# Towards an Energy–Landscape Integrated Analysis? Exploring the links between socio-metabolic disturbance and landscape ecology performance (Mallorca Island, Spain, 1956-2011)

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# Abstract

## *Context*

The role of agricultural landscapes in biodiversity conservation is an emerging topic in a world experiencing a worrying decrease of species richness. Farm systems may either decrease or increase biological diversity, depending on land-use intensities and management.

## *Objectives*

We present an intermediate disturbance-complexity model (IDC) of cultural landscapes aimed at assessing how different levels of ecological disturbance affect the capacity to host biodiversity depending on the land matrix heterogeneity. It is applied to the Mallorca Island, amidst the Mediterranean biodiversity hotspot.

## *Methods*

As independent variables, we use the disturbance exerted when farmers alter the Net Primary Production through land-use change as well as when they remove a share of it (*HANPP*), together with Shannon-Wiener indexes (*H'*) of land-cover diversity. The model is tested with a twofold-scalar experimental design (1:50,000 and 1:5,000) of a set of landscape units along three time points (1956, 1989, 2011). Species richness of nesting and wintering birds, taken as a biodiversity proxy, is used as dependent variable.

## *Results*

The results clearly show that when intermediate levels of *HANPP* are performed within high levels of complexity (*H'*) in landscape patterns, like agro-forest mosaics, great bird species richness and high socio-ecological resilience can be maintained. Yet, these complex-heterogeneous landscapes are currently vanishing due to industrial farm intensification, rural abandonment and urban sprawl.

## *Conclusions*

The results highlight the usefulness of transferring the concept of intermediate disturbance-complexity interplay to cultural landscapes. Our spatial-explicit IDC model can be used as a tool for strategic environmental assessment of land-use planning.

**Keywords**

Disturbance ecology; land-use change; socio-metabolic patterns; human appropriation of net primary production; land cover diversity; land matrix heterogeneity; landscape functioning; biodiversity; cultural landscape

## 1. Introduction

The role of agricultural landscapes in biodiversity conservation is an emerging research topic. This is by no means strange in a world where human population will approach nine billion people with a relevant portion of them still suffering malnutrition and hunger, together with a worrying decrease of species richness, and an unavoidable societal dependence on the environmental services biodiversity provides. World agriculture is at stake amidst this big challenge (Schröter et al 2005; Godfray et al 2010; Cardinale et al 2012). About half of the global usable land is already in intensive farming and grazing—and the more productive indeed. This has been a major driver of biodiversity loss, mainly after the 'Green Revolution' developed from the 1960s onwards (Matson et al 1997; Tilman et al 2002) whereas only some 6-12% is under any sort of nature protection (Bengston et al 2003; Tscharntke et al 2012).

No doubt, society needs other farm systems to meet this global challenge (Gomiero et al 2008). At the same time there is a growing acknowledgement that the environmental impact of agriculture, forestry and pasture is twofold. Depending on the land-use intensities and the type of management, agricultural systems may either entail a decrease or increase in biological diversity (Altieri 1999; Swift et al 2004; Cardinale et al 2012). Hence, scientific enquiry needs to focus on the relationship between the ecological disturbance exerted by farm systems and the biodiversity host in cultural landscapes (Tilman et al 2002; Benton et al 2003). This also means looking at farmers as providers of environmental services as well as producers of food, feed, fibre and fuel (Altieri 1999; Tress et al 2001; Agnoletti, 2006, 2014). If society wants to ensure both agricultural produce and ecological services then a dilemma between two seemingly opposite strategies arises: *i*) a land-sparing approach based on increasing agricultural intensification in some areas so as to devote the others to nature conservation and forest transition (Green et al 2005; Matson and Vitousek 2006); or rather *ii*) a land-sharing approach based on a wildlife-friendly farming able to provide complex agroecological matrixes connected with natural sites that jointly maintain high species richness at landscape level (Bengston et al 2003; Marull et al 2010; Perfecto and Vandermeer 2010; Tscharntke et al 2012).

Underlying this scientific and political controversy there exist contrasting bio-geographical features across the Earth, diverse human settlement patterns and socio-ecological trajectories, together with different intellectual traditions: e.g. island models of a binary landscape vs. continuous and heterogeneous landscape matrix; treating nature and agriculture as being opposite vs. enhancing environmental services in agroecosystems; considering humans separate from nature vs. seeing them as components of ecosystems (McDonnell and Pickett 1993; Farina 2000; Fischer et al 2008). Even those that advocate for combining these contrasting perspectives admit that this requires a major research step forward to know how biodiversity is kept in different landscape patterns and ecological processes (Phalan et al 2011).

A logical starting point for this research agenda is to resume the Intermediate Disturbance Hypothesis (IDH), one of the non-equilibrium explanations of biodiversity maintenance most debated in ecology (Connell 1978; van der Maarel, 1993; Wilson, 1994; Padisak 1993; Tilman 1994; Reynolds 1995; Chesson and Huntly 1997; Dial and Roughgarden 1998). Several authors had already claimed having applied the IDH to the anthropogenic disturbances exerted by agriculture, forestry and grazing as well, either from an ecological (Pickett and White 1985; Fahrig and Jonsen 1998), agroecological (Gliessman 1990) or biological conservation (Pierce 2014) viewpoint—and the time has come to undertake this task. Yet the empirical results accumulated over decades remain inconclusive, and the IDH still raises heated debates (Wilkinson 1999). Some authors are proposing its abandonment (Fox 2013), others remain strong supporters (Huston 2014), whereas some others explain the ambiguity of empirical tests by having used different indicators of biodiversity and disturbance measured at different spatial scales without taking into account the differences in biological productivity of each site (Collins and Glenn 1997; Sasaki et al 2009; Svensson et al 2012; Pierce 2014).

Many authors suggest keeping the IDH only as a general framework, and focus on developing clearer models and more accurate tests of the underlying mechanism that may actually bring about a hump-shaped correlation of spatiotemporal disturbances with species richness (Buckling et al 2000; Sheil and Burslem 2003; Shea et al 2004; Shreeve et al 2004; Barnes et al 2006; Miller at al 2012). There is a growing consensus in pointing out at the spatial environmental variations that create opportunities for a range of dispersal colonizers, either coming from the less undisturbed patches or the survivors in disturbed ones, as the key mechanism that avoids competitive exclusion and maintains a dynamic biodiversity peak at intermediate levels of ecological disturbance. This way undisturbed patches may preserve the 'ecological memory' (Bengston et al 2003) needed for an adaptive response to ecological disturbances by the species pool kept at landscape level (Shea and Chesson 2002; Loreau et al 2003; Perfecto and Vandermeer 2010). This approach stresses the spatial component of biological diversity (Tilman 1994), focuses on the interplay between disturbances and land cover diversity, and entails a significant shift towards considering the role of agroecological land management in ecosystem services provision (Tscharntke et al 2005). It also brings into light the insurance role played by the spatial heterogeneity of the land matrix to enhance the ecosystem complexity and resilience in human-dominated environments (Loreau et al 2001, 2003; Elmqvist et al 2003; Benton et al 2003).

These new approaches foreground the interplay between patch disturbance and land-cover diversity as the key mechanism that actually matters in biodiversity maintenance. They also highlight the role of agro-forest mosaics able to offer habitats to different inner species, and create greater amount of ecotones which provide more opportunities to edge species as well (Harper et al 2005). Much of this biological diversity is located at scales higher than plot or farm level, and depends on keeping a landscape-wide variety of land covers. When high species richness is kept at landscape level thanks to land cover heterogeneity, the inevitable decrease of biological diversity in the intensively cropped patches can be compensated (Swift et al 2004). This way, a disturbance-complexity interplay leads to divergent and compensatory trends followed by α-diversity at plot scale (within-patch or within each community), β-diversity at landscape level (between-patch or between communities), and γ-diversity of the species pool hosted at regional scale (Loreau 2000; Roxburgh et al 2004; Gabriel at al 2005; Loreau et al 2010). The colonizing capacity of the species hosted in a well-connected mosaic that combines early and late successional niches overrides the local decrease in α-diversity as a result of local or temporal disturbances.

Therefore, the predominance of β-diversity kept by the spatial heterogeneity of a variety of intermingled land covers becomes the key mechanism of biodiversity maintenance in cultural landscapes. A recent review by Tscharnkte et al (2012) stresses that under these circumstances dissimilarity of local communities determines landscape-wide biodiversity, overrides negative local effects of habitat fragmentation, generates spillover effects through the movement of organisms and resources across habitats in all directions (Blitzer at al 2012), and stimulates the selection for distinct traits on populations which facilitates their survival in human-managed landscapes. This landscape complexity enables spatial and temporal insurance, providing higher stability and resilience to ecological processes—such as biological pest control (Bianchi et al 2006). The effectiveness of farm management in increasing biodiversity reaches a peak at intermediate levels of landscape heterogeneity, given that simple landscapes tend to behave as a single monoculture poorly endowed of biological diversity whereas highly complex ones retain great biodiversity anyway. Hence, a wildlife-friendly agroecological matrix may enhance the overall biological diversity except when it comes to rare specialists species that require specific natural habitats and other conservation policies.

## 2. Research approach and methods

Testing these hypotheses requires a major research effort to define the thresholds where the disturbance-complexity interplay is more effective in providing biodiversity and ecosystem services. This task has to be undertaken from different disciplines and using different methods that range from conservation biology to agroecology, landscape ecology, land-use and land cover change, ecological economics and ecological modelling. It also needs a deeper interdisciplinary dialogue among them from a common sustainability science standpoint that seeks solution-oriented knowledge in a participatory manner (Berkes 2007; Rindfuss et al 2008; Lang et al 2012).

Our contribution stands at the crossroads between landscape ecology, land-use change, agroecology and ecological economics (Marull et al 2010). We adopt the socio-metabolic accounting of material and energy flow analysis used in ecological economics, as well as in agroecology, as a measure of anthropogenic disturbance carried out on landscape functioning (Haberl 2001; Fischer-Kowalski and Haberl 2007). Drawing on Margalef (2006), we then examine how disturbance exerted by farm systems correlates with landscape mosaics' complexity and biodiversity. To achieve this we use GIS methods of land cover and land-use change (Lambin and Geist 2006; Agnoletti 2006) to calculate landscape ecology metrics and assess how spatial patterns affect ecological processes (Forman 1995; Li 2000; Tischendorf 2001; Turner 2005; Turner et al 2007; Turner and Robbins 2008) which we deem them to play a role in biodiversity maintenance through landscape functions (Marull and Mallarach 2005; De Groot, 2006; Marull et al 2007; Helming et al, 2007; Verburg et al 2009; Pino and Marull 2012).

Our approach adopts a comparative long-term perspective (Antrop 2006; Matthews and Selman 2006). It is known that traditional organic farm systems maintained complex land-use mosaics, like those of Europe in the 19th century (Tscharntke et al 2005; Marull et al 2010), before the agricultural industrialization fuelled by cheap fossil fuels turned them into increasingly homogeneous land-covers polarized between intensive monocultures and afforestation of abandoned lands from the 1960s onwards (Gerard et al 2010; Parcerisas et al 2012; Marull et al 2014). This historical land-use change becomes a natural experiment that can be used for a comparative analysis of how different levels of anthropogenic disturbance, within different levels of land-use complexity, relate with landscape ecology indicators.

We present a mathematical model of how landscape processes are affected by different levels of ecological disturbance exerted when farmers alter Net Primary Production through land-use change, and remove a share of it. A multi-scalar experimental design of a set of landscape units in the island of Mallorca from 1956 to 2011 is used to check it empirically. We choose Mallorca for its heritage of a complex agricultural landscape located amidst the Mediterranean biodiversity hotspot (Myers et al 2000), and because its unique abundance of historical and cartographical sources allows long-term comparative analysis. The model is tested with a dataset of wintering and nesting birds in Mallorca, following other studies that use the decrease in common farmland bird populations as an indicator of landscape-wide biodiversity loss (Farina 1997; Donald et al 2001; Heikkinen et al 2004; Sirami et al 2008; Inger et al 2014). In the next sub-sections we explain the disturbance variable used and the multi-scalar research design. Then we present the intermediate disturbance-complexity (IDC) model applied to cultural landscapes taking resilience into account. Section three presents and discusses the results, and section four concludes.

### *2.1. Study Area*

The Mallorca Island (Figure 1) has a total area of 3,603 km$^2$ of calcareous origin. The mountain range of the Serra de Tramuntana runs parallel to the North coast and its highest peak reaches 1,445 metres. Between this range and the Eastern mountains of Serres de Llevant a plain occupies most of the island. Annual precipitation ranges from 300 mm (in the South) to 1,800 mm (in the North) with an average temperature of 16 ºC. The vegetation combines scrubland, pines and residual oak forests with a variety of annual crops (grains and vegetables) and arboriculture (olive groves, almonds, figs, carobs, vineyards). Six agro-ecological areas can be distinguished: *i*) '*Tramuntana*' is characterized by its hilly morphology and high precipitation (1,400-1,800 mm), and has most of its land devoted to olive groves and forest (our 3x3 km$^2$ site is the '*Esporles*' scene); *ii*) '*Raiguer*' is the piedmont between Serra de Tramuntana and the inland plain, whose soil, precipitation and edge condition allow intensive cropping of olive groves, vineyards and arboriculture with grains and vegetables (the 3x3 km$^2$ sites are the '*Santa Maria*' scene, and the '*Sa Pobla*' site which is characterized by watering intensification); *iii*) '*El Pla*' is the central plain mostly cultivated with grains (the 3x3 km$^2$ '*Sant Joan*' scene); *iv*) the Eastern '*Llevant*' combines small elevations with valleys that allow combining cereal cops and arboriculture with agro-forest mosaics, pastures and shrubs (with three 3x3 km$^2$ scenes: '*Aubocàsser*', '*Calicant*' and '*Marina*'); *v*) the Southeast '*Migjorn*' is characterized by water stress and barren land which largely hinder farming (the 3x3 km$^2$ site is the '*Santanyí*' scene).

We use this twofold-scalar experimental design in three time points (1956, 1973 and 2000) based on land-cover maps of Mallorca (GIST 2009):

1. Regional scale (1:50,000) takes into account the entire island divided into 3x3 km$^2$ cells, of which only 331 are used to avoid the sea edge effect. Biodiversity information on nesting and breeding birds has been obtained from 5x5 km$^2$ inland cell database (GOB 2008), and used to test our intermediate disturbance-complexity (IDC) model through principal components analysis (PCA) using as variables the bird species richness, the spatial land pattern, the human disturbance, and the proportion of land covers in each sample cell.
2. Landscape scale (1:5,000) takes into account eight 3x3 km$^2$ analysis scenes (Figure 1) distributed in five agro-ecological areas of Mallorca. Each scene is divided into nine 1x1 km$^2$ cells to better grasp the land-use change. We relate the human disturbance by the landscape dynamics captured at this scale by photo-interpretation of the three main land-use changes underway: *i*) abandonment of arboricultural rain-fed crops (almond groves change to cereals; olives groves change to forest); *ii*) spontaneous afforestation ensuing woodland abandonment (charcoal making, wood-pastures); and *iii*) urban sprawl (mainly tourism in coastal areas).

### *2.2. The Intermediate Disturbance-Complexity Model of Cultural Landscapes*

The IDC model is based on variables that describe both spatial land pattern (Shannon-Wiener index - *H'*) and human disturbance (Human Appropriation of Net Primary Production - *HANPP*), so as to assess how anthropogenic energy-use and land cover and land-use change affect landscape ecological functioning. We work with squared cells from land-unit (LU) maps, so that:

$$\sum_{i=1}^{k} p_i = 1$$

Where $p_i$ is the proportion of LU *i* in a specific cell, and *k* is the number of LU. We will refer to *p* as vector $p = (p_1, \ldots, p_k)$. In order to check the IDC with the LU diachronic maps we have first analysed the corresponding shifts in the spatial pattern of the study area, by using *H*' that measures the equi-diversity of LU in a cell.

$$H' = -\sum_{i=1}^{k} p_i \log_k p_i$$

Where *k* is the total number of LU in the study area, and $p_i$ is the proportion of LU *i* in a specific cell. *H'* reaches its highest value when: $p_i = \frac{1}{k}$ for $i = 1, \dots, k$ (i.e., all LU are equally probable). We can prove it by looking at its partial derivatives. Since $p_k = 1 - \sum_{i=1}^{k-1} p_i$, we can rewrite *H'* as $H' = -\sum_{i=1}^{k-1} p_i \log_k p_i - \left(1 - \sum_{i=1}^{k-1} p_i\right) \log_k\left(1 - \sum_{i=1}^{k-1} p_i\right)$. And $\frac{\partial H\prime}{\partial p_j} = \log_k \left(p_j / \left(1 - \sum_{i=1}^{k-1} p_i\right)\right)$, that is equal to zero when $p_i = \frac{1}{k}$, for all $i = 1, \dots, k$.

We use *HANPP* as an indicator of anthropogenic disturbance (Haberl et al 2004, 2007; Wrbka et al 2004; Firbank et al 2008). According to the standard *HANPP* accountancy, *NPP* is the net biomass produced by autotrophic organisms over a year that constitutes the main nutritional basis for all food chains. *HANPP* measures the extent to which humans reduce the *NPP* available for other species using the following identities: $HANPP = \Delta NPP_{LU} + NPP_h$; $\Delta NPP_{LU} = NPP_0 - NPP_{act}$.

Where $NPP_h$ is the *NPP* appropriation through harvest, and $\Delta NPP_{LU}$ is the change of *NPP* through human-induced land conversion. $\Delta NPP_{LU}$ is defined as the difference between the *NPP* of the potential ($NPP_0$), and the actual ($NPP_{act}$) vegetation. Therefore *HANPP* can be defined as the difference between the $NPP_0$ and the *NPP* remaining in ecosystems after harvest ($NPP_t$):

$HANPP = NPP_0 - NPP_t$; $NPP_t = NPP_{act} - NPP_h$.

*HANPP* has been assessed to each LU in each period. Hence, site-specific *HANPPs* are calculated multiplying a fixed coefficient ($w_i$) for some LU *i* by the surface occupied by this LU. So, *HANPP* can be expressed as follows:

$$HANPP = \sum_{i=1}^{k} w_i p_i$$

Where $w_i$ denote the weight of LU *i*. The $w_i$ values (in tonnes of dry matter per surface and year) have been adapted from Schwarzlmüller (2009).

The result is that we have one *H’* and *HANPP* value for each cell and time period. We are going to analyse the relationship between *H’* and *HANPP* assuming two LU (i.e., $k = 2$) Then:

$$p_1 \epsilon [0,1], \qquad p_2 = 1 - p_1,$$

$$H' = -(p_1 \log_2 p_1 + p_2 \log_2 p_2),$$

$$HANPP = w_1 p_1 + w_2 p_2.$$

When $p_1 = 1$ then $H' = 0$ and $HANPP = w_1$ (Figure 2a). Insofar as $p_1$ decreases in favour of $p_2$, the graphic *H’-HANPP* forms an arc whose peak is given by $p_1 = p_2 = 0.5$, where $H' = 1$ and $HANPP = \frac{w_1 + w_2}{2}$.

Supposing three different LU ($k = 3$) we will compare LU by pairs. We can assume $p_i + p_j = 1$, and $w_i, w_j$ to be their associated weights. The dispersion graphic *H’-HANPP* for these values forms an arc whose highest value is achieved when $p_i = p_j = 0.5$, and corresponds to the point $HANPP = (w_i + w_j)/2$, and:

$$H(0.5,0.5,0) = -\frac{1}{2}\log_k 0.5 - \frac{1}{2}\log_k 0.5 = \log_k 2.$$

In Figure 2b, starting from the curve formed by $(p_1,\ p_2, p_3) = (1, 0, 1)$ we get similar but higher curves when increasing $p_2$ and decreasing $p_1$ and/or $p_3$, accordingly. The same occurs starting from the curves (1, 1, 0) and (0, 1, 1). Hence, we get the whole area in Figure 2b. Notice that for any weight of *HANPP* there is a ‘leg’ formed by non-mosaic points (i.e., which have a predominant LU).

For $k > 3$ we obtain similar results to those in Figure 2b. For any $n < k$, if we have exactly *n* LU such that $p_i > 0$ for these *n* LU and $p_i = 0$ for the other *k*-*n* LU, we can be sure that the corresponding figure achieves its maximum at the point $(\overline{w}, \log_k n)$, where

$$\overline{w} = \frac{1}{n}\sum_{i=1}^{n} w_i,$$

$$\log_k n = -\sum_{i=1}^{n} \frac{1}{n} \log_k \frac{1}{n}.$$

Looking at the figure *HANPP-H’* it is clear that any sample data on these variables (obtained from the same LU cartographic data) must bear some relationship (Figure 2b). The issue is how to interpret the sample data according to the density of pair values of *HANPP-H'*. We assume that Figure 2b is mapping out any possible relationship between ecological disturbance and land cover diversity, where the actual disturbance-complexity interplays of a given landscape can be represented.

### *2.3. Taking Resilience into account*

Resilience is the capacity to recover after disturbance (Folke 2006). As explained, our model assumes that certain levels of disturbance-complexity in an agroecological matrix may lead to an increase in ecological resilience as long as this threshold is kept. Heterogeneous land cover mosaics enhance the resistance to change of the functional landscape structure. In order to test this, we look at the variation of *HANPP* and *H'* with respect to vector *p*, the proportion of LU *i* in a specific cell (Figure 2). First of all we should bear in mind that $\sum_{i=1}^{k} p_i = 1$, so $\sum_{i=1}^{k} \Delta p_i = 0$, where $\Delta p_i$ is the increase of component $p_i$. We should also remember that *HANPP* is a linear combination of *p*, so the variation of *HANPP* is quantified directly through $\Delta p_i$ and $\Delta w_i$:

$$\Delta HANPP = \sum_{i=1}^{k} (\Delta w_i \Delta p_i + \Delta w_i p_i + w_i \Delta p_i).$$

In order to measure variations of *H'* we look at the behaviour of $\frac{\partial H'}{\partial p_j}$ for each *j*. We have seen that *H'* reaches its maximum at $p = \left(\frac{1}{k}, \dots, \frac{1}{k}\right)$, so $\frac{\partial H'}{\partial p_j}\left(\frac{1}{k}\right) = 0$. So, we have to study this function for values of $p_j$ both smaller and bigger than $\frac{1}{k}$,

$$\lim_{p_j \to 0} \left| \frac{\partial H'}{\partial p_j}(p_j) \right| = \infty, \qquad \lim_{p_j \to 1} \left| \frac{\partial H'}{\partial p_j}(p_j) \right| = \infty.$$

This implies that the variation of *H'* for an unbalanced *p* (i.e., there are some $p_i < 1/k$) are greater than variations of *H'* for a balanced *p* (mosaics) for the same $\Delta p$. This means that the largest vertical variations fall on small *p* values (i.e., when *H'* is small). This mathematical behaviour is based on the IDC model (Figure 2) and can be described as resilience (i.e., the resistance of a point to be moved when it has reached low entropy values—or, conversely, high

$H'$). The opposite is observed for points with high values of entropy or lower $H'$ (i.e., great variations of entropy -$\Delta H'$ allow small changes in human perturbation -$\Delta HANPP$).

To relate the value of entropy with resilience we measure the changes at each point ($HANPP, H'$) by ($\Delta HANPP, \Delta H'$) and look at the slope and magnitude of the vector linking ($HANPP, H'$) with ($HANPP + \Delta HANPP, H' + \Delta H'$), to assess the change it has experienced. According to this, resilience can be measured multiplying the slope by the intensity of the movement from a time period to the next one:

$$S = \frac{\Delta H\prime}{|\Delta HANPP|+1} \cdot \sqrt{\Delta H'^2 + \Delta HANPP^2}.$$

Where $S$ is both the slope and the intensity of the movement between two time periods. In order to have the trend of $\Delta H'$, the absolute value of $\Delta HANPP$ is required, and a term which has been added in order to avoid dividing by zero. Consequently, resilience will be measured looking at $S$ with respect to $H'$. For higher values of $H'$ smaller values of $S$ are expected, and vice versa.

## 3. Results and discussion

### *3.1. Socio-metabolic disturbance and land-cover patterns (regional scale -SF1)*

Figure 3 shows the relationship between *HANPP* and $H'$ for data from 1x1km$^2$ cells at regional scale (SF-1) in the years 1956, 1973 and 2000. We have worked with a total of 10 land-covers having a specific $w_i$ for each typology and year. Land covers are divided into three categories, namely ‘natural’, ‘agricultural’ and ‘urban’. Natural land-covers include forests ($w_1$), scrubs ($w_2$), prairie and bedrock ($w_3$) and wetlands ($w_4$). Agricultural land-covers include dry cropland ($w_5$), irrigated cropland ($w_6$), rain-fed arboricultural groves ($w_7$), irrigated groves ($w_8$) and olive groves ($w_9$). Urban land-covers ($w_{10}$) are both urban and industrial areas. Figure 3 shows that the higher point density is concentrated on agricultural land-covers (mainly rain-fed groves $w_7$) which maintain high constant values of *HANPP* ($w_i$) along the years. Similar values of $H'$ with a decrease in *HANPP* can be observed along the period. Three different dynamics can explain these trends seen at a regional scale. First, there is a tendency to increase cells with a predominant urban use (urban sprawl), a fact that becomes apparent for 2000 where the value associated to urban areas ($w_{10}$) appears on the 'leg'. Second, the rain-fed groves ($w_7$) show a progressive decrease in *HANPP* due to rural abandonment. Third, there appears to be a combination between agricultural and forest land-covers in the arc connecting these two decks that becomes strongly enhanced, where transition from cropping to woodland becomes apparent.

We have to bear in mind that at regional scale (SF-1) the likelihood of finding agro-forest mosaics increases with cell size and the number of land-covers we are working with. Figure 4a (3x3 km$^2$) and 4b (5x5 km$^2$) show how cell's width affects the landscape mosaic. Comparing with Figure 3c, it can be seen that the points of the first graph are accumulated between zero and $\log_k 2$ (vertically) and form arches similar to the ones in Figure 2a. Conversely, for bigger cell size (4a, 4b) the point density is closer to 1 and to the central part of the graph. In addition, we can observe in Figure 3c that points tend to cluster on agricultural land-covers (mainly $w_7$), while diluted densities appear on the other land-covers. We infer from this that the latter mesh size is the most suitable for our study.

### *3.2. Testing the 'biodiversity assumption'*

As an initial test of this IDC model on biodiversity we have used data on nesting and wintering bird communities observed in Mallorca (GOB, 2008). For each database there is a different grid of 5x5 km$^2$, with 105 and 69 cells for nesting and wintering birds, respectively. Considering that it is not disturbance as such but the disturbance-complexity interplay (IDC) what matters, we do not presume a clear statistical relationship between species richness and *HANNP* when taken separately. Instead, we expect that it does exist between bird species richness and *HANPP* combined with *H'*. Two PCAs have been performed using nesting and wintering bird data separately, *H'* and *HANPP* values, and the proportion of land-cover in each cell. Then we introduce the variable *H'·HANPP* that is the multiplication of *H'* by *HANPP*, assuming that a higher bird diversity for higher values of *H'·HANPP* is to be expected. This PCA provides us with a representation that cannot be plotted in its entirety, together with a set of combinations of the original variables that help to discern types of relationships that exist between them so as to minimize the number of variables while losing the least amount of information. Table 1 shows the amount of variance of the new components.

We have taken the first two new components because they give a high enough percentage of variance explained by the original variables, 44.23% in the nesting PCA and 45.21% in the wintering PCA. The resulting components have been rotated so that the arrows are best placed on the axes, making it easier to interpret the results (the correlation of each variable with only one factor is as close to 1 as possible and 0 with the others). Figure 5 shows the projection of the original variables over each new dimension. The PCA both for wintering and nesting birds provides arrows placed in a fairly similar way. What changes comparing the two graphs is bird data, wintering birds being better explained between the first and second component than in the case of nesting ones whose arrow is shorter. In both analyses the first component is correlated with the variable *HANPP* and the land-covers olive groves ($w_9$), prairie and bedrock ($w_3$), forest ($w_1$), dry cropland ($w_5$) and dry groves ($w_7$). The second component is correlated with the variable *H'·HANPP* and the land-covers irrigated cropland ($w_6$), irrigated groves ($w_8$), wetlands ($w_4$) and bird richness. In turn, the variable *H*' is correlated with the first and the second component. Overall the variable *H'·HANPP* results are really important to explain bird species richness owing to the fact that the landscape of Mallorca is mainly a rain-fed agroecological matrix. While nesting birds are higher correlated with *H'* which implies landscape mosaic preference, wintering birds are more correlated with *H'·HANPP*, wetlands ($w_4$), irrigated groves ($w_8$) and irrigated cropland ($w_6$) which means that they look for wet and irrigated land-covers in order to find food in winter (Hawkins et al 2003).

### *3.3. Socio-metabolic change and landscape dynamics (landscape scale -SF2)*

Figure 6 shows the results for three time points (1956, 1989, 2011) of the eight scenes at landscape scale (SF-2). For the three years we have 13 different land-use types with a particular $w_i$. A perfect mosaic is understood as the one with $p_i = \frac{1}{n},\ i = 1, \dots, n,\ n < k$. In 1956 possible perfect agro-forest mosaics comprise up to five land-uses in a cell (the maximum value of *H'* is $\log_k 5$) while in 1989 and 2011 the number of possible land-uses in a cell increased up to seven (the maximum value of *H'* is $\log_k 7$). This may be due to forest regrowth in abandoned cropland that became intermingled with the rest within the selected areas. In addition, it becomes apparent that rural abandonment has taken place over the years: point density shifted to the left and concentrated on agricultural or natural land-uses (i.e., forest $w_1$, shelterbelts $w_2$, scrubland $w_3$, and rain-fed groves mixed with scrubs $w_4$). These trends can be seen by looking at the landscape scene of '*Esporles*' and '*Santa Maria*'.

On the whole, we can say that all areas are moving to the left, with a decrease in *HANPP*, except '*Sa Pobla*' that stays fairly constant on the axis corresponding to intensive irrigated cropland $w_{11}$ (Figure 6). At the same time values of *H'* grow up due to a wider diversity of land-uses, pointing at more agro-forest mosaic. Although '*Albocàsser*' and '*Santanyí*' practically remain at the same values, there appears to be a slight tendency towards a *H'* increase and a *HANNP* decrease. Similarly but stronger, a trend can be observed in the landscape scenes '*Calicant*' and '*Sant Joan*'. Only '*Marina*' breaks off this tendency in relation to *H'* due to a loss of land-use diversity driven by tourist urbanization. We conclude from these results that the main prevailing trends in Mallorca (1956-2011) were towards rural abandonment and forest transition on the one hand, and urban development on the other.

### *3.4. Testing the 'resilience assumption'*

Finally, we calculate the resilience capacity paying attention to the displacements of the points (*HANPP, H'*) from 1956 to 2011, at SF-2. Figure 7 shows the relationship between $H'_{1956}$, in the vertical axis, and *S* in the horizontal axis, where $\Delta H' = H'_{2011} - H'_{1956}$ and $\Delta HANPP =$

$HANPP_{2011} - HANPP_{1956}$. For higher values of $H'$ we find a smaller slope for the vector of displacement at any point ($HANPP$, $H'$) from 1956 to 2011, while the steepest slopes are observed for smaller values of $H'$. These results can be interpreted as the higher socio-ecological resilience that landscape mosaics provide. A particular case is observed for the points corresponding to the scene of '*Sa Pobla*', which despite having low values of $H'$ does not show large variations in slope. This is explained by the fact that '*Sa Pobla*' is an intensive irrigated landscape that has evolved towards monocultures, and is strongly affected by the decrease of $w$ associated to the main land cover ($w_{11}$). The same explains why there are no high variations of $\frac{\Delta H'}{|\Delta HANPP|+1}$. In future research, when we will be able to work with a larger database, a type of quadratic curve with a maximum at $H' = 0$ (i.e., decreasing when $S$ has negative values) is expected to be found.

## 4. Conclusion

We have built a spatial-explicit model that accounts for the joint behaviour of human appropriation of photosynthetic capacity ($HANPP$), and Shannon-Wiener ($H'$) indexes of land cover diversity of cultural landscapes, when they are correlated with species richness of nesting and wintering birds taken as a proxy of biodiversity. By adopting a long-term perspective the model can also grasp the dynamic trends at stake.

The results point out that agro-forest mosaics allow maintaining landscape patterns and processes that host great bird species richness in Mallorca and provide high socio-ecological resilience. Accordingly, actual species richness can be viewed as a resource offered by a legacy of historically built agroecosystems that created and maintained these landscape mosaics. Yet, this complex-heterogeneous landscape is currently disappearing due to industrial farm intensification, rural abandonment and urban sprawl. These results show the usefulness of transferring the concept of intermediate disturbance to LCLUC, by using $HANPP$ and land cover diversity $H'$ as variables. Additionally, a measure of LCLUC resilience has allowed analysing the resistance to spatial change of cultural landscapes and shedding some light on how entropy affects landscape functional structure (Cushman 2014).

Most of the species richness in the Mediterranean biodiversity hotspot appears to be located in complex agro-forest landscapes like these, created by former organic farm systems and currently endangered by a lack of an adequate land-use management. Current LCLUC has a long-term dynamics history behind it that is useful to know for a better biological conservation, particularly once biodiversity is no longer identified with wilderness. Further research is needed, however, either in the relationships between *HANPP* and *H'*, or in the non-lineal correlation with different components of biodiversity other than nesting and wintering bird locations. If this IDC model proves to be consistent and fruitful, it may offer a very useful tool to make robust assessments of the impact of land management on ecological landscape functioning and help to design better land-use policies.

## Acknowledgements

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# Tables

Table 1. Principal Component Analysis (PCA) for nesting (a) and wintering (b) bird species richness. Eigenvalues and correlation matrix among original variables and new components.

a) Nesting bird species richness PCA

| Components | variance | percentage of variance | cumulative percentage of variance | variance after rotation | percentage of variance after rotation |
|---|---|---|---|---|---|
| comp 1 | 3.576 | 25.545 | 25.545 | 3.571 | 25.401 |
| comp 2 | 2.617 | 18.689 | 44.234 | 2.680 | 19.063 |
| comp 3 | 1.375 | 9.82 | 54.054 | | |
| comp 4 | 1.297 | 9.266 | 63.321 | | |
| comp 5 | 1.067 | 7.62 | 70.941 | | |
| comp 6 | 0.96 | 6.858 | 77.799 | | |
| comp 7 | 0.853 | 6.093 | 83.892 | | |
| comp 8 | 0.717 | 5.121 | 89.013 | | |
| comp 9 | 0.542 | 3.873 | 92.886 | | |
| comp 10 | 0.507 | 3.622 | 96.507 | | |
| comp 11 | 0.483 | 3.452 | 99.959 | | |
| comp 12 | 0.006 | 0.041 | 100 | | |
| comp 13 | 0 | 0 | 100 | | |
| comp 14 | 0 | 0 | 100 | | |

Correlation matrix between original variables and rotate new components

| Variables | Component 1 | Component 2 |
|---|---|---|
| N. birds | -0.015 | 0.396 |
| H’ | 0.372 | 0.803 |
| HANPP | -0.953 | -0.045 |
| H.HANPP | -0.298 | 0.803 |
| $w_{1}$_Forest | 0.791 | -0.02 |
| $w_{2}$_Scrubs | 0.438 | 0.14 |
| $w_{3}$_Prairie and bedrock | 0.529 | 0.231 |
| $w_{4}$_Wetlands | -0.156 | 0.391 |
| $w_{5}$_Rain-fed annual crops | -0.415 | -0.029 |
| $w_{6}$_Rain-fed arboriculture | -0.532 | -0.656 |
| $w_{7}$_Irrigated crops | -0.38 | 0.498 |
| $w_{8}$_Irrigated arboriculture | -0.257 | 0.561 |
| $w_{9}$_Olives | 0.573 | 0.383 |
| $w_{10}$_Urban | -0.321 | 0.145 |

b) Wintering bird species richness PCA

| Components | variance | percentage of variance | cumulative percentage of variance | variance after rotation | percentage of variance after rotation |
|---|---|---|---|---|---|
| comp 1 | 3.421 | 24.434 | 24.434 | 3.394 | 24.084 |
| comp 2 | 2.909 | 20.776 | 45.211 | 3.028 | 21.487 |
| comp 3 | 1.529 | 10.924 | 56.135 | | |
| comp 4 | 1.386 | 9.898 | 66.033 | | |
| comp 5 | 1.108 | 7.912 | 73.944 | | |
| comp 6 | 0.972 | 6.945 | 80.889 | | |
| comp 7 | 0.899 | 6.421 | 87.31 | | |
| comp 8 | 0.681 | 4.867 | 92.177 | | |
| comp 9 | 0.507 | 3.618 | 95.795 | | |
| comp 10 | 0.314 | 2.246 | 98.041 | | |
| comp 11 | 0.27 | 1.927 | 99.968 | | |
| comp 12 | 0.004 | 0.031 | 100 | | |
| comp 13 | 0 | 0 | 100 | | |
| comp 14 | 0 | 0 | 100 | | |

Correlation matrix between original variables and rotate new components

| Variables | Component 1 | Component 2 |
|---|---|---|
| W. birds | -0.149 | 0.676 |
| H’ | 0.525 | 0.672 |
| HANPP | -0.912 | 0.15 |
| H·HANPP | -0.025 | 0.792 |
| $w_1$_Forest | 0.765 | -0.135 |
| $w_2$_Scrubs | 0.368 | -0.107 |
| $w_3$_Prairie and bedrock | 0.479 | 0.114 |
| $w_4$_Wetlands | -0.096 | 0.685 |
| $w_5$_Rain-fed annual crops | -0.48 | 0.046 |
| $w_6$_Rain-fed arboriculture | -0.69 | -0.568 |
| $w_7$_Irrigated crops | -0.22 | 0.59 |
| $w_8$_Irrigated arboriculture | -0.076 | 0.468 |
| $w_9$_Olives | 0.643 | 0.167 |
| $w_{10}$_Urban | -0.198 | 0.194 |

## Figure captions

Figure 1. Location of the study region in the Mediterranean Sea. Two-scale experimental design: SF-1 (1:50,000); SF-2 (1:5.000).

Figure 2. Shannon-Wiener Index (*H'*) - Human Appropriation of Net Primary Production (*HANPP*) theoretical dispersion graphics for two (a) and three (b) land units (LU).

Figure 3. Applying the Shannon-Wiener Index (*H'*) - Human Appropriation of Net Primary Production (*HANPP*) model to the Mallorca Land Cover Map (SF-1) at three time points (1956, 1973 and 2000; using a 1x1 km$^2$ sample cell scale).

Figure 4. Applying the Shannon-Wiener Index (*H'*) - Human Appropriation of Net Primary Production (*HANPP*) model to the Mallorca Land Cover Map (SF-1) at three different spatial scales (1x1 km$^2$ –see Figure 3c, 3x3 km$^2$ and 5x5 km$^2$ sample cells).

Figure 5. Principal Component Analysis (PCA) applied to nesting (a) and wintering (b) bird species richness, Shannon-Wiener Index (*H'*), Human Appropriation of Net Primary Production (*HANPP*), and land-covers of Mallorca (SF-1; 5x5 km$^2$ sample cells).

Figure 6. Applying the Shannon-Wiener Index (*H'*) - Human Appropriation of Net Primary Production (*HANPP*) model to eight Mallorca Landscape Study Areas (SF-2) at three time points (1956, 1989 and 2011; using a 1x1 km$^2$ sample cell scale).

Figure 7. Long-term change (1956-2011) of Shannon-Wiener Index (*H'*) and Human Appropriation of Net Primary Production (*HANPP*) in eight Mallorca Landscape Study Areas (SF-2). Resilience (inverse of *S*) is measured by the product of the pendent of the movements from a time period to the next one (see Figure 6) by the intensity of the change.

Fig. 1.

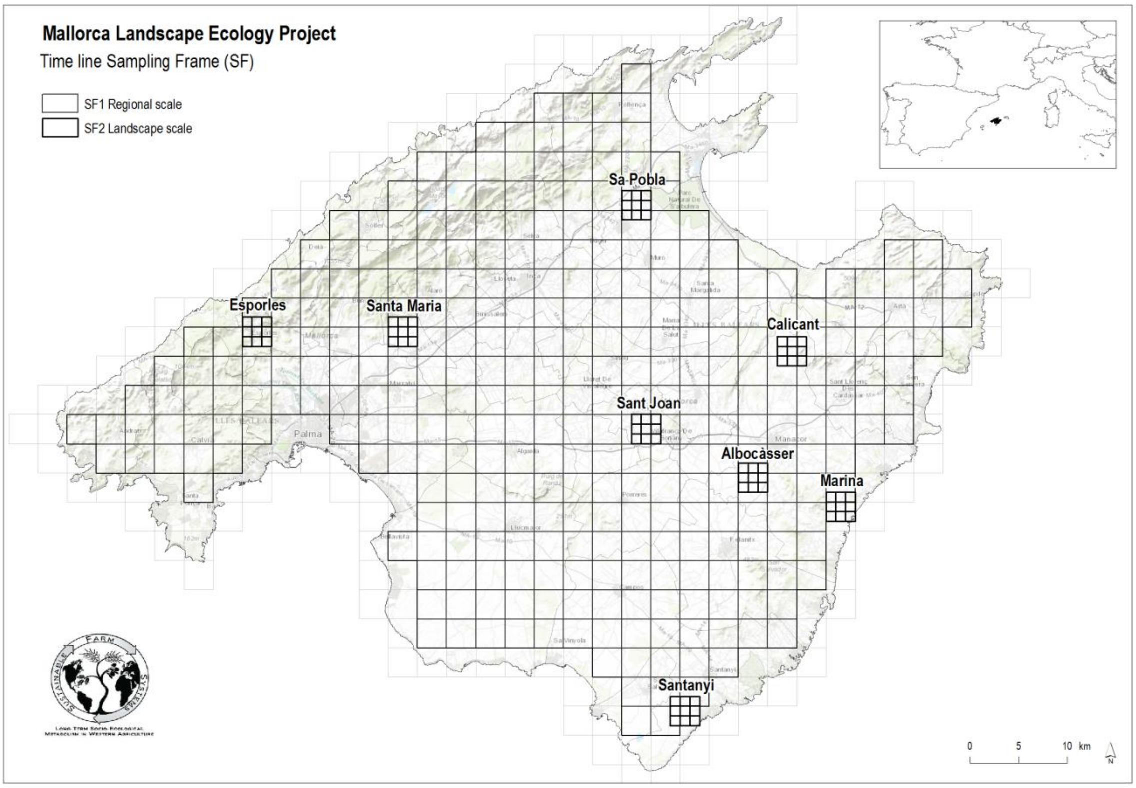
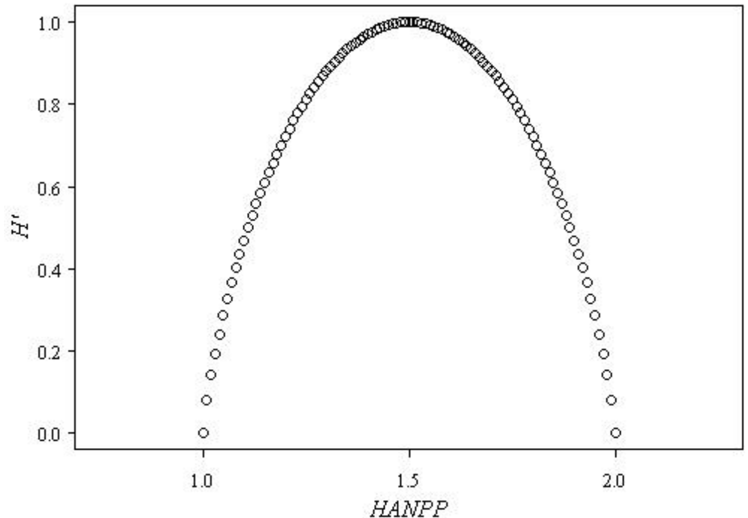
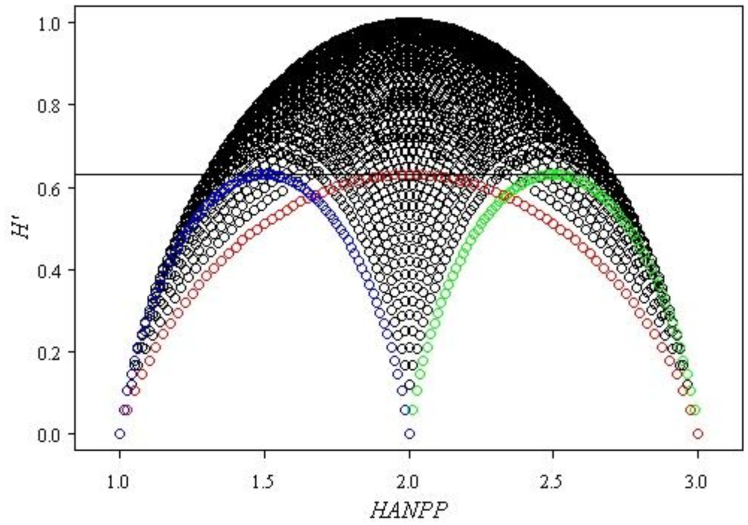

Mallorca Landscape Ecology Project
Time line Sampling Frame (SF)
SF1 Regional scale
SF2 Landscape scale
Sa Pobla
Esporles
Santa Maria
Calicant
Sant Joan
Albocàsser
Marina
Santanyi
Palma
Manacor
0
5
10 km
N

Fig. 2.

a) Two LU ($w_1$; $w_2$)



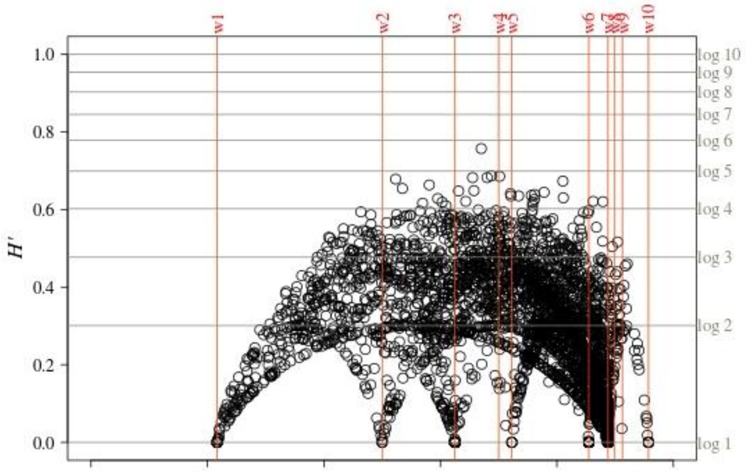
b) Three LU ($w_1$; $w_2$; $w_3$)



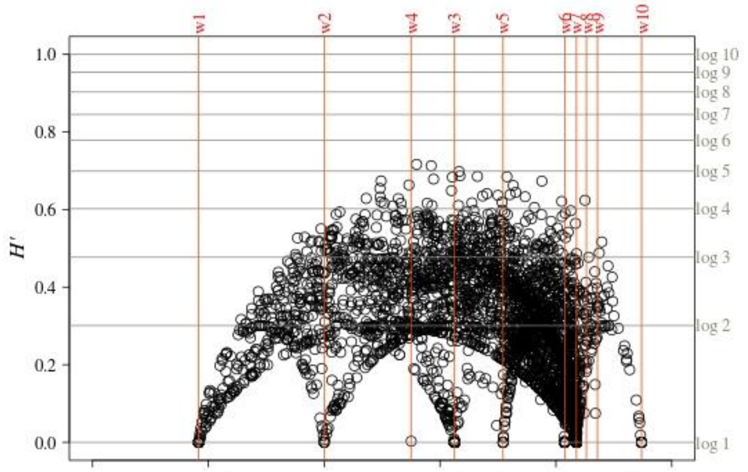
Notes: a) *H'-HANPP* dispersion graphic with $w_1 = 1$ and $w_2 = 2$. b) *H'-HANPP* dispersion graphic with $w_1 = 1$, $w_2 = 2$ and $w_3 = 3$; red points corresponding when $p_2 = 0$, green for $p_1 = 0$, and blue for $p_3 = 0$; and horitzontal line $H' = \log_k 2$.

Fig. 3.

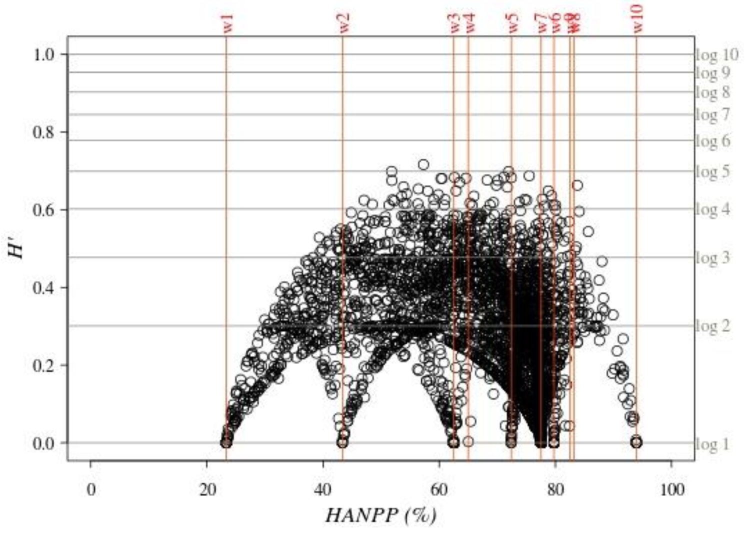
a) 1956



b) 1973



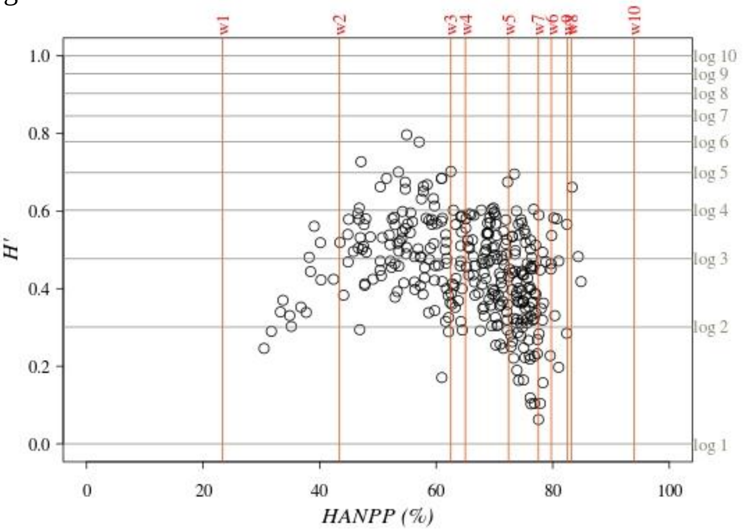
c) 2000



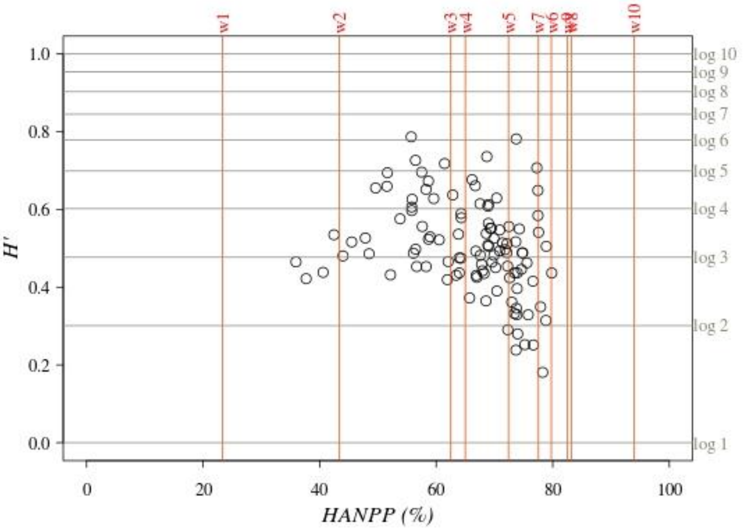
Note: $HANPP = \sum_{i=1}^{k} w_i p_i$. Where $w_i$ denote the weight of land-cover $i$: forest ($w_1$), scrub ($w_2$), prairie ($w_3$), wetland ($w_4$), dry cropland ($w_5$), irrigated cropland ($w_6$), dry grove ($w_7$), irrigated grove ($w_8$), olive ($w_9$), and urban ($w_{10}$).

Fig. 4.

a) 3x3 km$^2$ grid



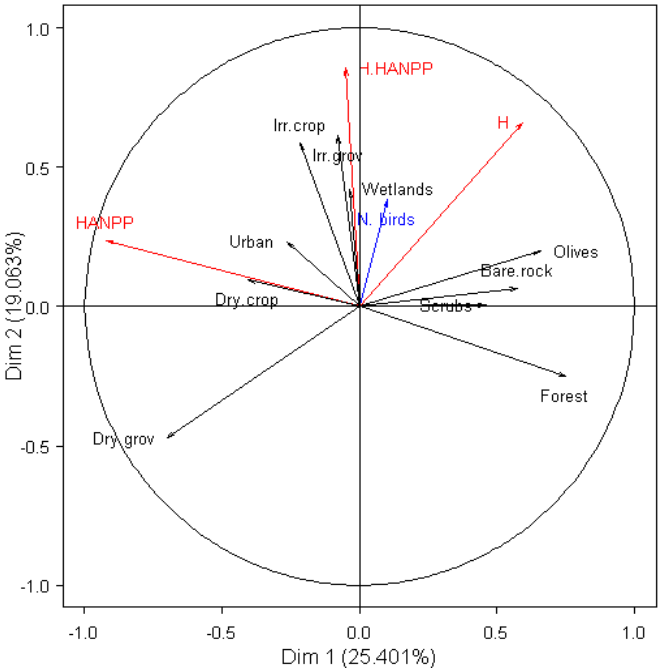
b) 5x5 km$^2$ grid



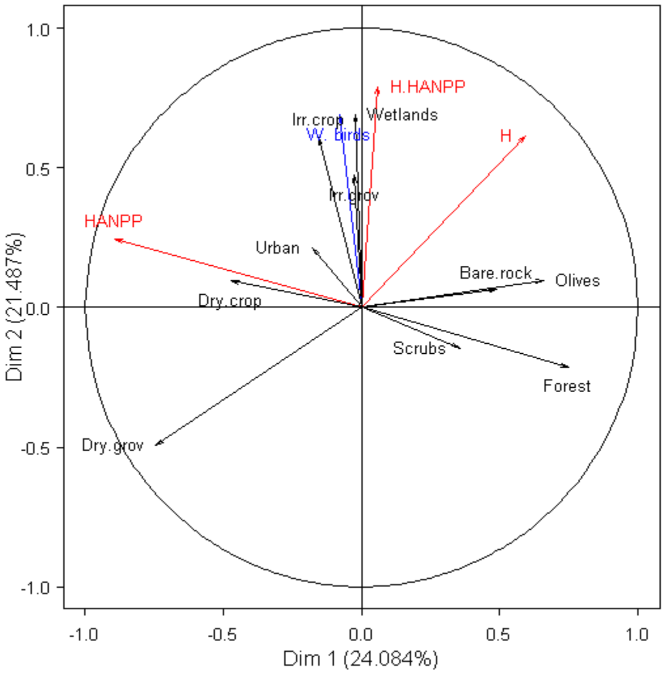
Note: $HANPP = \sum_{i=1}^{k} w_i p_i$. Where $w_i$ denote the weight of land-cover *i*: forest ($w_1$), scrub ($w_2$), prairie ($w_3$), wetland ($w_4$), dry cropland ($w_5$), irrigated cropland ($w_6$), dry grove ($w_7$), irrigated grove ($w_8$), olive ($w_9$), and urban ($w_{10}$).

Fig. 5.

a) PCA using nesting birds



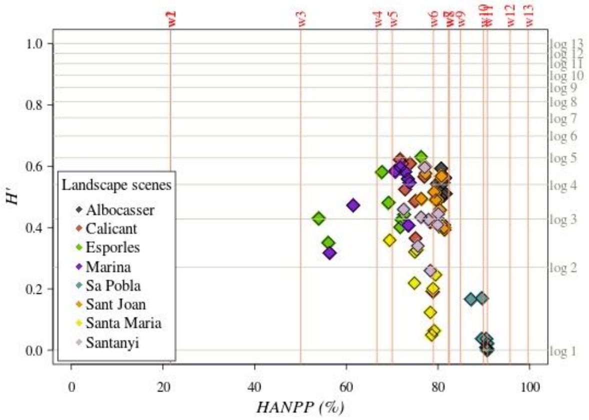
b) PCA using wintering birds



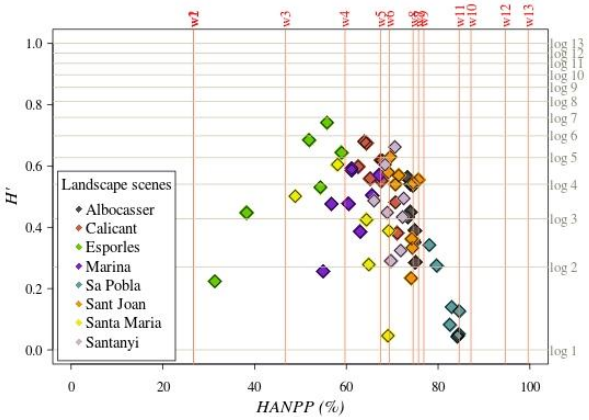
Notes: a) A 'varimax rotation' algorithm has been used in the analysis. b) Land-covers: forest ($w_1$), scrubs ($w_2$), prairie –bare rock ($w_3$), wetland ($w_4$), dry cropland ($w_5$), irrigated cropland ($w_6$), dry grove ($w_7$), irrigated grove ($w_8$), olives ($w_9$), and urban ($w_{10}$).

Fig. 6.

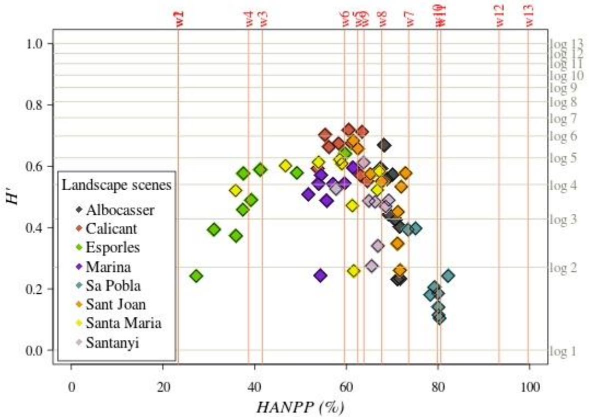
a) 1956



b) 1989

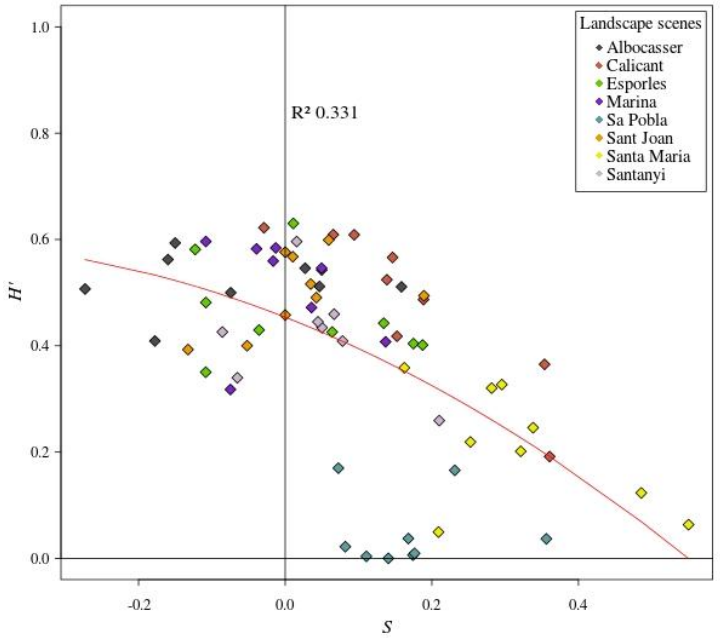


c) 2011



Note: $HANPP = \sum_{i=1}^{k} w_i p_i$. Where $w_i$ denote the weight of land-use $i$: forest ($w_1$), shelterbelt ($w_2$), scrub ($w_3$), dry grove mixed with scrub ($w_4$), grassland and pasture ($w_5$), dry grove high density ($w_6$), dry cropland ($w_7$), dry grove low density ($w_8$), vineyard ($w_9$), irrigated grove ($w_{10}$), irrigated cropland ($w_{11}$), urban area ($w_{12}$), roads ($w_{11}$).

Fig. 7.



Note: $S = \frac{\Delta H\prime}{|\Delta HANPP|+1} \cdot \sqrt{\Delta H'^2 + \Delta HANPP^2}$

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