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Spatial complexity and ecosystem services in rural landscapes

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ABSTRACT

Despite general agreement on antagonist relationships between ecosystems capacity to simultaneously sustain the availability of regulating services and agricultural production, it is not clear how these tradeoffs operate in response to complexity loss at the rural landscapes level. Here we present a novel evaluation framework of ecosystem services (ES) and pose different response models to landscape complexity. Therefore, we tested the hypothesis that complementarities among different ES types increase and the strength of their apparent tradeoffs diminishes with the spatial complexity of the rural landscapes, using a one million has basin of the Argentine pampas as study case. According to correlation and principal component analysis, main ES tradeoffs among ES availability observed at two spatial scales were represented by crop production *vs.* the other evaluated ES types (OES), and in contrast with our prediction, their strength was not higher for the fine- than for the coarse-scale (relatively large and internally complex observation units). Landscape composition and configuration indices showed a complementary capacity to explain spatial variation in OES, but combinations of configuration indices showed a higher explanatory value than composition ones. Widely accepted tradeoffs among ecosystem services at local levels, not only were able to explain their antagonistic but also their synergistic availability at intermediate levels of conversion of managed grasslands to croplands, depending on the evaluation scale. Despite intermediate complexity hypothesis was only partly supported by our results, these offer novel evidences about emergent responses in the form of nonlinearities and thresholds of total ES in relation to landscape complexity, which deserve further attention because of their relevance for land use planning.

1. Introduction

In contrast with a farming-centered point of view which dominates the analysis of agricultural landscapes, rural landscapes provide a wider knowledge-action arena where a mixed array of social actors (scientists included) meet to cooperate and/or to compete for production, conservation and recreation objectives, as well as for scientific understanding and management decisions. Therefore, rural landscapes actors must cope with difficulties in predicting system properties from their many and interacting landscape components, that is to say, they must cope with functional and spatial complexity of rural landscapes.

Spatial complexity of rural landscapes results from the dynamic interaction between the spatial distribution of biophysical cues and variable human actions. While simplification of rural landscapes (e.g. conversion of managed grasslands to croplands) favors the channeling of solar and subsidized energy and ultimately rises the agricultural production and economic profitability, the associated biodiversity loss and the impairment of different ecosystem processes can negatively affect the agricultural sustainability (Dauber et al., 2003; Honnay et al., 2003; Rodríguez et al., 2006; Dalgaard et al., 2007; Ryszkowski and Karg, 2007) as well as the availability of other ecosystem services (Bennett and Balvanera, 2007; Persson et al., 2010). Here we consider ecosystem services (short for ecosystem goods and services) as those benefits from ecosystem functioning available to human individuals and society; hereafter, ES) (Boyd and Banzhaf, 2007; Wallace, 2007).

Gains in productivity and predictability of agricultural production by the conversion of “natural” landscape elements and loss of ecosystem services (ES) are a source of stakeholders' conflicts. Notwithstanding a general agreement exists about tradeoff influences on the ecosystem capacity to sustain regulating ecosystem services while facing their agricultural conversion (MA, 2005), it is not clear how these tradeoffs operate in response to complexity loss at the rural landscapes level. In particular, while fixed land cover-ES relationships are frequently assumed in tradeoff analysis of ecosystem services (Guo et al., 2003; Viglizzo and Frank, 2006), other authors advocate for the existence of complementarity

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among different ES at the landscape level as support for the multifunctional land use concept (e.g. Chan et al., 2006).

Complementarity of ES could be considered a functional property of rural landscapes related to their landscape complexity (LC) among other emergent properties. While testing for ES–LC relationships has a clear relevance for environmental management and planning science, it has received little attention in the published literature.

Although many ecosystem processes not only vary with biophysical and social properties of the sites but also with properties of their spatial context (Boyd et al., 2001; Dalgaard et al., 2007), most studies address the complexity of rural landscapes by reducing it to the relative area of crop *vs*. non-crop "more complex" land cover classes (e.g. Menalled et al., 2000; Roschewitz et al., 2005a). However, human influences on ecosystem complexity cannot be linearly scaled from the ecosystem to the landscape level and scientific supporting for land use planning requires improving our ability to move from "how many biodiversity is enough" to "how many LC is enough" questions. Unfortunately, LC is a multidimensional property of landscapes depending both on their composition (e.g. proportion of non-arable land, covert types diversity) and their spatial configuration metrics (e.g. number, size, shape, diversity and connectivity of patches) which are only partly correlated among them (Roschewitz et al., 2005b), thus making difficult to select simple LC descriptors. For example, if the proportion of arable land is largely uncorrelated with the spatial configuration metrics, as reported for agricultural landscapes of North Germany by Roschewitz et al. (2005a,b), assessments of ES–LC relationships exclusively based on the proportion of non-arable land are probably overstating the occurrence of tradeoffs between crop production *vs.* complexity-dependent ES.

In this paper, we aimed to analyze the influence of spatial complexity on the availability of relevant ES provided within rural landscapes. As a general hypothesis we pose that the strength of tradeoffs among the availability of different ES diminishes, and their complementarity increases with the spatial complexity of the rural landscapes. Also we predict that: (a) because higher environmental heterogeneity is comprised within large than within small samples of a similar landscape, tradeoffs strength will increase with the resolution of the observation scale, (b) when at least some ES types are evaluated considering both local and context properties affecting the functional capacity of ecosystems, non-linear responses to LC can be expected, and ecological thresholds can give place to optimal LC levels maximizing overall ES availability.

In order to test for our predictions, first we describe an evaluation framework of ES and pose different response models to landscape structure. Second, we present and discuss the results of a static evaluation of ES within the Mar Chiquita basin, in the Argentine Pampas, where relative prices of crop and husbandry products have recently driven a new pulse of crop expansion over native grasslands and pastures (Manuel-Navarrete et al., 2009).

2. Evaluation framework of ecosystem services

Suitability of models and frameworks for testing our hypothesis greatly depends on their ability to take into account the influence of spatial context for the evaluation of context-dependent ES types, so we applied a recently proposed framework (ECOSER: Laterra et al., 2009, in press). ECOSER is aimed to evaluate ES availability in a spatially explicit manner, based on the integration of models and indexes describing ecosystem functions (ecosystem processes supporting ecosystem services, de Groot et al., 2002; hereafter, EF) into relative (unit-less) ES values (module 1), and the assessment of ES's vulnerability according to the social capture and distribution and ecosystem recovery after eventual agricultural replacement and abandon (module 2). Therefore, a functional evaluation of ES was performed here by applying the module 1 of the ECOSER procedure to a series of grid–grid-cells defined over a raster-based GIS (see Appendix A for a flowchart of this procedure).

A set of $i = 6$ ES types were selected and modeled at the grid-cell scale as the linear combination of $j = 8$ EF types (EF_j), where each EF_j was subjectively weighted according to a contribution factor expressing the relative influence of each EF_j on each ES_i, as follows:

$$ES_i = \sum (a_{ij} * EF_j)$$

where ES_i is the calculated value of the *i*-ES of the grid-cell, EF_j is the mean value of *j*-EF among the minimum spatial units (pixels) within the grid-cell, a_{ij} is the contribution factor of each *j*-EF to each *i*-ES.

All data analysis were performed on [0,1] normalized values of EF_j and ES_i and it is worth noting that although they are scaled to grid-cell size, they ultimately depend on model and indices about functional capacity of ecosystems calculated at the pixel scale. Models and indexes used here for EF evaluation are resumed below.

2.1. Functional capacity of ecosystems

Functional capacity of ecosystems within each pixel was evaluated adopting or developing models and indexes according to their suitability for handling the limited data base available for the study area, as detailed below.

2.1.1. Soil carbon storage

Carbon sequestration, the addition rate of carbon to its different sinks, dominates the analysis of ecosystem influences over the atmospheric composition. However, carbon sequestration rate is in general of little relevance when compared to C emissions associated to loss of soil organic content (SOC) after replacement of grassland ecosystems (the native vegetation cover in most of the study area) by annual. Global data compiled by Jobbágy and Jackson (2000) suggests that croplands offer a 50% of the SOC in grassland soils, and this figure agrees with differences observed between grasslands and croplands over similar soils in the study area (Costa and Aparicio, unpublished data). For simplicity, here we evaluate the soil carbon storage as the SOC of top soils according to soil types and their properties mapped at 1:500,000 scale (INTA and SAGyP, 1990), affected by a land use factor $F = 1$ for grasslands cover and $F = 0.5$ for annual crops.

2.1.2. Erosion control (EC)

EC is defined here as the capacity of ecosystems in the pixel for retaining sediments in response to large storm events and in relation to maximum sediment loss, and calculated as:

$$EC = RUSLE_{max} - RUSLE_j$$

where $RUSLE_{max}$ and $RUSLE_j$ are the Universal Soil Loss Equation (Renard et al., 1997) parameterized for bare soil and the cover class of the *j*-pixel, respectively.

2.1.3. Wetland water holding capacity (WWHC)

WWHC is the ability of wetlands to trap and slowly release surface water after water excess periods and thus exert a strong influence on the hydrological cycle (Bullock and Acreman, 2003). This function depends on the cover and spatial distribution of both flood plains and wetlands, but here we focused on the last for simplicity. The effectiveness of wetlands for flood abatement may vary, depending on the size of the drainage area, type and condition of vegetation, slope, location of the wetland in the flood path and the saturation of wetland soils before flooding. In this study, we assumed that WWHC for a given wetland pixel mostly depended on the combined influence of the wetland volume, and its mean wetness according to procedures detailed in Appendix C.

2.1.4. Aquifer protection by vegetation cover

Underground aquifers are the most important source of water of the Pampa region and the unique water source used for drinking, crop irrigation and industrial processes within study area. No local studies exist about dependence of aquifer recharge and quality on vegetation cover, except for some relationships between nitrate content and land use type (annual crops *vs.* grazing system over native grasslands (Costa et al., 2002). Here we assumed that the relevance of natural ecosystems for protecting the aquifer quality in the pixel depends on the intrinsic risk of aquifers to become contaminated by agrochemicals leaching, and it was calculated by using two components of the DRASTIC index (Aller et al., 1985), hydraulic conductivity and aquifer depth, which were selected because of their data availability, relevance and variability within the study area.

2.1.5. Runoff filtration by riparian vegetation (RFVR)

RFVR is the ability of strip belts at both sides of streams to retain sediments, nutrients and other contaminants transported by the runoff water before entering into superficial water bodies. In the practice, RFVR was calculated for those pixels neighbor to streams as a multiplicative index combining: (1) the contaminants loading rank (C), (2) the efficiency of sediment retention rank (*E*). See other details in Appendix A.

2.1.6. Water filtration by wetlands

The evaluation of this function was based on spatially explicit models of export, transport, accumulation, retention and decay of nitrogen and phosphorus, which were integrated in ArcGis 9.2, following procedures devised by Booman et al. (2010), which basically consisted in the simulation of nutrients loads in runoff meeting wetlands, for the calculation of wetlands potential retention capacity according to empirical equations (Kadlec and Knight, 1996; Byström, 1998). Models are mainly based on land use, topography, and soil type maps, as well as secondary data such as curve numbers, surface rugosity, water flow velocity and time for nutrient decay processes. A detailed description of models and their integration procedures is provided in Appendix C.

2.1.7. Water infiltration capacity

Water infiltration capacity is defined here as the portion of a stormy rain which is able to penetrate the soil instead to runoff, and it was calculated following the Soil Conservation Service curve-number (SCS-CN) approach. This method is based on an empirical index (CN) that represents the likelihood that rainfall will become runoff and results from the combined hydrologic effect of soil, land cover, land treatment, and antecedent soil moisture.

2.1.8. Productivity index

The capacity of a landscape portion (grid-cell) to support plant growth and primary productivity was characterized by a multiplicative productivity index (PI) developed by Riquier et al. (1970), who reported a linear relationship between crop yields and PI. The PI is composed by a series of soil (wetness, drainage, effective depth, texture and structure, alkalinity, soluble-salt concentration, organic matter, cation-exchange capacity, mineral reserves, soil erodability) and climate factors affecting primary productivity. The PI was previously applied for ES evaluation by Viglizzo et al. (2004).

2.2. Types of ecosystem services

Direct benefits of the above explained ecosystem functions were integrated into the following six ES types: (1) attenuation of flooding impacts, (2) maintenance of clean water bodies, (3) maintenance of aquifers quality, (4) crop production, (5) animal production, and (6) climate regulation. Crop production and animal production were estimated through the productivity index, assuming that at the study scale both of them mostly depend on productive properties of soil. Despite of both crop and animal production were calculated on basis the same ecosystem function, their flow within grid-cells were corrected by the relative cover of annual crops or grasslands plus cultivated pastures, respectively.

3. ES–LC models

Tradeoffs between crop production (CP) *vs.* other ecosystem services (OES) availability were previously represented by plotting them against the proportion of cultivated land, and optimal proportion of landscape cultivation for assuring equilibrate availability of different ES types was proposed at the cross cutting between the CP and the OES curves (Viglizzo and Frank, 2006). A modified approach for the identification of optimal level of land transformation, consist in the expression of OES and CP in relation to their respective maximum and minimum values within the landscape), and calculating the relative total availability of ecosystem services (TES) as the sum of relative CP and OES values, by analogy to the analysis of substitutive competition experiments commonly performed among plant species (Harper, 1977). The main advantage of the resulting ES–LC diagrams is that they allow for the identification of landscape transformation levels where ES tradeoffs may be minimized or even overcome through complementary among different land covers and land uses. Complex responses including possible thresholds for TES because of antagonistic ES relationships could also be expected (Fig. 1). In this way, ES–LC diagrams performed at multiple scales could provide criteria for identification of areas with high potential for multifunctional use, or for identification of areas with strong ES losses and potential stakeholder conflicts.

4. Application

Predictions about ES–LC relationships were tested by applying the ES evaluation framework to the analysis of the Mar Chiquita's basin, which consist in an agricultural landscape of about one million hectares located at the south east of the Buenos Aires province, in the Pampas ecoregion of Argentina. One of the less modified ecosystem within the study area consist of lowland grasslands (19% of total area), K. Zelaya (pers. comm.) remaining in non arable areas of the Flooding Pampa (León, 1991) and wetlands (4% of total area). Most of annual crops cover (48% of total area) is concentrated on slightly undulated plains around the Tandilia mountains in the Austral Pampa region, were the highland grasslands (2% of total area) remain over the non-arable mountains. No native forests cover the Austral Pampa nor the Flooding Pampa (except for small patches dominated by low trees near the Atlantic coast (León, 1991), but a 2% of the total study area is currently covered by cultivated forests (mostly *Eucalyptus* spp.). Variation of ES availability and landscape metrics within Mar Chiquita's basin was explored using two different scales: (a) a grid of 121 8 km × 8 km grid-cells (hereafter, "fine grain" scale) and (b) a grid of 30 20 km × 20 km grid-cells (hereafter, "coarse grain" scale).

Geo-referenced data about land cover and soil properties was provided by the Geomática Lab at the INTA Balcarce, and altitude plus slope maps were derived from a digital elevation model obtained from SRTM images with 76.69 m^2 of resolution. Land cover was reclassified into the following land-use/land-cover (LULC) classes: extensive crops (hereafter annual crops), intensive (vegetable) crops, cultivated pastures, lowland grasslands, highland grasslands, streams, wetlands, cultivated forests. Landscape within each cell of the grid was characterized by calculating a series of both composition and spatial configuration indices for the main

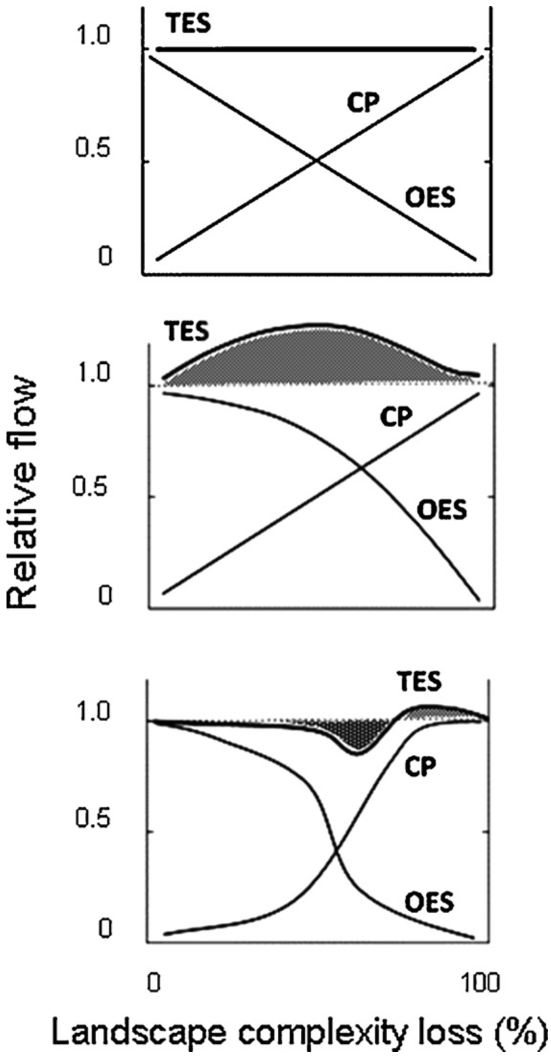

Fig. 1. Hypothetical relative flow of crop production (CP), other ecosystem services (OES), and total availability of ecosystem services (TES = CP + OES) in response to different levels of complexity loss by crop fields' expansion (ES–LC diagrams). Light gray filled areas correspond to landscape complexity levels where functional complementarity between transformed and untransformed areas leads to TES greater than 1 (synergistic ES availability); dark gray filled areas correspond to landscape complexity levels where CP gains are not able to compensate for OES losses.

cover classes, annual crops and lowland grasslands, using the Spatial Analyst and V-LATE 1.1 extensions in ArcGis 9.2.

Data, parameters and other details of EF evaluation and weighting factors of EF into their supported ES are provided in Appendices B and C, respectively.

4.1. Analytical procedures

Main landscape patterns within the study area were explored through principal component analysis (PCA) over standardized composition (cover of annual crops, cover of cultivated pastures, cover of lowland grasslands, cover of highland grassland, cover of wetlands, and cover of riparian vegetation strips), and configuration indices (number of patches, largest patch index, mean patch size, patch size coefficient of variation, total edge, edge density, mean shape index, mean nearest neighbor, mean proximity index) calculated for annual crops and lowland grasslands at grid-cell scales using ArcView GIS 9.1 and its extension Patch Analyst. Correlation structure among the ES types was explored through PCA on standardized availability of different ES (flooding attenuation, maintenance of clean water bodies, maintenance of aquifers quality, crop production, animal production, and climate regulation), and tradeoffs strength among different ES was estimated through correlation analysis. Pearson correlation coefficients (r) were compared following the Fisher procedure.

Relationships between ES and landscape metrics were described by simple and multiple regression analysis. The relative importance of composition *vs.* configuration indices for explaining SE availability was compared by considering the adjusted R^2 of the multiple regression analysis and the Mallow's Cp criteria using Infostat (Balzarini et al., 2008). Aiming to avoid usual redundancy and collinearity among landscape indices, ES variation was fitted to factor scores of PCA performed over landscape metrics instead of fitting to variation in the original indices. Notwithstanding some ES types were partly calculated from landscape attributes, non-trivial relationships between total ES availability and landscapes indices (LI) were expected because: (a) simulated total ES availability mostly result from combination of EF models considering other than landscape configuration indices (landscape metrics), and (b) while ES availability is expressed for arbitrary landscape units, their supporting EF were simulated at watershed scale. Moreover, we were not focused on testing the significance but exploring the structure and strength of ES–LI relationships, so we only applied regression and correlation analysis for descriptive purposes. Therefore, selection of analytical procedures was intended to highlight the influence of complexity in ES evaluation procedures as well as the ability of landscape features to predict on ES availability and their expected trade-off consequences.

ES–LC diagrams were constructed for contrasting ES groups according to the PCA results, which is crop production and the rest of ES. As descriptors of landscape complexity, here we used the relative cover of non-converted ecosystems, calculated as the difference between 100% and the cover of annual crops plus urbanized areas.

5. Results

5.1. Crop cover and landscape complexity

A 46% of the total variation in landscape composition plus landscape configuration indices calculated for the fine-grained scale was absorbed by the first principal component (PC1), which mainly increased with the cover of lowland grasslands, with their edge density and their patch size variability, with the number of patches of annual crops, and in minor extent, with the cover of cultivated pastures, wetlands and riparian vegetation. PC1 also decreased with the cover of annual crops, with their patches aggregation and with their border's irregularity, as well as with the aggregation of patches of lowland grasslands (Fig. 2).

Complementary (independent) variation pattern of landscape metrics offered by the second PC explained an additional 14% of total variation, and mostly consisted in a contrast between landscapes with relatively high cover of highland grasslands, wetlands and highly connected crop patches (MNN_C) *vs.* landscapes with relatively high cover of riparian vegetation strips, high edge density of annual crops (Fig. 2). Apart from its contribution to the PC1 variation, cover of annual crops did not significantly correlated with any other principal component.

Shannon's diversity index (SI) showed non-significant correlations ($R < 0.33$) with the first seven PC axis (altogether accounting for 90% of total landscape variation) except for the first PC ($r = 0.64$, $p < 0.001$). Therefore, first PC could be considered as a gradient of landscape complexity inversely related to the relative cover of annual crops level ($r = -0.86$, $p < 0.001$) and with mean terrain altitude ($r = -0.81$, $p < 0.001$) by grid-cell.

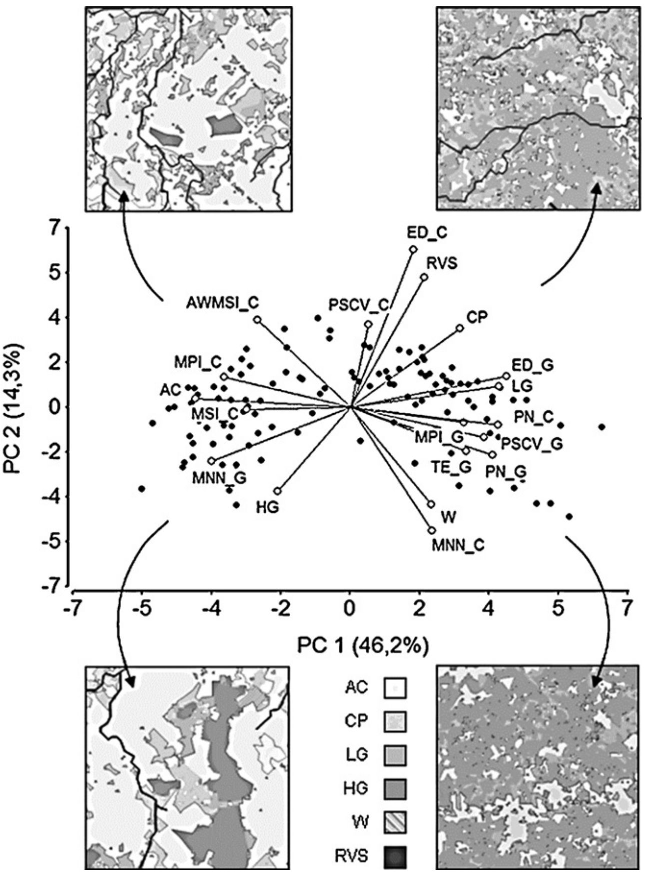

Fig. 2. Biplot of landscape metrics and 8 km × 8 km landscape cells (fine-grain grid) along the first and second principal components (PC 1 and PC 2, respectively) obtained from a principal component analysis performed over composition and configuration landscape indices calculated for annual crops (_C) and lowland grasslands (_G). AC: cover of annual crops, CP: cover of cultivated pastures, LG: cover of lowland grasslands, HG: cover of highland grassland, W: cover of wetlands, RVS: cover of riparian vegetation strips, PN: number of patches, LPI: largest patch index, MPS: mean patch size, PSCV: patch size coefficient of variation, TE: total edge, ED: edge density, MSI: mean shape index, MNN: mean nearest neighbor, MPI: mean proximity index. Figures between brackets are the percent of total inter-cell variation explained by the corresponding axis.

A similar PCA for the coarse-grained scale is not presented here because of space restrictions, but it is worth noting that mean SI was significantly greater for the large grid-cells than for the small grid-cells (1.39 and 1.18, respectively, $T = 6.84$, $p < 0.0001$).

5.2. Tradeoff analysis

Pearson correlation analysis revealed negative relationships between crop production within grid-cells and their capacity for providing animal production, and maintenance of clean water bodies, and maintenance of aquifers quality. In contrast, animal production, maintenance of clean water bodies, and maintenance of aquifers quality were all positively correlated among them (Fig. 3). Despite all these correlations were found at both analyzed scales, correlation strengths were slightly but significantly ($p \leq 0.05$) higher for coarse- than for the fine-grain scale (Fig. 3). Therefore, positive correlations among the flooding attenuation maintenance of clean water bodies, and maintenance of aquifers quality, as well as a negative correlation between flooding attenuation and climate regulation were observed at the fine-grain but not at the coarse-grain scales.

According to PCA on ES types, main variation patterns of simulated availability of different ES types among fine-grain landscapes are represented by two independent tradeoffs accounting for 73% of total ES variation among grid-cells. These tradeoffs consisted in a contrast between crop production and the rest of ES (PC1, 41.8% of total variation, loadings not shown), and a contrast between the flooding attenuation *vs.* the global climate regulation services (PC2, 25.4% of total variation, Fig. 3a), which agree with results from univariate correlation analysis. While PC1 increased with the mean terrain altitude and with the mean slope by grid-cell (Pearson $r = 0.78$, $p < 0.001$, and $r = 0.48$, $p < 0.001$, respectively), PC 2 showed an opposite and weaker correlation with these variables (Pearson $r = -0.22$, $p < 0.01$, and $r = -0.27$, $p < 0.001$, respectively). Despite main variation pattern of ES availability was very similar when

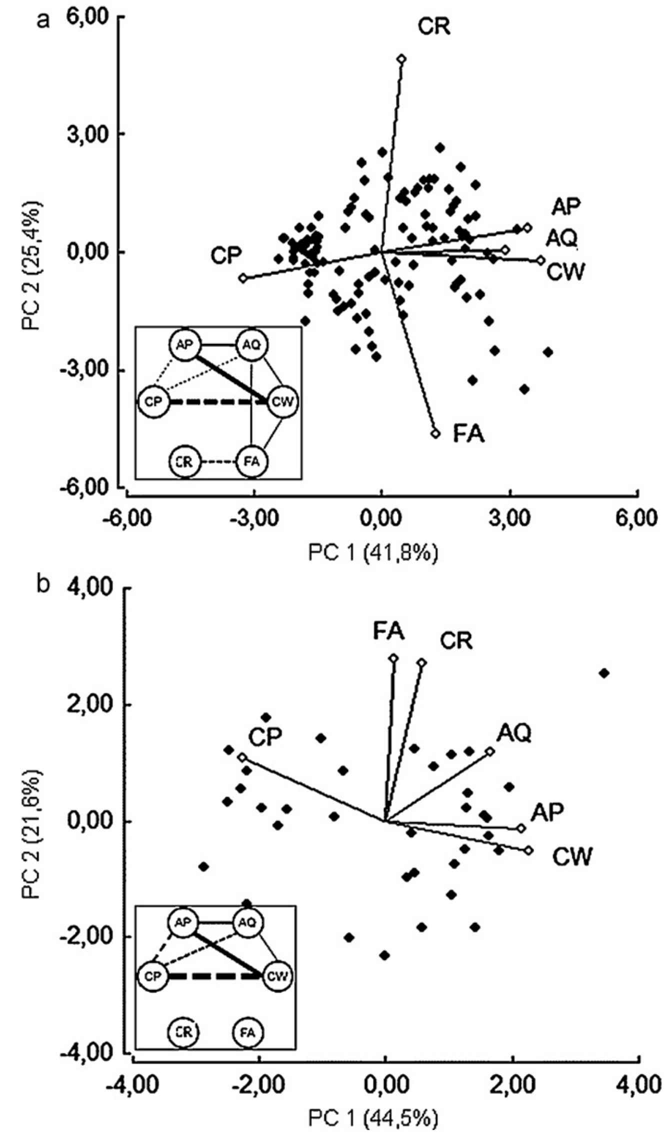

Fig. 3. Biplot of landscape cells defined by fine-grain (a) and coarse-grain (b) grids along the first and second principal components (PC 1 and PC 2, respectively), obtained from principal component analysis performed over availability of different ecosystem services types by cell. Figures between brackets are the percent of total inter-cell variation explained by the corresponding axis. Boxes within the biplots represent the correlation coefficients among ecosystem services calculated among landscape cells defined by fine-grain (a) and coarse-grain (b) grids, where FA: flooding attenuation, CW: maintenance of clean water bodies, AQ: maintenance of aquifers quality, CP: crop production, AP: animal production, CR: climate regulation. The thin, medium, thick and very thick lines linking different ES represent low, medium, high and very high correlation coefficients ($r < 0.40$; r between 0.41 and 0.60, r between 0.61 and 0.80, and r higher than 0.80, respectively); continuous and broken lines represent positive and negative r values, respectively. Only significant r values for $p < 0.05$ are represented.

Table 1
Simple and multiple regression models of crop production (CP) and other ecosystem services (OES) in relation to landscape composition and configuration indices.

Model[a]	Dependent variables	Adj R^2	Parameter[b]	Estimated beta values	SE parameter	Cp Mallows[c]
1	CP	0.66	Constant	0.75	0.05	–
N = 114			LG	−0.02	1.1E−03	–
2	CP	0.93	Constant	−0.16	0.02	
N = 114			AC	0.01	3.3E−04	
3	OES	0.68	Constant	0.12	0.02	–
N = 114			LG	0.02	9.7E−04	–
4	OES	0.65	Constant	0.85	0.03	–
N = 114			AC	−0.01	6.4E−03	–
5	OES	0.77	Constant	0.19	0.15	
N = 114			AC	−2.1E−03	1.7E−03	7.57
			LG	0.01	2.0E−03	41.56
			HG	0.01	2.8E−03	13.33
			CP	0.01	1.7E−03	16.56
			RVS	−4.3E−03	0.01	6.57
			W	−3.5E−03	2.8E−03	7.50
6	OES	0.82	Constant	0.22	0.14	
N = 113			AC	−1.8E−03	1.7E−03	12.16
			LG	0.01	2.3E−03	26.18
			HG	0.01	2.6E−03	24.07
			CP	3.5E−03	1.7E−03	15.31
			RVS	1.1E−03	0.01	11.04
			W	4.7E−03	3.2E−03	11.03
			PC 1	0.02	0.01	13.60
			PC 2	1.8E−03	0.01	11.05
			PC 3	0.05	0.01	33.46
			PC 4	0.02	0.01	13.48
			PC 5	−0.01	0.01	11.71
7	OES	0.81	Constant	0.44	0.07	
N = 113			PC 1	0.04	0.01	9.46
			PC 3	0.06	0.01	50.70
			LG	0.01	1.6E−03	22.74
			AC	3.5E−03	1.1E−03	15.09
			HG	0.01	2.1E−03	10.89

[a] Predictor variables: relative cover of the most extended cover classes (simple regression models 1–4 and multiple regression model 5), both composition and configuration indices (model 6), and a stepwise selection of both composition and configuration indices (model 7).
[b] Composition indices are cover of annual crops (AC), lowland grasslands (LG), highland grasslands (HG), cultivated pastures (CP), riparian vegetation strips (RVS) and wetlands (W). Configuration indices are the first five principal components of a principal component analysis performed over a set of 14 configuration indices.
[c] Mallow's Cp coefficients of independent variables were only calculated for significantly (p < 0.05) fitted models. Significance levels for complete models were not included because the analysis objective was focused on the relative predictive value of independent variables.

observed at fine and coarse-grain scales (Fig. 3a and b, respectively), the independent flooding attenuation *vs.* climate regulation trade-off described for the fine-grain scale was missing in the coarse one.

5.3. ES and landscape relationships

When the main variation pattern for the simulated availability of ES was separately analyzed for its two opposite components (crop production *vs.* the rest of ES), they showed good fits to simple linear functions for the two most important cover types (Table 1) but the rest of the cover types did not show a good predictive capacity for the summed availability of other ES (R^2 < 0.35). While crop production variation with the cover of annual crops were satisfactory described by simple linear models (model 2, Table 1), fitting to the rest ES (OES) was improved through different multiple linear models. Predictability of the OES availability was 13% improved by fitting a model composed by all cover classes set where, according to Cp Mallows index, lowland grasslands contributed to the predictive capacity of the model in more than 250% of any other independent variable of the model (model 5). Adjusted R^2 increased an additional 6% when including into the model all cover classes set plus main landscape configuration patterns as predictor variables (complete model, model 6), leading to the highest Cp Mallows index value for the configuration descriptor PC 3. A similar fitting level to the complete model was obtained by applying a stepwise selection of both composition and configuration indices (model 7) where the Cp Mallows index for PC 3 was more than 100% higher than any other independent variable of the model. According to their Pearson correlations with the original configuration variables, the main synthetic predictor of the landscape-configuration influence on OES variation (PC 3) consisted in a contrast between the edge density of annual crops (r = 0.71, p < 0.001), the mean fractal dimension, and mean shape index of lowland grassland patches (r = 0.51, p < 0.001, and r = 0.38, p < 0.001, respectively) *vs.* the total edge, mean patch size, and the mean nearest neighbor of lowland grassland patches (r = −0.40, p < 0.001, r = −0.40, p < 0.001, and r = −0.39, p < 0.001, respectively), and the mean patch size of annual crops (r = −0.40, p < 0.001). The other descriptor of landscape configuration entering within model 7 (PC 1) represented a contrast between the landscape shape index (r = 0.95, p < 0.001), edge density (r = 0.92, p < 0.001) and total edge (r = 0.84, p < 0.001) of lowland grasslands *vs.* the largest patch index (r = −0.88, p < 0.001), mean proximity index (r = −0.74, p < 0.001) and mean patch size (r = −0.71, p < 0.001) of annual crops. Therefore, according to model 7, OES availability not only increases with cover of highland and lowland grasslands, but most importantly, when the landscape is a complex and inter-

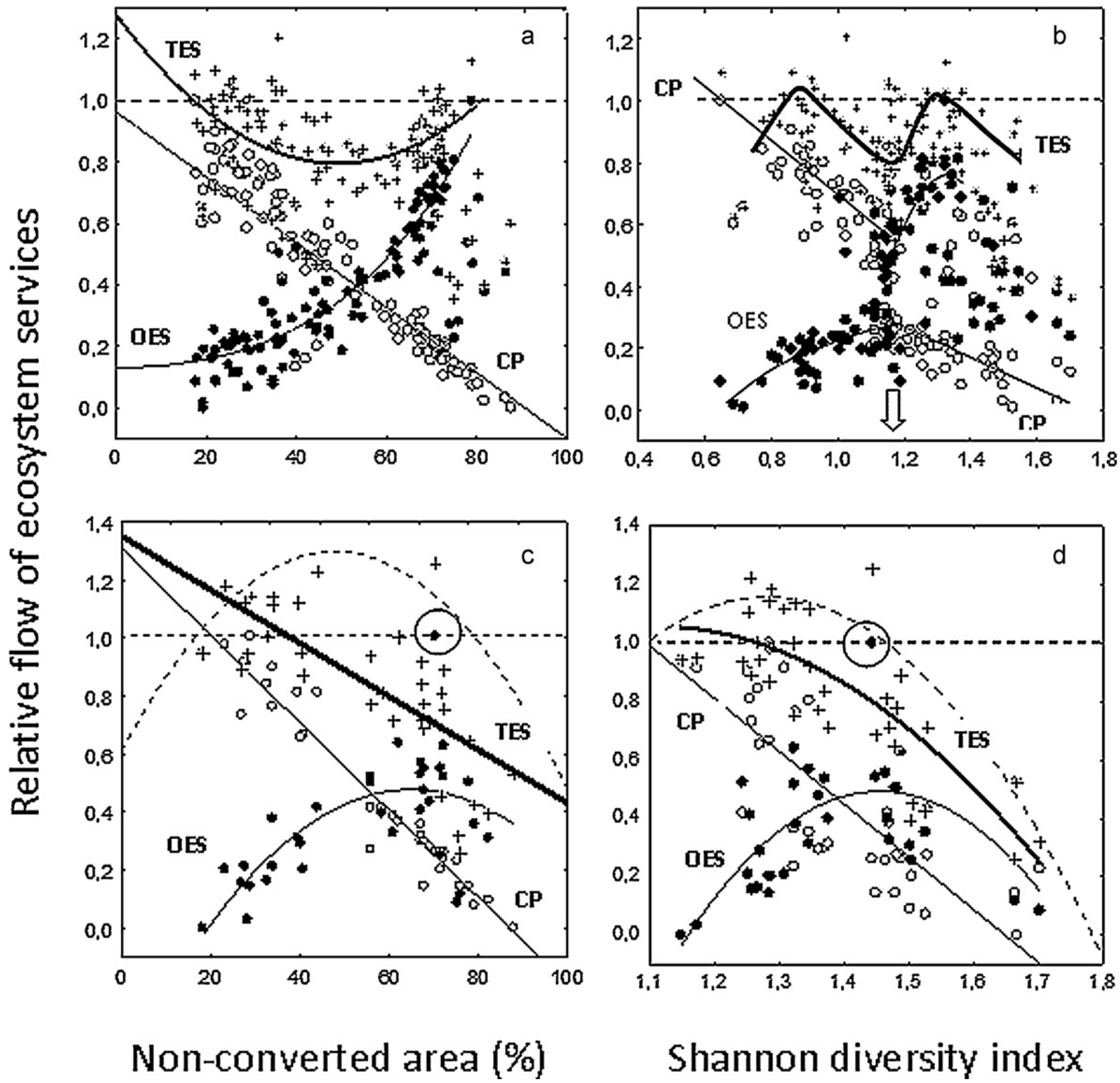

Fig. 4. Variation of ecosystem services with landscape complexity (ES–LC diagrams) obtained from the evaluation of high (a and b) and low (c and d) resolution grids. Curves were obtained from fitting of linear or polynomial models, except for Fig. 5b, were hand held curves were traced because no simple models provided satisfactory fittings. Curve fitting of OES and TES variation in Fig. 5a excluded annual crops cover over 75% in order to avoid too complex models. See other references in legend of Fig. 1. Note that landscape complexity grows in opposite directions of the independent axis of Figs. 1 and 5. Arrow in (b) indicates a breaking point in both CP and OES responses. Discontinuous curves of Fig. 5d and b represent a polynomial curve fitting to re-normalized TES values after the encircled outlier points were omitted.

mingled mixture of distant and irregular patches of annual crops and lowland grasslands.

Variation in the offer of total ecosystem services (TES) to simple descriptors of LC did not always peaked at intermediate complexity levels as predicted, but alternative ES–LC models were obtained for the different combinations of LC descriptors and scales (Fig. 4). Main contrasts among those models were represented by a clear reduction of TES at intermediate LC levels under fine-scale analysis and nearly an opposite trend under the coarse-scale analysis, when an erratic point was suppressed (cfr. Fig. 4a *vs*. c and b *vs*. d). Non-linear responses to LC were generally shown by OES but not for CP in response to both LC descriptors and at both scales, except for responses to landscape diversity in the fine-grained analysis, where both CP and OES showed a clear diversity threshold (Shannon Index, SI = 1.17, Fig. 4b). This threshold was associated to the grid-cell altitude (mean altitude of pixels within grid-cells), the main physical driver controlling the grassland conversion extent within Mar Chiquita basin. While from 0 m to 60 m of altitude there is a sharp decline of the Shannon index (SI) until aprox. SI = 1.17, that relationship becomes more diffuse above the 60 m altitude (Fig. 5).

6. Discussion

While Mar Chiquita's rural landscapes vary largely according to the cover of two contrasting LULC classes, annual crops and lowland grasslands, nearly a half of total variation in landscape composition and configuration was turned out to be independent of these two cover categories (Fig. 2). Not surprisingly, linear regression models combining both composition and configuration metrics of rural landscapes showed better explanatory power for the OES flow patterns set than models based on landscape composition alone. However, incorporation of different landscape configuration metrics did not improve the explanatory power of variations in crop production, because this ES was exclusively based on site properties.

Dependence of some OES on landscape composition and configuration reflects that their availability is an emergent property of the landscape level, and therefore they could be better considered as landscape services rather than ecosystem services. This is the case of, for example, the maintenance of clean water bodies which according to the applied protocol not only depends on the filtration and depuration of runoff water by riparian vegetation and

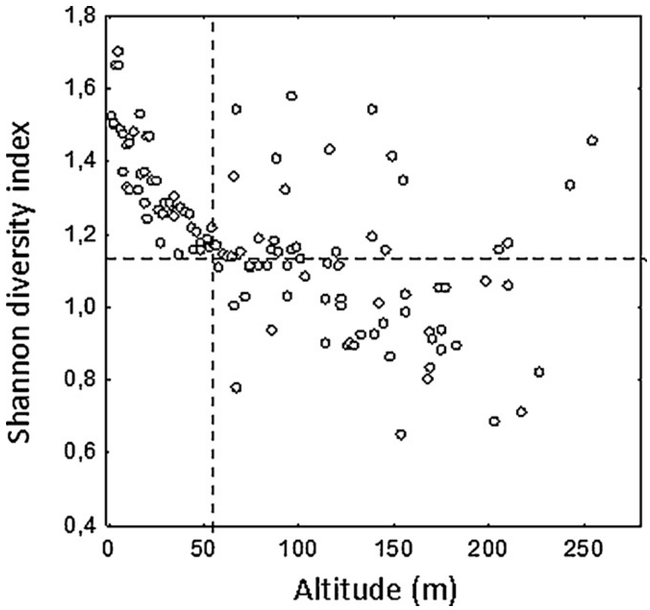

Fig. 5. Variation of the Shannon diversity index of rural landscapes within the Mar Chiquita basin with the mean altitude of pixels within the grid cells. Vertical discontinuous line indicates altitude value corresponding to the threshold Shannon index value (horizontal discontinuous line) observed in Fig. 4(b).

wetlands, but also on landscape attributes which ultimately affects the nutrients and sediment loadings entering them.

In contrast with our prediction, CP-OES tradeoffs were robust enough to be observed at both examined landscape scales (Fig. 3), probably because of their strong dependence on the variation in the relative cover of grasslands and crop fields and relatively low dependence on more scale-dependent metrics of the landscapes (Wu et al., 2000). On the other hand, the global climate regulation *vs*. flooding attenuation relationship was clearly scale-dependent. The tradeoff observed at fine-grain scale is reflecting the negative relationship between cover of cultivated pastures plus lowland grasslands (with relatively high soil organic content, SOC) *vs*. wetlands (see de PC2, in Fig. 2). In exchange, the global climate regulation *vs*. flooding attenuation relationship reflected by PCA at the coarse-grain scale (Fig. 3b) mainly results from the altitude-dependent contrast between the mostly cultivated (Austral Pampa) *vs*. the mostly animal-husbandry devoted and pasture or grassland covered (Flooding Pampa) regions within the Mar Chiquita basin.

The relative cover of annual crops was able to provide good predictive power for individual and aggregated ES availability (CP, OES and TES). However, different models were set for the variation in TES responses according to the scale of analysis, mainly as a consequence of different responses of OES to the non-converted area (Fig. 4a and b). In this way, our results revealed that negative CP-OES correlations commonly described as tradeoffs, can be masking different combinations of linear and non-linear responses (Fig. 1) with different meanings for land use planning. In the case of our study area, while maintaining intermediate levels of landscape complexity (LC) seems to be the better strategy for assuring maximum flow of TES at the coarse observation scale, the opposite seems to be true for the fine-grain scale, which showed maximum values at opposite extremes of LC gradients and disagrees with the ES models of saturation at low levels of landscape diversity hypothesized by (Roschewitz et al., 2005a). This results illustrate that tradeoffs usually described among separated ES at local levels do not necessarily support their antagonistic but also their complementary (synergistic) availability at the landscape level, according the observation scale and landscape complexity, among other factors.

Threshold responses were posed or shown for different ecological processes (Huggett, 2005; Groffman et al., 2006) but our results represent one of the first evidences about this kind of responses for other than biodiversity-conservation ES in relation to landscape complexity (but see Concepción et al., 2008). Since the observed patterns of ES and landscape complexity in this study do not exclusively reflect the consequences of human decisions but the consequences of their interactions with natural sources of biophysical heterogeneity (where for example, cover of annual crops is not independent of altitude and soil types), tradeoffs and thresholds reported here are not directly applicable to land use planning. However, our analytical framework could be advantageously applied to scenario analysis, where our results suggest that ES availability are affected by spatially dependent tradeoffs which results from different land use patterns not only in terms of landscape composition but also of landscape configuration.

The observed ES–LC responses improve the theoretical basis of the diversity paradigm for landscape planning, which sates the advantages of maintaining high heterogeneous mosaics of man-made and natural ecosystems (e.g. Jørgensen, 2007). However, the analysis of aggregated availability responses of ES sets (TES) to agricultural conversion cannot be transferred to landscape planning, management and/or decision making without caution because of several factors. First, since our results illustrate that intermediate landscape conversion level can be associated to maximum or minimum TES according to scale, benefits from landscape diversity may be elusive to some administrative levels but achievable to others. Second, complementary availability of different ES types cannot be directly interpreted as a measure of compensation or substitution among them, unless society requirements for different ES types are taken into account (e.g. translating functional complementarity into compensation of benefits by weighting ES types in TES calculus). Third, ecosystem benefits to human individuals and society not only depends on weighted ES availability but also on society capacity for ES use or capture. Finally, land use planning for sustainable scenarios must consider consequences of ES capture on their future availability (i.e. ES vulnerability).

Additional caution for ES–LC analysis arises from properties of CP, OES and TES indices. Normalized indices are typically affected by reference values of maximum and minimum ES availability. In this way, indices can be aggregated but they are only able to measure changes over space or over time instead of absolute quantities. Furthermore, when reference values are the extreme values within the study area (like in our study case), outliers can drastically modify CP or OES values and then the response function of TES, as illustrated in Fig. 4c and d. Through judicious removal of outliers, these ES indices can be forced to a more or less uniform distribution over their range of values (see Fig. 4c and d). Despite of this shortcomings, TES utility goes beyond its precise values, because identification of optimal or threshold values for landscape complexity mostly depends on relative maximum or minimum of TES.

The growing need for ES assessment has elicited an evolving set of methods, which have progressed from the evaluation of isolated to relevant sets of ES types, and from the simple transference of cover-specific ES supply to the ES modeling based on site-specific biophysical attributes. Since important local ecosystem processes which ultimately control the local ES delivery depend on lateral flows and filter effects from the spatial context (van Noordwijk, 2002), further improvements on ES assessment were limited by the lack of methods capable of integrating local and context-dependent processes for the assessment of ES sets. Recently proposed methods for the context-dependent evaluation of ES, like INVEST (Nelson et al., 2009) and ECOSER, might be the key for answering how much landscape conversion, ecosystem conservation or ecosystem restoration is needed for different ES demands. In this context, by providing different evidences about the influence of the spatial complexity of rural landscapes on scale-dependent tradeoffs and complementarities among relative ES flows, our study offers a novel insight into neglected properties of landscapes which were recently acknowledged as priority research areas for ecosystem management and land use planning (Nicholson et al., 2009).

7. Conclusions

Composition and configuration indices of Mar Chiquita's rural landscapes showed a complementary capacity to explain the overall spatial variation in ecosystem services other than crop production, but combinations of configuration indices showed a higher explanatory value than composition ones. According to our results, widely accepted tradeoffs among ecosystem services at local levels not only were able to explain their antagonistic but also their synergistic availability at the landscape level, depending on the evaluation scale. Multifunctionality potential of rural landscapes, as reflected by a synergistic availability of relevant sets of ecosystem services, was only promoted by intermediate levels of conversion of managed grasslands to croplands when the evaluation scale was large enough to match the scale of the largest ecosystem processes considered. Despite intermediate complexity hypothesis was only partly supported by our results, these offer novel evidences about emergent responses in the form of nonlinearities and thresholds of total ecosystem services in relation to landscape complexity, which deserve further attention because of their relevance for land use planning.

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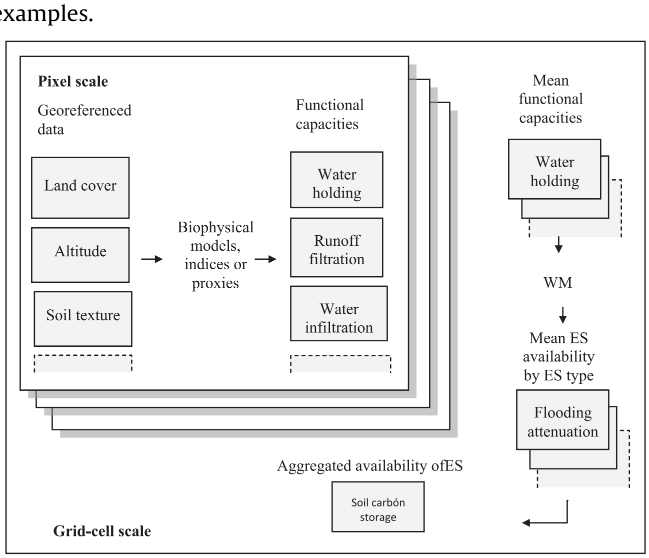
Appendix A.

Evaluation flowchart applied for evaluation of ecosystem services in the study area. WM is the weighting matrix of ecosystem functions into ecosystem services availability (see Table 1). Only some ecosystem functions and ecosystem services are included as examples.



Appendix B.

(See Table B.1).

Table B.1
Conversion table of ecosystem functions (EF) evaluated within the Mar Chiquita Basin into their potential benefits to human society (ecosystem services, ES).

Ecosystem functions	Ecosystem services					
	FA	CW	AQ	CP	AP	CR
SCS	0.00	0.00	0.00	0.00	0.00	**1.00**
EC	**0.33**	**0.67**	0.00	0.00	0.00	0.00
WWHC	**0.33**	0.00	0.00	0.00	0.00	0.00
APC	0.00	0.00	**1.00**	0.00	0.00	0.00
RFRV	0.00	**1.00**	0.00	0.00	0.00	0.00
WFW	0.00	**0.33**	0.00	0.00	0.00	0.00
WI	**1.00**	0.00	0.00	0.00	0.00	0.00
PI	0.00	0.00	0.00	**1.00**	**1.00**	0.00

Cell values received one of four possible values (0.0, 0.33, 0.67 or 1.00) representing the relative contribution of each ES according to subjective criteria. FA: flooding attenuation, CW: maintenance of clean water bodies, AQ: maintenance of aquifers quality, CP: crop production, AP: animal production, CR: climate regulation, SCS: soil carbon storage, EC: erosion control, WWHC: wetland water holding capacity, APC: aquifer protection by vegetation cover, RFRV: runoff filtration by riparian vegetation, WFW: water filtration by wetlands.

Appendix C.

Evaluation of functional capacity of ecosystems. Equations, parameter values selected for the study case and other supplementary details to Section 2.1.

C.1.

Wetland water holding capacity (WWHC) was calculated by

$$WWHC = WA * TW \tag{C.1}$$

where wetland area (WA) was used as a proxy of wetland volume, and TWI is the Topographical Wetness Index (Beven and Kirkby, 1979), calculated by

$$TWI = \ln\left(\frac{a}{\tan\beta}\right) \tag{C.2}$$

where a is the upslope contributing area, and β is the mean slope in the pixel. TWI combines local upslope contributing area and slope to quantify topographic control on hydrological processes, and higher TWI values means higher flood risk. The slope and catchment area grids were calculated using the *Dinf* approach (Tarboton, 1997), which assigns a flow direction based on steepest slope on a triangular facet, and provides better results than other slopes calculations on DEMs. Slope and specific catchment area layers were obtained by running TauDEM 3.1 tools in ARCGIS 9.2. Finally, both layers (wetland areas and mean wetland TWI) were normalized and multiplied to obtain a final layer.

C.2.

Aquifer protection by vegetation cover (APC) was calculated by

$$APC = I * P * \frac{1}{D} \tag{C.3}$$

where I is the water infiltration factor calculated for a rain event of 100 mm, P is the protection factor of cover type in the pixel ($P = 0$ for annual crops and $P = 1$ for cultivated pastures and native grasslands), and D is the aquifer depth. Correlations between APC calculated with this reduced set of DRASTIC parameters showed a poor correlation with that calculated on basis to all DRASTIC parameters for restricted areas within the study area, so particular caution should be taken about ES depending on this ecosystem function.

Runoff filtration by riparian vegetation (RFRV) was calculated by

$$RFRV = C * E \tag{C.4}$$

where C is the contaminants loading rank, and E is the efficiency of sediment retention rank. The C rank of pixels was obtained by combining models of export, transport, and accumulation of sediments, nitrogen and phosphorus, according the procedures devised by Orúe et al. (in press). The efficiency of sediment retention rank (E) was estimated from

$$SRE = 53.35 + 235 * RA \tag{C.5}$$

where SRE is the efficiency of sediment retention, and RA, ratio area, is the ratio between the area of the riparian vegetation strip area and source area. Parameters of Eq. (C.5) were obtained by fitting simulated values using VFSMOD model (Muñoz-Carpena and Parsons, 2003) applied to riparian vegetation strips consisting in grasslands dominated by perennial species. The source area parameters applied for calculating C consisted in a 50 mm of type II rain of 4 h of duration; CN (curve number, NRCS, 1986): 86; source area: 10 ha.; mean flow slope: 3%; soil type: loam; Dp (Sediment particle size diameter): 35 μm; K factor (soil erodability factor of RUSLE): 0.04; C Factor (conservation factor of RUSLE): 0.3; P Factor (practices factor of RUSLE): 1. For simplicity, biophysical attributes of riparian vegetation strips were assumed homogeneous along the study area (grassland dominated by tall fescue, 5% mean terrain slope, silt loam soil, friction factor Manning = 0.04 in the soil surface, variable strip width from 3 m to 100 m and constant strip length of 100 m).

C.3.

Water filtration by wetlands included the following steps, (1) nutrient runoff modeling in ArcGis 9.2, (2) wetlands mapping and characterization, and (3) modeling the potential filtration capacity of wetlands.

1. Nutrient runoff modeling in ArcGis 9.2. The general decay rates of total nitrogen (TN) and total phosphorous (TP) typically follows a first order kinetics (Liu et al., 2006; Rossman, 2004; Skop and Sørensen, 1998)

   $$X_t = X_0 * e^{-kt} \tag{C.6}$$

   where X_t is the nutrient mass that will persist in runoff after being transported from each pixel during a travel time t (days), X_0 is the initial mass that is exported from each pixel, and k is the decay coefficient (day^{-1}). In this case, we applied a k = 0.05 per day for both nitrogen and phosphorus, value within the range found in literature (i.e. SWAT model, in Neitsch et al., 2005). To determine the travel time of nutrients, distance to wetlands as well as speed of transport calculations were performed considering the topography. To calculate the velocity of surface flow (laminar or channeled), we used the following equation (Brown et al., 2001)

   $$v = K * \sqrt{S} \tag{C.7}$$

   where v is runoff velocity, K is the runoff coefficient, which depends on land use type and hydrologic radius, and S is the slope. K values resulted from the adaptation of the classification made by Brown et al. (2001). The calculation of the distances where performed in ArcGis 9.2.

   The volume of runoff was modeled in GIS following the Curve Number method (NRCS, 1986)

   $$SRO = \frac{(P - 0.2 * S)^2}{P + 0.8 * S} \tag{C.8}$$

   where SRO is the surface runoff (mm), P is the precipitation in mm for a given rainfall event, S is the initial loss due to evaporation plus infiltration calculated by

   $$S = \frac{1000}{CN} - 10 \tag{C.9}$$

   where CN is the curve number value for a particular hydrological type of soil and land use. For this calculation we used an average rainfall event over the past 10 years in the study area (49 mm). The runoff volume from each pixel was calculated based on the runoff mm per pixel and the pixel size.

   The mass of nutrients to be exported from each pixel was calculated from the export values for TN and TP for each land use (Jeje, 2006) and from the SRO volume layer. Then these layers were used for the calculation of X_t using Eq. (C.6). Finally we obtained the runoff flow accumulation weighted by TN and TP reaching the streams and wetlands in ArcGis 9.2.
2. Wetlands mapping and characterization. The wetlands in the Mar Chiquita basin were mapped through Landsat TM classifications for the 2005–2006 period (Zelaya and Cabria, 2008). Then the resulting map was incorporated to the GIS, where the area of each wetland was calculated.
3. Modeling the potential filtration capacity of wetlands. The nitrogen retention by wetlands is controlled primarily by three processes: denitrification, uptake and sedimentation (Mitsch and Gosselink, 2000). However, denitrification is the most important process explaining between the 60 and 90% of the total nitrogen retention in wetlands (Jansson et al., 1994). In the absence of specific models for wetlands in the area, and assuming that nitrogen retention can be explained only by denitrification, we applied an exponential empirical equation that includes both the area of the wetland and the nutrient income (Byström, 1998)

$$N_{ret} = WA^{0.51} * N_{in}^{0.49} * 7.56 \tag{C.10}$$

where N_{ret} is the rate of TN retained by the wetland area, WA is the wetland area (ha), and N_{in} is the amount of TN entering the wetland area annually. To obtain the annual amounts of nitrogen reaching the wetland, the flow of nitrogen calculated for the rainfall event were extrapolated according to the average annual accumulated rainfall over the past ten years in the area (900 mm).

The phosphorous retained by the wetlands was calculated from an empirical equation obtained by Kadlec and Knight (1996) for a large number of wetlands

$$P_{out} = P_{in}^{0.96} * 0.34 \tag{C.11}$$

where P_{out} is the rate of TP output by wetland area, and P_{in} is the rate of non point source TP load entering by wetland area. It is important to note that the flow of nutrients entering wetlands depend on the drainage area of the wetland, and its land use and topology, so the P_{in} value depends on the position of the wetland in the landscape and the upstream land uses.

C.4.

Water infiltration was calculated by

$$I = P - Q \tag{C.12}$$

where P is mean annual precipitation in mm ($P = 50$ mm), Q is the runoff deep and was computed following the Soil Conservation Service curve-number (SCS-CN) approach

$$Q = \frac{(P - I_o)^2}{P - I_o + S} \tag{C.13}$$

where S is the potential maximum retention after runoff start (mm); I_o initial abstraction (mm) includes water retained in surface depressions, water intercepted by vegetation, evaporation, and infiltration. I_o was found to be approximated by the following empirical equation: $I_o = 0.2S$ and substituting this equation into the previous one gives

$$Q = \frac{(P - 0.2 * S)^2}{P + 0.8 * S} \tag{C.14}$$

S is related to the soil and cover conditions of the watershed through the CN. CN has a range of 0–100, and S is related to CN by

$$S = \frac{1000}{CN} - 10 \tag{C.15}$$

The major factors that determine CN are the hydrologic soil group (HSG), cover type, treatment, hydrologic condition, and antecedent runoff condition (ARC). Another factor considered is whether impervious areas outlet directly to the drainage system (connected) or whether the flow spreads over pervious areas before entering the drainage system.

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