-benefits for other services, while carbon hotspots have the lowest. This finding calls for cautiousness in relation to expectations that forest-based mitigation initiatives such as REDD (reducing emissions from deforestation and forest degradation) can automatically maximize bundled co-benefits for biodiversity and local ecosystem services.

Keywords: adaptation, biodiversity, carbon, climate change, environmental services, mitigation, REDD, scenic beauty, spatial analysis, water

INTRODUCTION

Ecosystem services (ES) have recently become a key concept in understanding the way humans benefit from ecosystems. The Millennium Ecosystem Assessment (MEA) popularized the approach, and showed how humans depend on provisioning (products such as fibres, fuel and foods), regulating (for example climate, disease or water regulation) and cultural (recreation, education or heritage) services (MEA 2005). Humans modify the structure and functions of ecosystems, and thus affect the flow of services and human well-being (Costanza & Farber 2002). Hence, many conservation organizations and environmental decision makers worldwide have restructured their interventions around the concept of ES.

Payments for ecosystem (or environmental) services (PES) aim at promoting land-use practices that maintain or improve the provision of ES benefiting people other than the land stewards, such as regulating and cultural services. PES are voluntary conditional economic transactions through which ES beneficiaries provide land managers with economic incentives to adopt sustainable land uses (Wunder 2005). A pioneer national PES scheme has operated in Costa Rica since 1996 (Pagiola 2008). It considers four forest ES that have dominated PES schemes worldwide: biodiversity conservation (for global and national benefits), carbon storage (for global climate change mitigation), hydrological services (for downstream human consumption, irrigation and hydropower production), and scenic beauty (for ecotourism and recreation). Eligible land uses for PES are natural forest, plantation and agroforestry. In 2005, the programme covered *c.* 270 000 ha, of which 95% were allocated for forest conservation (Pagiola 2008).

In Costa Rica, the initial assumption in PES implementation was that standing forests per se are important for all these four services equally, without significant service trade-offs (Zhang & Pagiola 2011). However, if the ES concept is to become a fully operational planning tool, it is necessary to move beyond this simplistic perception. Important trade-offs have been recognized between ecosystem management for extracting tangible products (such as food and fibre) versus maintaining intangible services (for example water regulation) (MEA 2005; Rodríguez *et al.* 2006), but less attention has been given to the relationships between intangible ES (Daw *et al.* 2011).

Four categories of previous studies on the relationships between ES can be defined according to their spatial explicitness and their consideration of temporal dynamics. Using a static non-spatial approach, Kessler *et al.* (2012) measured carbon and biodiversity in different agroforestry plots in Sulawesi (Indonesia), and found little evidence of links between carbon storage and biodiversity. With a dynamic non-spatial approach, Chisholm (2010) modelled the temporal effects of afforestation on ES in a catchment

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in South Africa and showed that the benefits of carbon sequestration and timber production are balanced against the losses in water supply. Similarly, Bullock *et al.* (2011) showed that interventions to restore ecosystems for increasing the provision of one ES can benefit other ES, but that trade-offs can also arise. Several studies used a spatial static approach (Turner *et al.* 2007; Egoh *et al.* 2008; Naidoo *et al.* 2008; Pagiola *et al.* 2010; Raudsepp-Hearne *et al.* 2010; Larsen *et al.* 2011). For example, Bai *et al.* (2011) found positive correlations and high overlap between the hotspots of biodiversity and the three ES (water yield, soil retention and carbon sequestration) in a watershed in China. A few studies used spatial and dynamic approaches (Nelson *et al.* 2008, 2009; Haines-Young *et al.* 2012; Willemen *et al.* 2012). For example, Swallow *et al.* (2009) mapped the temporal evolution of two ES (erosion control and agricultural production) in a watershed in East Africa and found no significant relationships between these ES, which shows that presumptions of particular patterns of trade-offs between regulating and provisioning ES should be avoided.

Previous spatial studies on ES relationships have used three kinds of comparisons. First, some studies compare the priority areas of ES conservation policies. For example, Zhang and Pagiola (2011) found significant overlaps between the areas targeted for watershed and biodiversity conservation in Costa Rica, and discussed the spatial and financial feasibility of implementing PES in synergies, but without considering the ecological feasibility (i.e. a land use that provides one ES must also provide the other). Second, other studies compare ES by assessing either the spatial congruence between ES hotspots or the spatial correlations between ES provision. For example, Strassburg *et al.* (2010) analysed the congruence between biodiversity and carbon at the global scale using species and biomass indicators and found a strong positive relation between them. Third, some studies compare ES priority areas with ES provision. For example, studies showed that habitats under conservation (for example in protected areas) provide more regulating and cultural ES than other habitats in Europe (Eigenbrod *et al.* 2009; Maes *et al.* 2012*b*). Most of these studies focus on the effects of biodiversity conservation policies, such as protected areas or agrienvironmental schemes, on other ES (Chan *et al.* 2006; Egoh *et al.* 2009, 2011). With the prospect of large global investments in reducing emissions from deforestation and forest degradation (REDD), some studies have analysed how carbon policies could benefit biodiversity (Strassburg *et al.* 2010; Busch *et al.* 2011).

Mapping ES is at the heart of spatial analyses of ES relations (Eigenbrod *et al.* 2010; Maes *et al.* 2012*a*). Most mapping approaches assess only the provision of ES by ecosystems (Fig. 1), with primary information, land-cover proxies or causal relationships (Martínez-Harms & Balvanera 2012). As, by definition, ecosystem functions or processes become ES if they benefit people (Fisher *et al.* 2009), other studies consider both the ecological side of ES provision and the socioeconomic side of ES use or demand, but without analysing ES flows, either because demand is not assessed spatially or because ES provision and demand are assumed to occur at the same location (Luck *et al.* 2009; Eigenbrod *et al.* 2010; Raudsepp-Hearne *et al.* 2010; Willemen *et al.* 2012). Attention has been recently given to the scale of ES provision, the location of beneficiaries, and the flows of ES from ecosystems to humans, which are particularly relevant for spatially-confined ES (Locatelli *et al.* 2011*b*; Bagstad *et al.* 2013; Luck *et al.* 2012; Schröter *et al.* 2012). For example, Wendland *et al.* (2010) considered the location of beneficiaries of water ES in Madagascar, as well as directional water flows in landscapes.

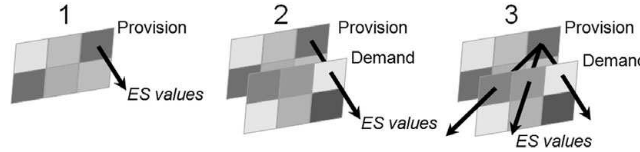

Figure 1 Three approaches to mapping ES values. (1) ES provision is spatially explicit but the spatial distribution of demand is not considered; (2) ES provision and demand are spatially explicit but ES is assumed to be produced and used at the same location; (3) ES flows are assessed from where they are produced to where they are used.

The aim of this study is to reflect on the synergies and trade-offs between ES, considering the insights gained from an empirical analysis in Costa Rica. We assess the spatial distribution of four ES at a resolution of 1 km and at the national scale, using indicators of service provision and demand. We analyse the correlations and spatial congruence between pairs of ES, and the synergies between policy instruments (national parks and PES) and the conservation of multiple ES. We hypothesize that ES are positively correlated in Costa Rica, and that areas in national parks or under PES provide high levels of ES.

METHODS

Assessment framework for matching provision and demand

We considered that different ecosystems have different capacity to provide ES (for example forests' water regulation depends on soils and slope), and that the values of ES produced by a specific ecosystem depend on the spatial characteristics of demand (such as the number of downstream water users) (Balvanera *et al.* 2001; Reyers *et al.* 2010; Locatelli *et al.* 2011*b*). We assessed and ranked ES by analysing the flows of ES between ecosystems and users.

We applied a multicriteria analysis with indicators of ES provision and demand (Fig. 2). Indicators were aggregated into provision and demand criteria, with normalization (if indicators had different units) and sum. In order to match provision with demand, we aggregated provision and demand criteria into ES values with the logical operator 'AND',

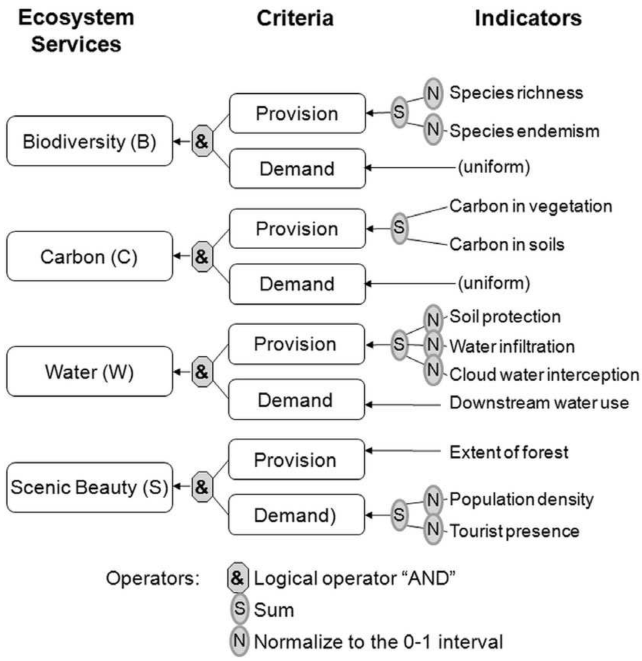

Figure 2 Assessment framework.

corresponding to the following logical proposition: 'The value of ES provided by a pixel is high IF the provision of ES by the pixel is high AND the population benefiting from the ES provided by the pixel is large'.

This approach is inspired by the fuzzy set theory (Zadeh 1965), which has been applied to sustainability assessment (Cornelissen *et al.* 2001), environmental impact evaluation (Enea & Salemi 2001) and natural resource management (Bender & Simonovic 2000). At the heart of fuzzy set theory is the notion of possibility, the degree of truth of a statement. Using the values of provision (or demand) indicators, we calculated the possibility that provision (or demand) is high. This possibility is equal to 0 if the value of the indicator is lower than the 10th percentile, equal to 1 if the value is higher than the 90th percentile, and linearly calculated between these two thresholds. We then aggregated the provision and demand criteria with the AND operator, assuming that both provision and demand must be high for an ES to have a high value and that a low value of demand is not compensated by a high value of provision (and vice versa). For example, if the statement 'provision is high' has a possibility (or truth value) of 0.31 and 'demand is high' has a possibility of 0.88, the statement 'ES value is high' has a possibility of 0.31, namely the minimum of the two possibilities.

Demand for ecosystem services

The provision of biodiversity-related ES, defined here as the conservation of the diversity of species, benefits society at local to global scales, for instance through the conservation of locally used species, strategic species for the national ecotourism sector, and globally rare species. Because of the diversity of scales at which the service is delivered and the lack of data on local biodiversity uses, we assumed that the demand was uniform, as in other studies (Wendland *et al.* 2010). This means that we accounted only for the benefits of biodiversity for the country as a whole and for the global society. Similarly, the demand for carbon was assumed to be uniform because the benefits of carbon for climate change mitigation are global, regardless of where carbon is stored.

In contrast, we assumed spatially heterogeneous demand for the other two services. We considered that the demand for hydrological services provided by a pixel was high if downstream water use or extraction was high (for example local use for irrigation or extraction, and transport to cities). As a proxy for water ES demand, we calculated an aggregated index of water intake as the mean of four normalized indices of abstracted volumes (for example by an aqueduct inlet) per square kilometre of upstream watershed (surface water for human consumption, agriculture and energy production) or aquifer (underground water for human consumption) (data sources are provided in Table S1, Appendix 1, see supplementary material at Journals.cambridge.org/ENC). Regarding demand for scenic beauty, we considered both people living in, and tourists visiting, the surrounding areas. As respective proxies, we used population density and the density of hotel rooms within a 5-km radius of a forest pixel.

Provision of ecosystem services

For the provision of biodiversity-related ES, we considered indicators of species richness and endemism. These indicators were taken from a regional database overlaying the distribution of thousands of species (Anderson *et al.* 2008). For carbon, we used indicators of above- and belowground carbon in vegetation, taken from a benchmark map of forest carbon density at 1-km resolution (Saatchi *et al.* 2011), and carbon in soils, calculated from data on soil organic matter, bulk density and gravel content (FAO [Food and Agriculture Organization of the United Nations] *et al.* 2009).

For the provision of water-related services, we took into account soil protection, water infiltration and interception of water from clouds. First, we considered that soil protection and the reduction of soil erosion represent key services of forests, as high sediment loads in water affect many water users (for example for drinking water, hydroelectricity generation and irrigation). The proxy used was the difference of soil erosion rates between forest and alternative land uses (pasture and cropland), and was estimated with the revised universal soil loss equation and data on precipitation, soil texture, soil organic matter and elevation to estimate rainfall erosivity, soil erodibility and slope factor (Table S1, Appendix 1, see supplementary material at Journals.cambridge.org/ENC). Second, we considered that forests that enhance water infiltration into soils and facilitate groundwater recharge contribute to the reduction of peak flows and the conservation of base flows in watersheds (Locatelli & Vignola 2009).

The proxy for water infiltration was the product of soil infiltration capacity and the effect of forests on infiltration. Although some studies have shown that primary forests contribute more to increasing water infiltration than secondary or degraded forests (for example Deuchars *et al.* 1999), no map of secondary forest was available for Costa Rica, so we assumed that the contribution by forests to increased infiltration depends only on soil infiltration capacity. Third, even though forests generally have higher evapotranspiration rates and produce lower annual water yields than pastures or annual cropping land uses (Bruijnzeel 2004), some forests, such as cloud forests, intercept water from the clouds and contribute significantly to seasonal water regulation in Costa Rica (Mulligan & Burke 2005; Imbach *et al.* 2010). To capture this important role of forests, we used as a proxy the amount of water intercepted by forests from clouds (Mulligan & Burke 2005).

For scenic beauty, we recognized that the capacity of a forest to provide this service is subjective, as different people may value the beauty of a landscape differently (for example human-modified versus pristine landscapes). Despite the usefulness of considering which features of scenic beauty are valued by different beneficiaries, we used the simplified approach applied in other studies (Wünscher *et al.* 2008) and supported by a study showing that residents and tourists in Costa Rica associate the enjoyment of scenic beauty with the presence of pristine forest areas (Biénabe & Hearne 2006). As a proxy of the provision of scenic beauty, we used the extent of forests within a 5-km radius.

Analytical method

All calculations and analyses were made with Matlab (The MathWorks Inc. 2008). The different proxies were mapped at a 1-km resolution. The indicators were summed and the truth-values of statements such as 'the provision of ES is high' were calculated. The truth-values for provision and demand were combined using the AND logical operator.

The spatial distributions of ES and their indicators were mapped. The correlations between the four ES and the indicators were evaluated using Spearman rank correlation. A pixel was defined as a hotspot (coldspot) for a given ES if its ES value was in the highest (lowest) 25% of values. The spatial overlaps among hotspots, and between hotspots and coldspots, were calculated for each pair of ES, in order to assess the probability for a hotspot of a given ES to be a hotspot or coldspot of another ES. Hotspots and coldspots were mapped for identifying areas with congruence or divergence between pairs of ES. We named the priority areas for each ES, using a division of the country in watersheds (a unit used for territorial planning).

The analysis was conducted across all forested areas in Costa Rica, including primary and secondary forests and mangroves (Fig. S1, Appendix 1, see supplementary material at Journals.cambridge.org/ENC). Although mangroves and public lands (such as national parks or biological reserves) are not allowed to receive payments under the national PES scheme, our study included them because we aimed at analysing the spatial relationships between ES in the whole country, independently of the existing PES scheme. However, we tested whether areas under PES or in national parks provide more ES than other areas by using a non-parametric Mann–Whitney U test. The location of the areas under PES between 2003 and 2010 was retrieved from the Fondo Nacional de Financiamento Forestal (FONAFIFO 2011) and the location of national parks from the Instituto Tecnológico de Costa Rica (ITCR 2004).

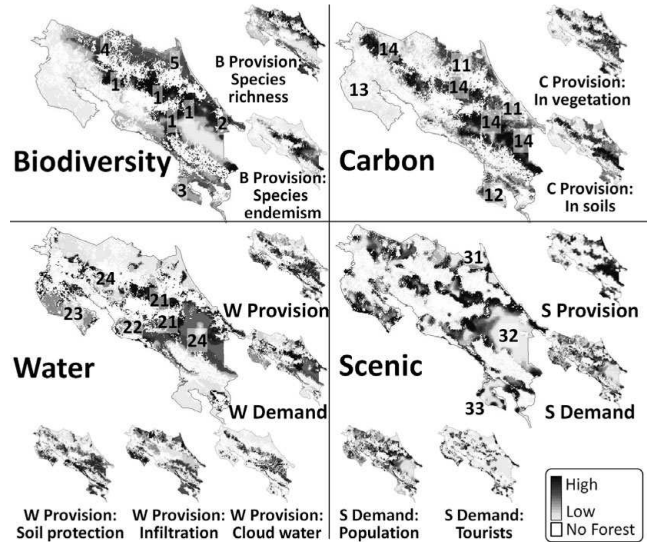

Figure 3 Maps of ES levels (four large maps) and their indicators of provision or demand (13 small maps) in Costa Rica forests (B: biodiversity, C: carbon, W: water, S: scenic beauty). Numbers refer to the sites mentioned in the text.

RESULTS

Correlations between indicators of service provision

The correlations between the indicators of ES provision show two groups of correlated indicators (Table 1). In the first group, positive correlations were observed between species endemism, carbon in vegetation, carbon in soils, cloud water interception, soil protection and the extent of forests. In the second group, positive correlations were observed between species richness and water infiltration. Detailed maps of ES indicators (Fig. 3) show that the indicators of the first group had high values in the central mountains (for example in sites 21 and 24) and low values in the lowlands (for example in sites 2, 3, 5 or 23), whereas the contrary was observed for the indicators of the second group. Only carbon in vegetation did not present such a contrast between mountains and lowlands.

Table 1 Spearman correlation values between the indicators of ES provision (ns = not significant at $p < 0.05$; *non-trivial absolute values above 0.50; B = biodiversity; C = carbon; W = water; S = scenic beauty).

	B. Species richness	*B. Species endemism*	*C. Carbon in vegetation*	*C. Carbon in soils*	*W. Soil protection*	*W. Water infiltration*	*W. Cloud water interception*
B. Species richness	1						
B. Species endemism	–0.37	1					
C. Carbon in vegetation	+0.18	+0.35	1				
C. Carbon in soils	–0.31	+0.69*	+0.38	1			
W. Soil protection	–0.31	+0.21	+0.10	ns	1		
W. Water infiltration	+0.13	–0.42	–0.23	–0.32	ns	1	
W. Cloud water interception	–0.53*	+0.64*	+0.26	+0.50*	+0.43	–0.27	1
S. Extent of forest	–0.20	+0.30	+0.38	+0.39	+0.11	–0.17	+0.31

Maps of service values

Biodiversity-related values were high in the forests of the centre of Costa Rica (for example site 1 in Fig. 3), in the south of the Caribbean Coast (site 2) and, to a lesser extent, in the Osa Peninsula (site 3), the north (site 4), and the north-east (site 5). Maps of biodiversity indicators show that biodiversity values resulted from trade-offs between species richness, high in the humid lowland forests (sites 2 to 5), and species endemism, high in the central mountains (site 1). Carbon-related values were higher in the tropical rainforests of the Atlantic lowlands (site 11) and Peninsula de Osa (site 12) than in the dry forests of the north-west (site 13). Highest values were found in the mountain humid forests of the central mountain range (site 14), particularly because soil carbon was very high.

Hydrological services had high values in the centre of the country around the capital city (site 21), where upland forests provided services to a large number of downstream water users. The indicators of water ES provision had different distributions: the service of soil protection was particularly high in the central Pacific region (site 22), where soils are erodible and slopes are steep; the service of water infiltration was high in the western Nicoya peninsula (site 23), where deep and sandy soils have high infiltration capacity; the service of cloud water interception was, as expected, high in the cloud forests of the central mountain range (site 24). Scenic beauty had high values in some localized spots at the edges of large forested areas and close to population or tourist centres. As demand and provision were negatively correlated ($r = -0.53$), scenic beauty values resulted from clear trade-offs between provision and demand (Fig. 3). For example, provision was very high in Peninsula de Osa (site 33), but demand was concentrated around a few touristic spots at the forest edge.

Correlations between service values

The correlations between ES values (the result of aggregating provision and demand) show that biodiversity and water were positively correlated to all other services (Table 2), whereas carbon and scenic beauty were positively correlated to two others. Higher hotspot overlaps were observed between biodiversity and any other service than for other pairs of services (Table 2). Biodiversity hotspots were more likely to be hotspots of multiple services than other ES hotspots. Similarly, a biodiversity hotspot had a low probability of being a coldspot of other services (Table 3).

Table 2 Spearman correlation values between ES (ns = not significant at $p < 0.05$; *the three highest non-trivial absolute values).

	Biodiversity	*Carbon*	*Water*
Biodiversity	1		
Carbon	+0.33*	1	
Water	+0.11	+0.23*	1
Scenic beauty	+0.26*	ns	+0.12

Synergies between policies and ES conservation

Our estimated values of biodiversity, carbon and scenic beauty were higher in areas under PES than in other areas, but the differences were slight (< 10%). Water ES were similar in PES and in other areas. Our estimated values of carbon and water ES were substantially higher in national parks than other areas (> 40% difference). With the chosen indicators for scenic beauty, the estimated values of this service were lower in national parks than in other areas, and biodiversity values were similar.

Maps of service hotspots and coldspots

The maps of hotspots and coldspots of pairs of ES (Fig. 4) show areas of congruence and divergence between ES in the country. For example, the central mountains (area 1) were hotspots for all four ES. La Amistad (area 2) was a hotspot for carbon, but a coldspot for biodiversity and scenic beauty. In Tempisque (area 3), hotspots for water services coincided with coldspots for biodiversity and carbon. Nicoya (area 4) was a hotspot for scenic beauty, but a coldspot for biodiversity and carbon. In Hitoy Cerere (area 5), hotspots for biodiversity and water services were observed along with coldspots for scenic beauty.

For management purposes, the identification of priority areas for ES conservation can be done at the scale of the 23 major watersheds of the country (Fig. S2, Appendix 1,

Table 3 Spatial congruence between ES hotspots and between hotspots and coldspots (B = biodiversity, C = carbon, W = water, S = scenic beauty). Expected values with random distributions = *25%, **57.8%, ***15.6%.

Probability		*If a hotspot of this service is selected (%)*			
		B	*C*	*W*	*S*
Probability of selecting a hotspot of:	B *	–	39	49	40
	C *	39	–	33	31
	W *	49	33	–	37
	S *	40	31	37	–
	At least one other service **	73	54	68	61
	At least two other services ***	42	36	39	34
Probability of selecting a coldspot of:	B *	–	22	18	15
	C *	4	–	20	20
	W *	14	9	–	17
	S *	16	24	22	–
	At least one other service **	28	39	38	35
	At least two other services ***	5	17	17	16

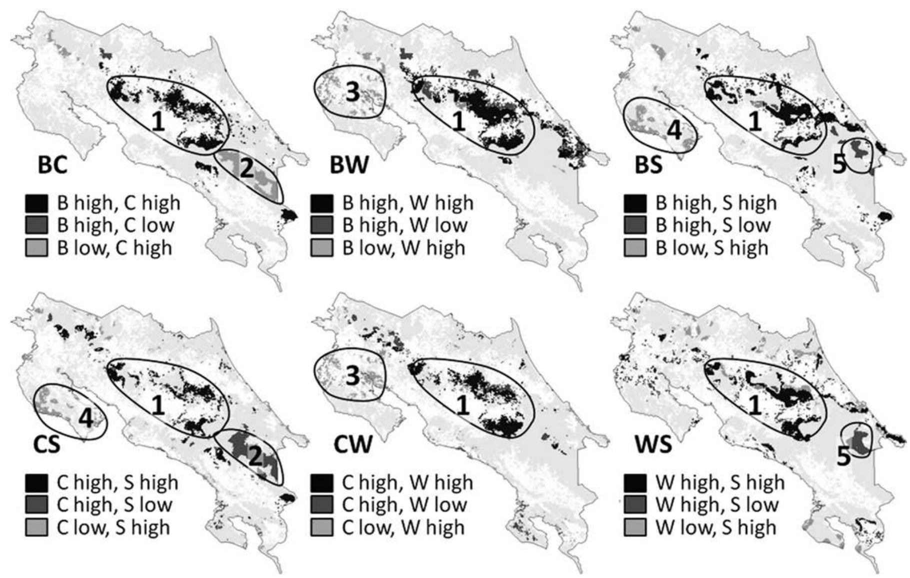

Figure 4 Maps of congruence and divergence between pairs of ES (B: biodiversity, C: carbon, W: water, S: scenic beauty). Numbers refer to the areas mentioned in the text.

see supplementary material at Journals.cambridge.org/ENC). The six most important watersheds for carbon and biodiversity host around 80% of the hotspots for these services. Water and scenic beauty hotspots were spread across the country, and the six most important watersheds for these services hosted only 65% of hotspots. Two watersheds were among the top six for all ES: Reventazon-Parismina, with hotspots for the four ES observed at 650–2000 m altitude, and Chirripo-Tortuguero, at altitudes > 550 m.

DISCUSSION

Explaining spatial relationships between services

The correlations between indicators of ES provision can be explained by ecological or geographical factors, such as topography, climate and biogeography. Some indicators (species endemism, carbon in soils, soil protection and cloud water interception) have higher values in the forests of the central mountains than in the lowlands. Other studies have shown that cloud forests and topographically dissected mountain areas have high endemism in the tropics (Gentry 1992; Aldrich 1997), and wet and highly organic soils in humid mountains store large amounts of carbon (Aldrich 1997; Raich *et al.* 2006). Steep slopes explain the importance of mountain forests in soil protection, whereas atmospheric moisture, temperature gradients, prevailing winds, topography and the orientation of the mountains explain the importance of cloud water interception (Bruijnzeel 2001).

Other indicators (species richness and water infiltration) have higher values in the lowlands than in the mountains of Costa Rica. For water infiltration, this is due to the distribution of soil types. For species richness, some authors have shown that tropical lowlands with high and evenly distributed rainfall present high species richness (Gentry 1992), which is the case in the northern and eastern lowlands of Costa Rica. The same contrast between lowlands and mountains is not observed for carbon storage in vegetation: it is high in wet or moist lowland forests, medium in the mountain forests, and low in dry lowland forests of the country, as confirmed by other studies in the tropics (Fehse *et al.* 2002; Raich *et al.* 2006; Keith *et al.* 2009).

The spatial distribution of the values of some ES provision indicators can also be explained by human factors. For example, the extent of forests in the south-east mountain range is related to patterns of development: cities and agriculture have developed in the central valley and the lowlands, while forests have been conserved in this mountain range (Veldkamp & Fresco 1997). The influence of human factors on ES values is clear for local services (water and scenic beauty), as their evaluation takes into account spatial variations in human demand. The distribution of these local ES is explained by the interface between ecology and society: values are high where people meet flows of services from ecosystems. The spatial patterns of settlements and economic development are thus important in explaining ES priorities and distribution.

In addition, past and present conservation policies can help explain the congruence between biodiversity, water and scenic beauty: large national parks in the mountains surrounding the densely populated central valley have preserved the essential provision of local ES (Veldkamp & Fresco 1997; Locatelli *et al.* 2011*b*). These forests are biodiversity hotspots thanks to biogeography factors combined with conservation policies, yet they also provide local ES to a large population who benefit from hydrological and recreational services alike.

Strengths and limitations of the approach

Our framework for mapping ES emphasizes the spatial congruence between the ecological side of ES production and the socioeconomic side of ES use or demand, following ES definitions stressing that a service is not an ecosystem function or process but the benefits that ecosystems provide to humans (Fisher *et al.* 2009). The explicit link between ecosystems and people is a strong point of our approach, but also a weakness compared to approaches based on purely ecological indicators, because adding demand indicators increases the normative loading of the set of indicators (Müller & Burkhard 2012). This weakness applies to local ES, for which demand was assessed.

For scenic beauty, we aggregated the demand from tourists and local residents, but we could not differentiate the way these two groups valued scenic beauty. We assessed the provision of scenic beauty by the extent of forests around a given point, because there is limited information about how different landscape features are valued by people. In addition, we considered that the spatial congruence between provision and demand was determined only by the distance from touristic or population centres to scenic views. This explains why our assessment resulted in low values for scenic beauty in large national parks, as their cores are far from touristic or population centres. Further work with a refined approach should consider where people travel, what landscapes they value, and how much they invest (in time or money) to enjoy scenic beauty. This would require collecting data on recreational preferences and practices of tourists and local populations.

For water ES, our approach assessed demand with the volumes of water abstracted for human consumption, agriculture and energy. An improvement would be to include other beneficiaries of services, such as recreational users or people living in flood-prone areas. The dependence of water users on ES and their capacity to adapt to the loss of ES could also be assessed (see Luck *et al.* 2009). For example, the contribution of forests to purifying water or conserving base flows is more valuable if people downstream depend only on water from rivers and have no alternative for water supply. A refinement of the method would be to disaggregate the services included in the water and scenic beauty categories, and consider different indicators for the demand of these services: for example, within the water ES, soil protection and water infiltration have different beneficiaries.

Another strength of our approach is to combine different spatial indicators of provision and demand from different data sources. However the choice of the indicators was constrained by data availability, as in most ES mapping studies (Eigenbrod *et al.* 2009; Bai *et al.* 2011; Luck *et al.* 2012). Biodiversity provision was derived from maps of species richness and endemism at the country scale. These maps do not consider fine-scale effects of disturbance or landscape fragmentation on biodiversity. This may explain why national parks, where disturbance and fragmentation are limited, did not appear with higher biodiversity values than in other areas. Our method could be improved by using the results of a meta-analysis on these effects (Alkemade *et al.* 2009), coupled with landscape analysis. The demands for biodiversity and carbon were assumed to be similar across the country, as in Wendland *et al.* (2010). While carbon storage contributes to climate change mitigation globally, biodiversity demand could be assessed differently, by considering local beneficiaries (such as ecotourism businesses or local communities).

In our framework, provision and demand were combined with the 'AND' logical operator, in line with our definition of ES, in which a service results from both provision and demand. This operator means that, if provision is high and demand is low at a given place and time, current ES value is low and the conservation of this ES is not prioritized. However, demand can change rapidly, for example because of new settlements where the ES is delivered, new recreation habits, or the installation of a water pumping station in the watershed. A refinement of our method could consider socioeconomic future scenarios, in order to explore whether a service with a low current value may be valuable in the future.

We identified ES hotspots and analysed their spatial overlaps, for example in the central mountains of the country. Identifying ES hotspots is a useful way to analyse spatial congruence and to help managers target interventions (Egoh *et al.* 2008). But the threshold for defining ES hotspots is arbitrary: here, as for Gimona and van der Horst (2007), we chose the quartiles as cut-off points, but other thresholds would have led to different results on spatial congruence. Furthermore, hotspot maps convey an uncompromising message to policymakers, namely that some areas are worth conserving, while others are not. Using ES values rather than hotspots would help better decisions to be made on conserving multiple ES.

We observed no negative correlations between ES, but this may be due to the few regulating and cultural services considered in this work, thus making it impossible to compare with the negative correlations between provisioning services and other ES that have been found in other studies (Chan *et al.* 2006; Raudsepp-Hearne *et al.* 2010)

Policy implications

As the assessment and mapping of ES are still at an early stage (Nelson *et al.* 2008), further research is needed on the relationships between ES to provide advice to policy making. Despite the limitations of our study, some implications can be drawn for policies in Costa Rica. The positive correlations between carbon, biodiversity and local services makes it possible to develop conservation policies with synergies for multiple ES, as in other countries (Chan *et al.* 2006; Turner *et al.* 2007; Bai *et al.* 2011; Egoh *et al.* 2011; Luck *et al.* 2012). According to our results, current conservation policy mechanisms in Costa Rica contribute to the delivery of multiple ES: protected areas provide high levels of carbon and water-related services, and PES areas provide high levels of biodiversity, carbon and scenic beauty. Spatial targeting to high-service areas has recently attracted interest in Costa Rica, particularly with respect to watershed and biodiversity protection. For example, a new water tariff will help in targeting PES at the most critical watersheds, offering higher per-hectare forest conservation payments than the previously uniform rate (Pagiola 2008). As five out of the six priority watersheds for water-related services in our analysis are also priority areas for other ES, this targeting will benefit multiple services.

Carbon and biodiversity appear to be positively correlated in Costa Rica, as in other studies with different spatial coverage and resolution (Egoh *et al.* 2009; Strassburg *et al.* 2010; Bai *et al.* 2011). However, our results show that more services are provided by biodiversity hotspots than carbon hotspots. Although it is specific to Costa Rica, this result calls for increased attention on environmental regulations focusing on carbon only, in line with recommendations from other studies (Strassburg *et al.* 2010; Busch *et al.* 2011). If instruments for climate change mitigation, such as REDD, are applied strictly from a carbon maximization viewpoint, they may not protect the forests that provide the greatest societal benefits in terms of biodiversity and local ES in Costa Rica. This does not mean that a REDD initiative would degrade services other than carbon, but rather that such an initiative could have greater co-benefits for local people and the country if priority areas were selected based on multiple ES values. This selection criterion could also foster synergies between policies for climate change mitigation (such as REDD) and adaptation (Locatelli *et al.* 2011*a*), as hydrological services can reduce the vulnerability of local populations to climate-related problems, and biodiversity conservation can increase the resilience of ecosystems to climate change.

The spatial patterns that we found also have implications for strategies to sell ES in bundles to the same buyer or layers to different buyers (Wunder & Wertz-Kanounnikoff 2009). For instance, the Global Environment Facility (GEF), with its mandate vis-à-vis carbon and biodiversity services, can bundle both services in PES interventions, as has already occurred in Costa Rica and elsewhere (Pagiola 2008). Yet, in Costa Rica, the GEF should not expect priority areas for these two services to automatically coincide; rather, only with detailed spatial information and analysis in hand, synergies between them could be optimized. Organizations focused on biodiversity conservation seem to have well-founded options to co-finance PES schemes through layering strategies involving either water users or ecotourism companies. While the first strategic alliance is already widely implemented in Latin America (Southgate & Wunder 2009), the second is still nascent.

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