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Using thermodynamics to understand the links between energy, information, structure and biodiversity in a human-transformed landscape

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Abstract

According to classical ecological theory, biodiversity at ecosystem scale can be viewed as the direct product of landscape complexity and information, and the inverse product of energy dissipation. The main difference between natural ecosystems and agroecosystems is the external energy driven by farmers. Hence, it could be argued that biodiversity in biocultural landscapes can be explained by an energy-information-structure model. We developed an Energy-Landscape Integrated Analysis (*ELIA*) to predict biodiversity levels in human-transformed landscapes. *ELIA* combines the energy-flow accounting in agricultural landscapes from abioeconomic point of view and landscape ecological metrics that assess the functional structure of the land cover. It uses indicators to assess the energy stored in internal loops (*E*) and the information incorporated into the energy network (*I*) to establish a correlation with the resulting patterns and processes in biocultural landscapes (*L*). We tested the model on biodiversity data using butterflies and birds. The results showed positive correlations between butterfly and bird species richness and *ELIA*, and, above all, between *I* and *ELIA*. This emphasizes how different strategies of agricultural management combined with nature conservation can be employed at certain optimal points in the relationship between the energy-information-structure of biocultural landscapes and the biodiversity present therein. *ELIA* modelling is the key to a new research agenda that will be very useful for designing more sustainable agroecosystems, metropolitan green infrastructures, and land-use policies, in line with the forthcoming Agroecology Transition planned by the European Commission and the Food and Agriculture Organization.

Keywords

agroecosystem complexity; social metabolism; disturbance ecology; biocultural landscapes; species richness; biodiversity conservation.



1. Introduction

For centuries, global human-driven Land Use and Cover Change (LUCC) has stimulated the spread of human-modified habitats in many regions including the Mediterranean, thereby affecting biodiversity and ecosystem functioning in human-transformed landscapes (Grove and Rackham, 2001). Its impact has been manifold and created a very different landscape from the mosaics of the past: today, we see the results of organic mixed farming adapted to site-specific natural conditions, land-cover homogenization driven by industrial farming, the use of animal feed based on fossil fuels, and spontaneous reforestation causing rural abandonment (Giampietro et al., 2013; Sterling and Ducharme 2008; Ellis et al., 2008). The effects of LUCC on biodiversity are already well known (Newbold et al., 2005; IPBES, 2019) and include a general decrease in species richness but also changes in species composition due to the rarefaction of habitat specialists and expansion of generalists and cosmopolitan species, as well as invasions by alien species (González-Moreno et al., 2013; Gaertner et al., 2017) facilitated by increasing propagule pressure and disturbance levels (Vilà and Ibáñez, 2011; Basnou et al., 2015). All these impacts lead to biotic homogenization in the most human-transformed regions (McKinney, 2006).

Human-transformed landscapes are today the outcome of a shifting interplay between the spatial patterns of land-use types driven by the energy flows of human activity and their associated ecological processes (Haberl, 2001; Wrבka et al., 2004). A widely acknowledged consensus in conservation biology, known as the intermediate disturbance hypothesis (Cornell, 1978), accepts that landscape heterogeneity is key to maintaining high biodiversity levels at intermediate disturbance levels through the interaction between, on the one hand, ecosystem patch diversity and, on the other, the ecological requirements that activate the dispersal abilities of species originating from less disturbed patches or allow colonization from the most disturbed ones (Perfecto and Vandermeer, 2010; Loreau et al., 2010). However, the outcome also depends on the intensity and



spatial distribution of the metabolic (i.e., energy) flows driven by society (Swift et al., 2004; Marull et al., 2016b). This recurrent interaction between landscape patterns and socioecological pressures has opened up a research field that investigates how the complexity of the energy flows driven by farming, livestock rearing and forestry ‘imprint’ diverse spatial patterns of human land-uses that give rise either to heterogeneous or homogeneous landscapes able to house very different levels of biodiversity (Matthews and Selman, 2006; Parrotta and Trosper, 2012) that can be addressed through a network perspective (Jordán, 2022).

The fundamentals of this research agenda can be found in Morowitz’s theorem that states that a flow of energy through a system is a necessary and sufficient condition for generating an organized, albeit ephemeral, structure (Morowitz, 2002). The structures of living systems that emerge and evolve towards self-reproducing complexity allow us to keep information organized and to transfer energy with greater efficiency away from thermodynamic equilibrium (Gladyshev, 1999). This increase in internal complexity is achieved by exporting entropy to the environment, since all living organisms are dissipative structures with multiple metabolic cycles embedded in a heterogeneous functional organization over space and time (Schrödinger, 1944). This thermodynamic concept of organisms has close similarities to ecosystems’ functioning, which is directly related to information-complexity and inversely to entropy (Ho and Ulanowicz, 2005). When a living system becomes more complex, it is also metabolically more efficient because it increases its internal information rather than its energy intake, thereby also reducing entropy (Ulanowicz, 2003).

Margalef (1958, 1963) indicated that ecosystem succession tends to a decrease in the photosynthetic Net Primary Production (NPP) growth rate. In other words, energy combined with information increases diversity and does not produce greater uniformity. Similarly, complex agroecosystems can store more energy and information at some points that reduce their internal



entropy, thanks to the exploitation of other spaces of less complexity that have larger NPP rates. Many traditional Mediterranean agroecosystems are the result of this type of balance between exploitation and conservation due to the spatial localization of different gradients of human intervention, a wise intermediate disturbance pattern resulting in heterogeneous landscape mosaics (González-Bernáldez, 1981).

The combination of an energy-flow pattern driven by complex information regarding how energy is redistributed across space is a good starting point for modelling human-landscape relationships. According to Margalef (1991), “the relationship between the external energy inputs and the dimensions that characterize the spatial patterns of its distribution” gives rise to the functional structure of landscape mosaics able to host higher biodiversity than other homogeneous landscapes. To test this hypothesis, Marull et al. (2016a, 2019b) developed an Energy-Landscape Integrated Analysis (*ELIA*) of agroecosystems that considers both the investment of energy stored within (*E*) and the information held in the whole network of socio-metabolic energy flows (*I*) to correlate their interplay (*E·I*) with the functional structure of the resulting biocultural landscape (*L*). This implies assessing whether the energy reinvested and redistributed by farming-driven metabolic flows can lay the foundations for studying the linkages that exist between social metabolism, landscape ecology and biodiversity, which in the final instance will help generate resilient agroecosystems (Ho et al., 2018) and sustainable land-use policies (Padró et al., 2020).

Testing Margalef’s hypothesis requires specifying and accounting for the ecological disturbance exerted by the information-driven external energy that farmers incorporate into the landscape. The Human Appropriation of Net Primary Production (HANPP) is a quantitative estimate of the potential annual biological productivity reduced by human activities (Haberl et al., 2007; Krausmann et al., 2013). It represents an initial approach to the interplay between anthropogenic disturbances and wildlife’s ability to withstand them. Intermediate HANPP values



are able to sustain greater biodiversity in human-modified landscapes than higher ones that largely decrease habitat differentiation and negatively affect the provision of food chains free from human colonization (Barnes et al., 2006). Thus, Marull et al. (2016a) developed an Intermediate Disturbance Complexity (*IDC*) model to assess how different levels of anthropogenic disturbance at regional scale affect landscape functional structure. Results show a hump-shaped relationship between landscape complexity, free NPP available for non-domesticated species, and biodiversity levels (Marull et al., 2016a, 2018). However, it depends greatly not only on the overall flux balance of photosynthetic biomass but on the intensity and distribution of socio-metabolic flows associated with either land-use mosaics or homogeneous land covers in agroecosystems (Swift et al., 2004; Peterseil et al., 2004).

The *ELIA* modelling goes a step further than the previous *IDC* explorations of the links between intermediate levels of socio-metabolic human disturbance, and the ecological functioning of biocultural landscapes carried out at regional scale (Marull et al., 2018). It measures *E* as the proportion of energy remaining in the agroecosystem, and *I* as the network of flows that allows farmers to reproduce the landscape *L* ‘fund components’ due to the information embedded in the system. According to the fund-flow bioeconomic approach, all biophysical flows that sustain societal metabolism are provided by living funds that, to continue providing them, they also need to be nourished and reproduced (Georgescu-Roegen, 1971). This approach leads to a circular bioeconomic view that assesses the sustainability of socioecological systems in terms of the reproducibility of the living fund components within the biophysical structures of our societies. In agroecosystems, this means both the reproduction of living funds such as soil fertility, which requires replenishment with organic matter and nutrients (Maeder et al., 2002), and aboveground biodiversity, which requires heterogeneous landscapes with sufficient NPP free from human appropriation (Tschardt et al., 2012). The way in which these internal energy flows of agroecosystems recirculate and temporarily store energy within agroecosystem is by interlinking



their living funds with each other through a set of bioconversions, similar to how food chains in ecosystems do it.

We use this energy-information-structure model (Fig. 1) to predict the locations of two important and particularly well-known biodiversity components, butterflies and birds, in the human-transformed landscapes here employed as empirical example. The aim is to test Margalef's hypothesis that the complex landscape mosaics of traditional organic agriculture were – and continue to be – good for biodiversity conservation (Margalef, 1991). Using butterfly and bird transects in the Barcelona Metropolitan Region (BMR), we account for the association between landscape patterns (composition and spatial configuration), *ELIA* components (*E*, *I*, *L*) and biodiversity (species richness and total observations). After applying the *ELIA* model, we use Structural Equation Modelling (SEM) to assess how social metabolism affects the capacity of metropolitan landscapes to host these indicators of biodiversity.

2. Materials and Methods

2.1. Study area

Covering 3,200 km² and with a population of 4.5 million, the BMR is one of the most densely populated regions in Europe (Fig. 2). However, this region still possesses several important natural and semi-natural areas boasting considerable ecological diversity and valuable biocultural landscapes. Contrasting topography (elevations ranging from 0 to 1700 m a.s.l.) and climate (with NE-SW gradients from moist to dry and from less to more continental) afford it greater climatic and land cover variability than most Mediterranean areas and are responsible for the great biodiversity present in this highly human-transformed territory. The region contains more than 40 habitat types of European interest (according to 92/43 EU Directive), including natural (forests, scrublands and grasslands; 60% of the region) and semi-natural habitats (croplands; 21%).

2.2. The Energy-Landscape Integrated Analysis (ELIA)



As explained, *ELIA* is a spatially explicit model for an energy-information-landscape integrated analysis based on information theory applied to ecology (Marull et al., 2016b). It combines the landscape functional structure (*L*) with the interlinking pattern of energy flows driven by farming (*E*) and the information they contain (*I*). *ELIA* summarises both natural and cropland production in agroecosystems (Fig. 3) through a combination of internal (vertical axis) matter-energy flows derived from photosynthesis, and external matter-energy flows coming from human society through the farmers' labour and knowledge (left-hand side of the horizontal axis). These flows interact across the agroecosystem functioning and give rise to a final product consumed and dissipated by the human society as well (right-hand side of the horizontal axis). The *ELIA* graph is the depiction of this socio-metabolic biophysical interaction with nature in human-transformed ecosystems. Accordingly, the flows of energy carriers from the solar radiation photosynthetically converted into biomass (i.e., the itinerary of the photosynthetic Net Primary Production – NPP – along the vertical axis) interact with the flows farmers invest (i.e. the itinerary of the external energy carriers moving along the horizontal axis). All matter-energy flows that arrive at a node split into two, one incoming flow recirculates within the agroecosystem, and another outgoing flow ends up in the agri-food basket of consumable products delivered to society (which, in some cases, is wasted).

The *ELIA* graph (Fig. 3) resulting from this pairwise distribution of flows distinguishes between three main internal loops that characterize agroecosystem functioning: 1) the most 'natural' cycles (e.g. forestry and livestock grazing on natural pastures), which merely extract some of the *NPP*; the rest is left to internal recirculation without directly interfering with the reproductive natural cycling of these flows, which end up decomposed as organic matter that temporarily accumulates energy in fertile soils where ecological turnover recommences; 2) the 'cropland' cycles, which require a direct input of farmers' labour through ploughing, seeding, weeding, harvesting and fertilizing the soils, where *NPP* is reinitiated on arable land; and 3) the livestock-



raising cycle, through which a share of the previous biomass flows that circulate in loops 1 to 2 are diverted to feed farmers' herds that, in turn, recirculate manure into cropland and pastureland while provisioning livestock products to the societal agri-food chains. The more linked the flows of matter and energy moving through these three cycles of a mixed farming, the more complex and endowed with information the agroecosystem is.

The plant biomass obtained from ecosystem photosynthesis is the *actual Net Primary Production* (NPP_{act}), i.e., the energy source for all the heterotrophs that live there. The biomass included in the NPP_{act} that becomes available for heterotrophic species splits into *Unharvested Biomass* (UB) and the share of *Net Primary Production harvested* by farmers (NPP_h) (Fig. 3). The UB generally remains in the same place as it was originally grown and can feed farm-associated biodiversity. It becomes a source of the *Agroecosystem Total Turnover* (ATT), which closes the cycle of the 'natural' subsystem. This subsystem maintains the farm-associated biodiversity and, in turn, the production of NPP_{act} , again through the trophic net of non-domesticated species either aboveground or in the edaphic decay processes of the soil. NPP_h splits into *Biomass Reused* (BR) inside the agroecosystem and *Farmland Final Produce* (FFP) that flows outside the system. BR is an important flow that remains within the agroecosystem thanks to the farmers' investment aimed at directly or indirectly maintaining two basic funds: livestock and soil fertility. Hence, BR closes the 'farmland' subsystem circle.

Then, BR is split into the share that goes to feed and bed domestic animals as *Livestock Biomass Reused* (LBR), which can be added to the *Livestock Total Inputs* (LTI) and *Farmland Biomass Reused* (FBR). In turn, these flows add up to *Farmland Total Inputs* (FTI) as seeds, green manure, and other plant-based fertilizers (Fig. 3). These energy linkages in the graph enable us to see to what extent land-use management is carried out by integrating or not the basic living funds of the agroecosystem. Finally, domestic animals perform bioconversion, and then the LBR flow



splits into *Livestock Final Produce (LFP)* and internal *Livestock Services (LS)*. *LFP* includes a wide range of food and fibre products, while *LS* services include driving force and animal manure. Together they make up *Livestock Produce and Services (LPS)*.

The ‘farmland’ and ‘livestock’ subsystems are partially closed within agroecosystems and offer a *Final Produce (FP)* that is consumed and dissipated outside, and also receive *External Inputs (EI)*. Therefore, *UB*, *BR* and *LS* regulate the internal flows that lead to a higher or lower circularity in the pattern of energy networks in agroecosystems (Fig. 3). They constitute important flows of recirculating biomass that contribute to the maintenance of the agroecosystem living funds, that is, associated biodiversity, soil fertility and livestock. Conversely, their weakening denotes an increase in the linearity and external dependence of the agroecosystem.

The circularity of matter-energy flows is kept within the agroecosystem because the outputs of one subsystem serve as inputs for the next subsystem, thereby allowing for the temporary storage of energy carriers and information within its dissipative structure interlinking their living funds through a set of energy bioconversions. That said, there is an exception to this rule that occurs when energy carriers circulating inside the agroecosystem, due to farmers’ mismanagement, are converted into a ‘resource out of place’, i.e. waste. We consider waste an energy flow that cannot be integrated into the structured recirculation of matter-energy of the agroecosystems, either because it exceeds their carrying capacity or because the way it is disposed of does not render it useful for neither keeping alive the agroecosystems’ funds nor to meet societal goals. In some cases, the monetary cost of certain biomass flows is larger than the benefits they generate, and this can lead to misuse. The result is a waste flow.

Sometimes a fraction of NPP_{act} can be wasted, such as crop stubble or tree pruning, and are burnt rather than properly composted and used as fertilizer, as it often occurred in past times when they were used as bedding (straw), home heating (branches), or animal feed (leaves and green shots

browsed). The same may happen with a fraction of the *LPS* generated by agro-industrial feedlots whose excess is spread on cropland beyond its carrying capacity, and eventually contaminates the water table (a resource out of place). If they exist, *Farmland Waste (FW)* and *Livestock Waste (LW)* do not contribute to the renewal of the agroecosystem's funds; they neither enhance its internal complexity nor meet human needs.

2.2.1. Measuring energy storage as a reinvestment of energy cycles (E)

We understand agroecosystem complexity to be the differentiation of dissipative structures (e.g., metabolic cycles) that allows for a diversity of potential ranges in the system's behaviour. The more complex the space-time differentiation of these structures, the more energy is stored within a living system. Hence, higher mean values of even β_i mean that agroecosystems are increasing in complexity because the different cycles are connected, and the residence time of the stored energy increases thanks to a greater number of interlinked energy transformations circling within. Accordingly, our way of calculating the energy stored and needed to keep the agroecosystem's funds functioning is as follows (Eq. 1):

Eq.1

$$E = \frac{\beta_2 + \beta_4}{2} k_1 + \frac{\beta_6 + \beta_8}{2} k_2 + \frac{\beta_{10} + \beta_{12}}{2} k_3.$$

$$k_1 = \frac{UB}{UB + BR + LS}, k_2 = \frac{BR}{UB + BR + LS}, k_3 = \frac{LS}{UB + BR + LS}$$

Where the coefficients k_1, k_2, k_3 account for the share of reusing energy flows that are circulating through each of the three subsystems (Fig. 3), which allows us to differentiate the agroecosystems' fund composition and make their energy patterns comparable. E remains within the range [0,1]. An E close to 0 implies a low reuse of energy flows, usually associated with industrial agroecosystems, which are highly dissipative and dependent on external inputs. An E



close to 1 implies the existence of internal cycles only, meaning land abandonment (which is associated with the loss of biocultural landscapes) or to a simple extractive use of the land (i.e., foraging or hunting).

E assesses the amount of all the energy flows that are returned to the agroecosystem relative to the total amount of energy flowing across each one of the three subsystems. If we pool the three subsystems together, we are adopting a landscape agroecology standpoint focused on what happens with the energy carriers flowing across the different land units driven by farmers. This allows us to link farming energy analysis with landscape ecology assessment.

2.2.2. Measuring information as the complexity of energy flow patterns (*I*)

According to Information Theory applied in ecology (Hirata and Ulanowicz, 1984; Grueber et al., 2011), agroecosystems have a quantity of information embedded in their network structure that allows their reproduction to take place over time. This information can be assessed through the graph complexity, i.e., the degree to which energy flow is equally distributed across all edges and nodes of the graph or, conversely, is concentrated only on some edges and nodes. An equal distribution of energy flows across the edges that link the nodes of a graph (Fig. 1) means that the information carried cannot be known beforehand (Shannon and Weaver, 1949). Therefore, the information given by each event is the highest that can be transmitted by the channel considered (in this case the agroecosystem to the farmers that manage them). This type of information accounting can be seen as a measure of uncertainty, or the degree of freedom for the system to behave and evolve. It is called ‘information-message’ and registers the likelihood of the occurrence of a pair of events.

Energy Information (I) is always site-specific (Font et al., 2020), an important trait from a cultural standpoint. In general, when the *I* of balanced agroecosystem decrease, information has been lost or transferred from the site-specific traditional agroecological knowledge possessed by

farmers, and located at the landscape level, towards higher hierarchical scales (i.e., big corporations that produce and sold the seeds, fertilizers, herbicides and pesticides to industrial farmers). Some important parts of agroecosystem functioning are thus no longer controlled at landscape level but linked to increasingly globalised agri-food chains (Tello and González de Molina, 2017).

We used a Shannon-Wiener Index for a metric of I , adapted to be applied over each pair of β_i , so that this indicator will show whether the β_i pairs are evenly distributed or not. This metric accounts for the balance of pairwise energy flows that exit from each node in every sub-process (Eq. 2):

Eq. 2

$$I = -\frac{1}{6} \left(\sum_{i=1}^{12} \beta_i \log_2 \beta_i \right) (\gamma_F + \gamma_L) (\alpha_F + \alpha_L),$$

$$\gamma_F = \frac{UB + NPP_h}{2(UB + NPP_h + FW)}, \gamma_L = \frac{LS + LFP}{2(LS + LFP + LW)}$$

$$\alpha_F = \frac{FEIr}{2(FEIr + FEInr)}, \alpha_L = \frac{LS + LFP}{2(LEIr + LEInr)}$$

Base 2 logarithms are applied as the probability is dichotomous. The introduction of the information-loss coefficients γ_F, γ_L ensures that I values remain lower than 1 when the agroecosystem presents farm and/or livestock waste. We have also introduced the coefficients α_F, α_L as a penalization for the use of non-renewable external inputs, which entail an internal information loss given that the agroecosystem functioning is no longer self-reproductive.

I values close to 1 have an equal distribution of incoming and outgoing energy flows, where the ‘information-message’ embedded in the agroecosystem structure is high; on the other hand, I values close to 0 indicate probability patterns that are far from equally distributed, containing and providing less information. These lower I values correspond to disintegrated agroecosystems with

either low site-specific information, which may be related to an industrialised farm system, or, conversely, to an almost ‘natural’ turnover with no external inputs and no harvests. Conversely, agroecosystems where $I = 1$ have equally well-distributed incoming and outgoing energy flows in each interlinked sub-process, which probably correspond to mixed farming systems where external inputs are balanced with the local energy recirculation. Therefore, E measures the energy reinvested and temporarily stored in the agroecosystem, and I assesses how farmers redistribute this energy in the land-matrix. Needless to say, the more complex (i.e., internally differentiated and interlinked) an agroecosystem is, the greater the farming information required to manage it.

2.2.3. Measuring energy imprint through the landscape structure (L)

To assess the energy imprinted in the landscape we use L , a metrics of landscape heterogeneity that indicates the capacity of differentiated landscape mosaics to offer a range of habitats that sustain biodiversity (Loreau et al., 2010). The underlying assumption is that species richness associated with agricultural landscapes depends on the landscape heterogeneity of land covers measured at scales larger than plot and farm scale (Eq. 3).

Eq. 3

$$L = - \sum_{i=1}^k p_i \log_{k+1} p_i$$

where k is the number of different land covers (potential habitats) in each case and there are $k+1$ possible land covers in each unit of analysis. We consider that the existence of urban land cover results in a loss of potential habitats. Thus, p_i is the proportion of land covers i in every unit of analysis. These L values can be seen as a proxy for guaranteeing farm-associated biodiversity, whereby species whose populations are disturbed by agriculture can find safe haunts nearby by activating their own dispersal abilities. The more diverse the vegetated land cover of an

agroecological landscape, the more likely it is to be able to withstand discontinuous disturbances through dispersion towards less disturbed or undisturbed spaces in the landscape.

2.2.4. Measuring the Energy-Landscape Integrated Analysis (ELIA)

After having defined the three *ELIA* indicators (*E*, *I* and *L*), we can analyse their relationship. We surmise that the interplay between *E* and *I* will jointly lead to complexity, understood as a balanced level of intermediate self-organisation. We assume that an agroecosystem's complexity of energy flows ($E \cdot I$) is related to the most diverse landscapes where the ecological patterns and processes that sustain farm-associated biodiversity are stronger. Therefore, the *ELIA* index that combines the agroecological landscape functional-structure with the complexity of the interlinking pattern of energy flows, and can be taken as a proxy for the agroecosystem's biodiversity (Marull et al., 2019a) (Eq. 4):

Eq. 4

$$ELIA = \left(\frac{(E \cdot I) L}{\max\{EI\}a} \right)^{1/3}$$

where *E* is the energy storage, *I* the information carried by the network structure of energy flows, and *L* the diversity of land covers, viewed as the energy imprint on the landscape structure. The equilibrated $\max\{EI\}e = 0.6169$ ($k_i = \frac{1}{3}$) implies subsystem equilibrium and no waste. When there is no such equilibrium, the absolute $\max\{EI\}a = 0.7420$ ($k_i = 1$) and, even though this last combination is unlikely in an agroecosystem, it is possible in a theoretical mathematic case. Hence, *ELIA* theoretically ranges from 0 to 1 for any value of the parameters considered.

In order to understand the relationship between the stored energy (*E*), the information it contains (*I*) and its impact on the landscape (*L*), we should consider a three-dimensional model (Fig. 3c; see a 3D video in Supplementary Material) that can be interpreted in the sense that it is culture (the



site-specific knowledge passed down from generation-to-generation, combined with knowledge of opportunities originating from outside the farm system) what allows farmers to manage the energy entering the agroecosystem in order to meet their needs and societal goals while ensuring the reproduction of its living funds in a healthy state.

The socio-metabolic analysis is based on the BMR's energy flow-fund approach to agroecosystems (Tello et al., 2016), and uses data from the Spanish Ministry of Agriculture and the Catalan Institute of Statistics (Cattaneo et al., 2018). The landscape composition and configuration was calculated using the 2009 Land Cover Map of Catalonia (www.creaf.uab.es/mcsc/).

2.3. Species studied

Birds and butterflies are recognized as excellent biodiversity indicators in both natural and human-modified landscapes. Their use as bioindicators comes from the variability between species and their ability to respond quickly to environmental changes such as agricultural intensification and land abandonment (Santos et al., 2008; Melero et al., 2016; Stefanescu et al., 2010; Vallecillo et al., 2008). We used butterfly data generated by the Catalan Butterfly Monitoring Scheme (CBMS; <http://www.catalanbms.org/>), a project that has been running for the past 25 years. The survey consists of a network of sites where visual counts of adult butterflies along transects (Fig. 2) are undertaken by volunteers. At each site butterfly surveys are performed weekly during the flight period of the imagoes (March–September) along lineal transects of ca. 700-2500 m in length (mean and median length = 1715 and 2010 m, respectively; 5 m in width). Each transect is divided into smaller sections according to the dominant habitat type, giving 6–14 sections per transect. The number of individuals (i.e., observations) are then recorded per species in each section, and then summarized per transect. We used 91 butterfly transects from the CBMS (2009). In the case of birds, we obtained data from the Catalan common bird monitoring scheme (SOCC; www.giraffa.co/ico-catalan-ornithological-institute/). Transects consist of a 3-km walk with six



sections of 500 m along which observers record all birds seen and heard, and then summarize data per transect (Fig. 2). Two censuses are performed annually for breeding species (April/May and May/June) and two for wintering species (December and January). We used 23 bird transects from the BMR (2009).

2.4. Landscape factors

A land cover map of the BMR (2009) was used to evaluate the landscape structure in both butterfly and bird transects. These biodiversity databases consist of 91 bird transects (linear buffer: 500 m) and 23 butterfly transects (circular buffer: 750 m). In these buffers (Fig. 2), a set of landscape metrics of landscape composition and configuration were obtained using GIS (ArcGIS) methods. For landscape composition, we calculated the proportion of main land-cover categories (forest, scrubland, cropland and built-up) per buffer, while for landscape configuration (Marull et al., 2019), we used the land heterogeneity (i.e., land-cover diversity), edge density (i.e., the sum of edge length divided by buffer area), polygon density (i.e., the amount of patches per buffer area), the largest patch index (i.e., the area percentage of the largest patch in the buffer), effective mesh size, a defragmentation measure proposed by Jaeger (2000), and, finally, the ecological connectivity, inferred from the ecological connectivity index proposed by Marull and Mallarach (2005).

2.5. Statistical analyses

As a test of *ELIA* using biodiversity data components, we used the observed abundance (i.e., total number of butterfly observations) and species richness of butterflies and birds along the study transects. Despite species richness and abundance are often considered weakly related with ecosystem function, we have preferred using them because of their simplicity instead of other proxies (e.g., redundancy or richness in functional groups) that could need an ad hoc definition of these groups. In order to disentangle the direct and indirect effects on biodiversity of (i) energy

storage and distribution and (ii) landscape composition and configuration, Structural Equation Models (SEM) were built for each of the studied biodiversity groups (butterflies, and breeding and wintering birds). Specific SEM were performed for species richness and the abundance of all pooled butterfly species and, in the case of birds, separately for nesting and wintering species. The SEM took into account the direct effects of the three *ELIA* components (*E*, *I*, *L*) and their indirect effects reflected in landscape composition (*C_m*) using land covers as variables, and in landscape configuration (*C_n*) using landscape metrics as variables. In order to reduce the number and the redundancy of variables in the SEM, we performed a Principal Component Analysis (PCA) on *C_m* and *C_n* (Table 1). Analyses were performed using the SEM package in R (Fox et al., 2016).

3. Results and discussion

3.1. Testing the *ELIA* model against empirical biodiversity data

Our study provides evidence that the societal metabolic flows driven by farming imprint different landscapes (*L*) with agroecosystems which enhance or decrease populations and species richness of butterflies and birds depending on the interplay between energy storage and its distribution pattern (*E·I*). The significant results of SEM are summarized in Figs. 4 and 5; the complete data are given in Tables S1 to S8 in the Supplemental Material.

The butterfly Principal Component Analysis (Table 1) shows that the first factor is the land-cover composition of the landscape (*C_{m1}*; 43.9% of variance), which obtains the highest loading for forest, while the second (*C_{m2}*; 35.5%) has the greatest loading for cropland. The first component of land metrics assessing landscape configuration through land metrics (*C_{n1}*; 72.4%) has negative loadings for diversity and fragmentation but positive loadings for grain size and connectivity, while the second component is more heterogeneous and contributes much less to explaining the variance (*C_{n2}*; 12.2%) despite being mostly associated with connectivity metrics (including effective mesh size).

The SEM results (Fig. 4) show that total butterfly observations (TBOB) are positively associated to *ELIA* values; species richness (TBSR) shows no significant correlation with this model. *ELIA* is negatively associated with Cm1 in the TBSR model but not in the TBOB model. In both models, Cm1 and Cn1 were negatively associated. The R^2 for the endogenous variables of TBSR and TBOB models were 0.316 and 0.266, respectively. When disentangling the effects of *ELIA* components (*E*, *I* and *L*), *I* has a positive association with both TBSR and TBOB, while *E* and *L* are only significant and positively associated with TBOB. Landscape composition (Cm) and configuration (Cn) are not significantly associated with any biodiversity component, although Cm1 is negatively associated with *ELIA* values in both models and Cm2 is negatively associated with *I* only in the TBOB model. The R^2 for the endogenous variables of TBSR and TBOB are 0.420 and 0.334, respectively.

In the bird Principal Component Analysis, the first factor of landscape composition (Cm1; 39.3% of variance) has the highest loading for forest, while the second factor (Cm2; 31.8%) has the greatest loadings for scrubland and cropland (Table 1). The first factor of landscape configuration (Cn1; 53.6%) has higher (negative) loadings for landscape diversity and fragmentation, while the second (Cn2; 27.3%) has greater (positive) association for ecological connectivity and effective mesh size.

The SEM results (Fig. 5) show that breeding bird species richness (BBSR) and wintering bird species richness (WBSR) are positively related to *ELIA* values and Cm2 but negatively related to Cn2. *ELIA* is negatively related to Cn1 in both models but only to Cm1 in the BBSR model. Cn2 and Cm1 are also negatively associated in this model. The R^2 for the endogenous variables of BBSR and WBSR are 0.244 and 0.210, respectively. If we disentangle the effects of *ELIA* components (*E*, *I* and *L*), *I* and *E* are positively and negatively correlated, respectively, to both BBSR and WBSR. *L* is only associated negatively with WBSR. *E* is negatively associated with Cm2 in both models,



and with Cm1 only in the BBSR model. L and Cm1 are negatively associated in this last model. The R^2 for the endogenous variables of BBSR and WBSR are 0.321 and 0.329, respectively.

3.2. Comparing ELIA results with Margalef's hypothesis

We checked Margalef's hypothesis regarding the capacity of biocultural landscape mosaics resulting from a complex distribution of external energy flows of farming to host high biodiversity by comparing the links present within the spatial energy-information structure with the species richness of butterflies and bird populations in the Barcelona Metropolitan Region (Margalef, 1991; Marull et al., 2018, 2019a). The results obtained suggest that agroecosystems could play a key role in halting the serious decline of butterfly populations in Europe (Van Swaay et al., 2012), a finding that can also be taken as proxy for many other current biodiversity threats (Thomas, 2005). The importance of the energy redistribution (I) to structure landscape mosaics carried out by farmers, coincides with recent research highlighting the worrying decline of common bird populations in European biocultural landscapes, which is related to the abandonment of age-old land-use patterns in human-configured agroecosystems (Inger et al., 2015).

The Energy-Landscape Integrated Analysis should be an efficient predictor of butterfly and bird locations in the studied human-transformed landscapes. Indeed, *ELIA* can better predict these biodiversity locations than if only landscape composition or configuration metrics are taken into account. Recent studies in the area have evidenced a parallel decline in species richness and functional diversity of butterfly and bird species in human transformed landscapes (Sol et al., 2020; Pla-Narbona et al., 2022). The results suggest that farmers' uneven spatial distribution of the biomass energy flows (I) in agroecosystems could be the key factor explaining not only butterfly observations and species richness but also breeding species richness and wintering bird species richness. This is an important outcome that points to the role farmers' knowledge plays in the design of the ecological functionality of biocultural landscapes through a subtle human-nature relationship



(Marull et al., 2019a). It also confirms the hypothesis that the interplay between the energy reinvested (E) and redistributed (I) by farmers affects the landscape functional structure (L) and its associated biodiversity via the harnessing of biomass flows that loop within these human-transformed landscapes.

The analytical advances and positive empirical results obtained mean that the usual methodology of energy flow analysis of social metabolism and classical landscape ecology metrics need to be adapted, enlarged and integrated to account for the complex cyclical character of human-driven land use changes in biocultural landscapes. Traditional farm systems with a solar-based metabolism tended to organise their land usages according to different gradients of spatiotemporal intensity, thereby ensuring an integrated management of different land patches given that their whole subsistence depended on the endurance of that very landscape functional structure (Marull et al., 2019a). In order to offset the energy lost in the inefficient human exploitation of animal bioconversion, on which farmers once had to rely to obtain traction and manure, past organic farmers guaranteed that livestock breeding was carefully integrated into their use of cropland, pastureland and forestland (Cattaneo et al., 2018).

While traditional organic farm management schemes with closed energy cycles in complex agroecosystems led to landscape mosaics that allowed a *land sharing* strategy for biological conservation (Tschardt et al., 2012), the agro-industrial farm systems that rely on external flows of inputs from underground fossil fuels now enable society to overcome the traditional energy dependency on bioconverters (Schaffartzik et al., 2014). As a result, integrated land-use management became redundant and the overcoming of this necessity led to the loss of its agroecological virtues (i.e. its reproduction of the landscape ‘living fund components’). Nowadays, biodiversity conservation in land matrices mostly occupied by biocultural landscapes cannot be guaranteed merely through the protection of nature protected areas (*land sparing*) to compensate



for the ever-more intensive industrial agriculture. It requires, rather, an improvement of the ecological connectivity and functionality of the whole land matrix by recovering and enhancing agroecological landscape mosaics (*land sharing*). This also means agroecosystems' functioning at landscape level need to be scaled up to cope with and offset the land cost of sustainability (Guzmán and González de Molina, 2009). Given that the relationship between energetic and biological processes that influence species richness may be due to the intermediate disturbance that characterizes biocultural landscape, the integration between social metabolism and landscape ecology approaches will be crucial in future developments of sustainable land-use planning.

4. Conclusion

The environmental change caused worldwide by the decoupling of energy flows and land uses makes it increasingly urgent that societies recover their former landscape efficiency (Marull et al., 2010). Depending on the energy storage-distribution ($E \cdot I$) and how these energy flows are imprinted on the landscape (L), agroecosystems either enhance or decrease biodiversity (Marull et al., 2019a). Since the lack of an integrated management of energy flows and land-uses is inherent to the current global socioecological crisis, its recovery is crucial for sustainable human-transformed landscapes. As Margalef suggested (Margalef, 1991), “the patterns of energy distribution” shaped by farmers' knowledge (i.e., the distribution of energy flows according to an aim) and labour (i.e., the energy investments needed to maintain an agroecosystem's funds over time) are determinant for understanding the locations of bird and butterfly species richness and abundance in Mediterranean biocultural landscapes.

The landscape scale is crucial for managing the challenge of increasing agricultural production while improving the state of the environment via a climate-smart and resilient farming transition. Neither agroecological intensification nor the application of a circular economy to agriculture will be possible without a rearrangement of the landscape complexity that can close



their main biophysical cycles and improve their ecoefficiency. This innovative line of research aims to contribute to the economic and environmental viability of scaling-up organic agriculture and agriculture in general. This can become possible if we learn to use the sustainable design of human-transformed landscapes to close socio-metabolic cycles, reduce our dependence on non-renewable external inputs, and improve ecological processes in order to maintain biodiversity.

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Figures and Tables

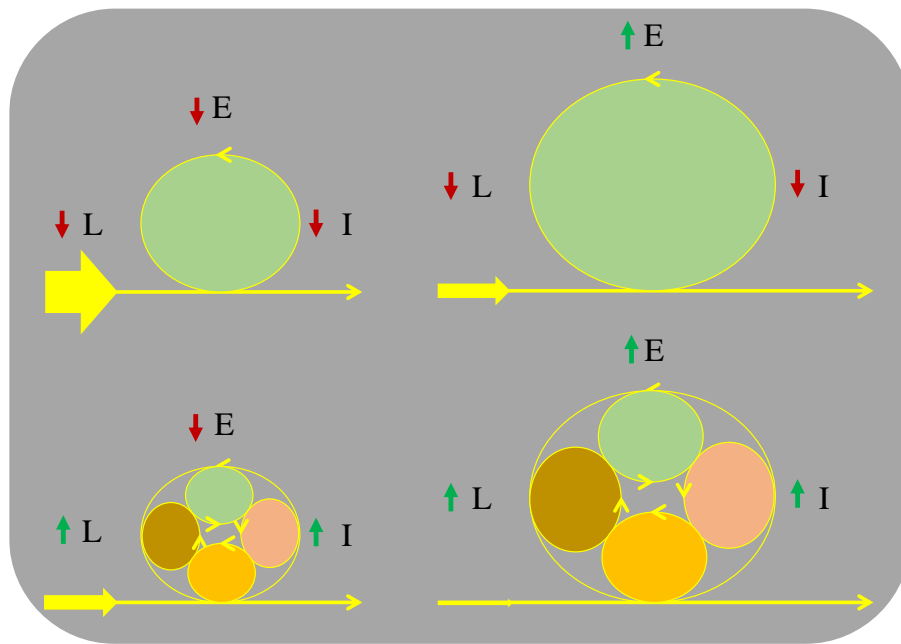


Figure 1. Our conceptual approach is based on a fundamental idea of Margalef (1991) according to which the relationship between the external energy reinvested in the system (E) and the spatial ‘distribution pattern’ (I) of this energy flows need to be considered to understand how society affects the functional structure of biocultural landscapes (L).

Note: The figure shows: a small metabolic cycle (low E , I and L values); a large metabolic cycle (high E , and low I and L values); many small interconnected metabolic cycles (low E , and high I and L values); and many large interconnected metabolic cycles (high E , I and L values). The latter case has stored more energy within and has greater capacity to organize the territory in a landscape mosaic (L) that becomes less dependent on external energy flows.

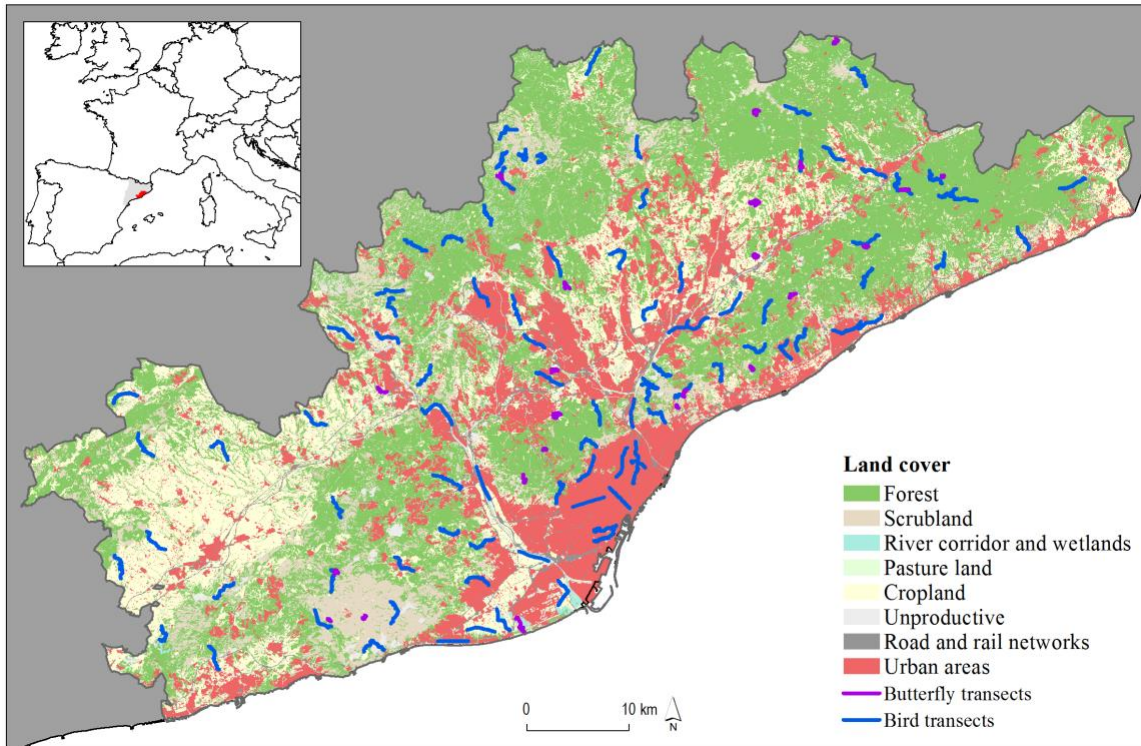


Figure 2. Butterfly transects (circular buffer: 750m; N=23) and bird transects (longitudinal buffer: 500m; N=91) analysed in the Barcelona Metropolitan Region (NE Spain) and represented over a Land-cover Map (2009).

Source: Catalan Butterfly Monitoring Scheme and Catalan Ornithological Institute datasets.

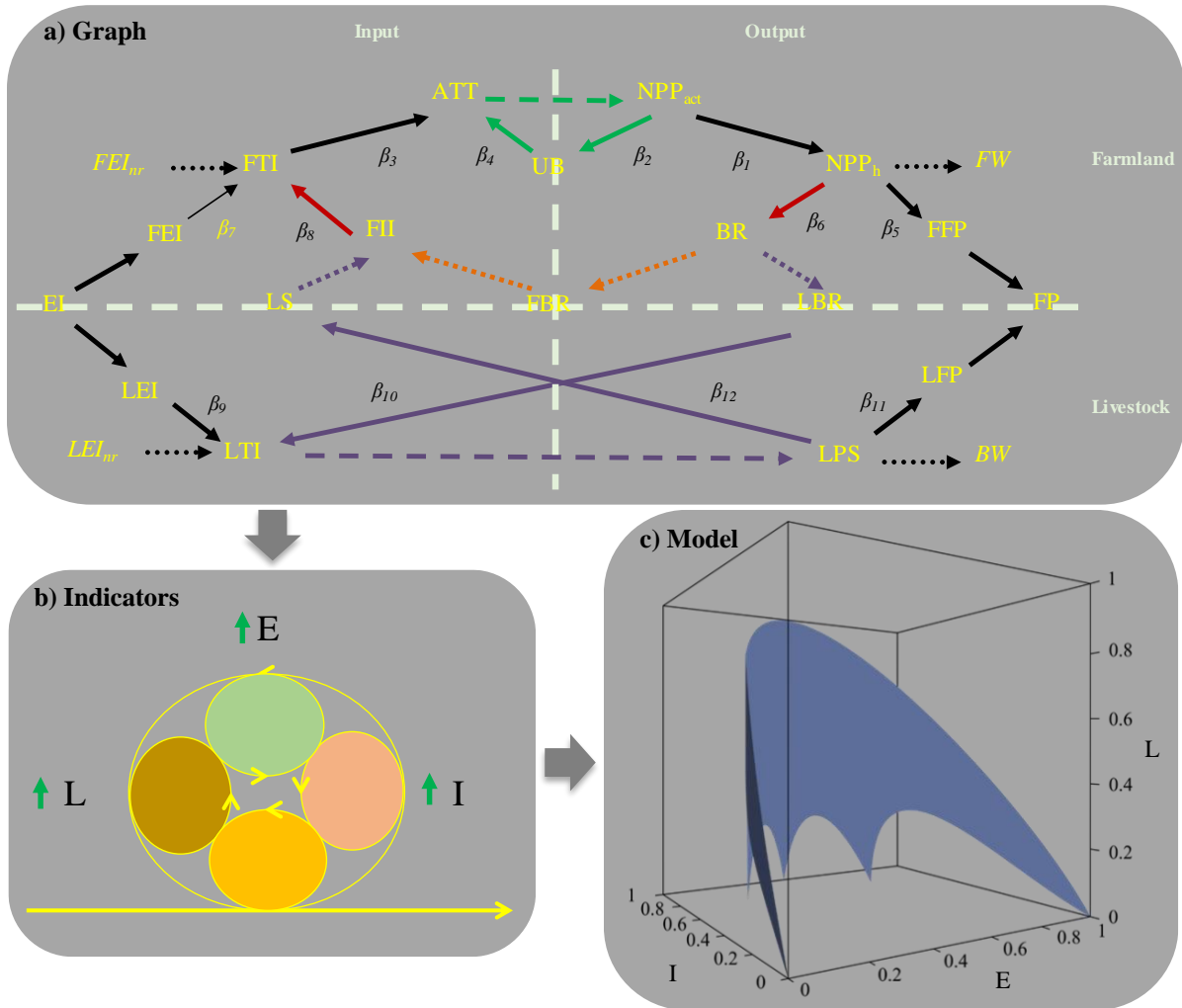


Figure 3. Methodological approach of the energy-information-structure model: a) Graph model of the interlinked energy carriers flowing in an agroecosystem. b) From the graph model, we can calculate the energy investment (E), the energy information (I), and the energy ‘imprint’ in the landscape structure (L). c) The resulting mathematical model allows the calculation of a three-dimensional relationship among E , I and L (as an example five land-cover typologies are represented), conforming a particular human-transformed landscape.

Variables: Actual Net Primary Production (NPP_{act}); Unharvested Biomass (UB); Harvested Net Primary Production (NPP_h); Biomass Reused (BR); Farmland Biomass Reused (FBR); Livestock Biomass Reused (LBR); Farmland Final Produce (FFP); External Input (EI); Farmland External Input (FEI); Livestock External Input (LEI); Livestock Total Input (LTI); Livestock Produce and Services (LPS); Livestock Final Produce (LFP); Livestock Services (LS); Final Produce (FP); Agroecosystem Total Turnover (ATT); Farmland Total Input (FTI); Farmland Internal Input (FII); Farmland Waste (FW); Livestock Waste (LW). nr means no-renewable. β_i 's are the incoming-outgoing coefficients. Relations between variables: $NPP_{act}=UB+NPP_h$; $NPP_h=BR+FFP$; $BR=FBR+LBR$; $EI=FEI+LEI$; $LTI=LEI+LBR$; $LPS=LFP+LS$; $FP=FFP+LFP$; $ATT=FTI+UB$; $FTI=FII+FEI$; $FII=FBR+LS$. Solid-line arrows show the energy flows that represent the internal and external exchange of energy carriers. Squared-line arrows indicate flows that require biological energy conversion (photosynthesis and animal metabolism). Point-line arrows show energy carriers which are no renewable external inputs or resources out of place (waste).

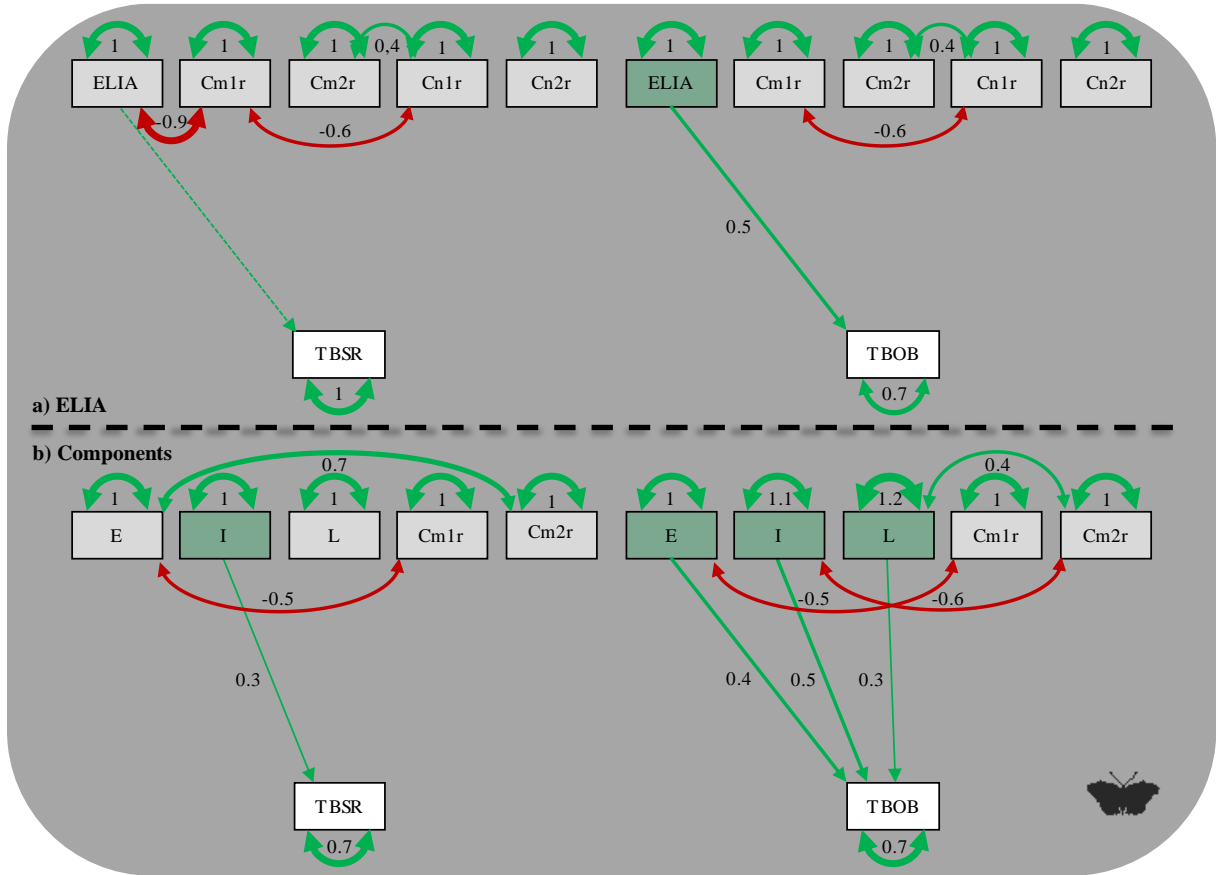


Figure 4. Structural Equation Model (SEM, see Supplemental Material) applied to the variables Total Butterfly Species Richness (TBSR) and Total Butterfly Observations (TBOB), taking into account: a) the Energy-Landscape Integrated Analysis (ELIA); and b) the ELIA components (Energy Storage, *E*; Energy Information, *I*, and Landscape Complexity, *L*). We have included Landscape Composition (Cm; in a and b) and Landscape Configuration (Cn; only in a, because in b we have included *L* using Principal Component Analysis (Table 1).

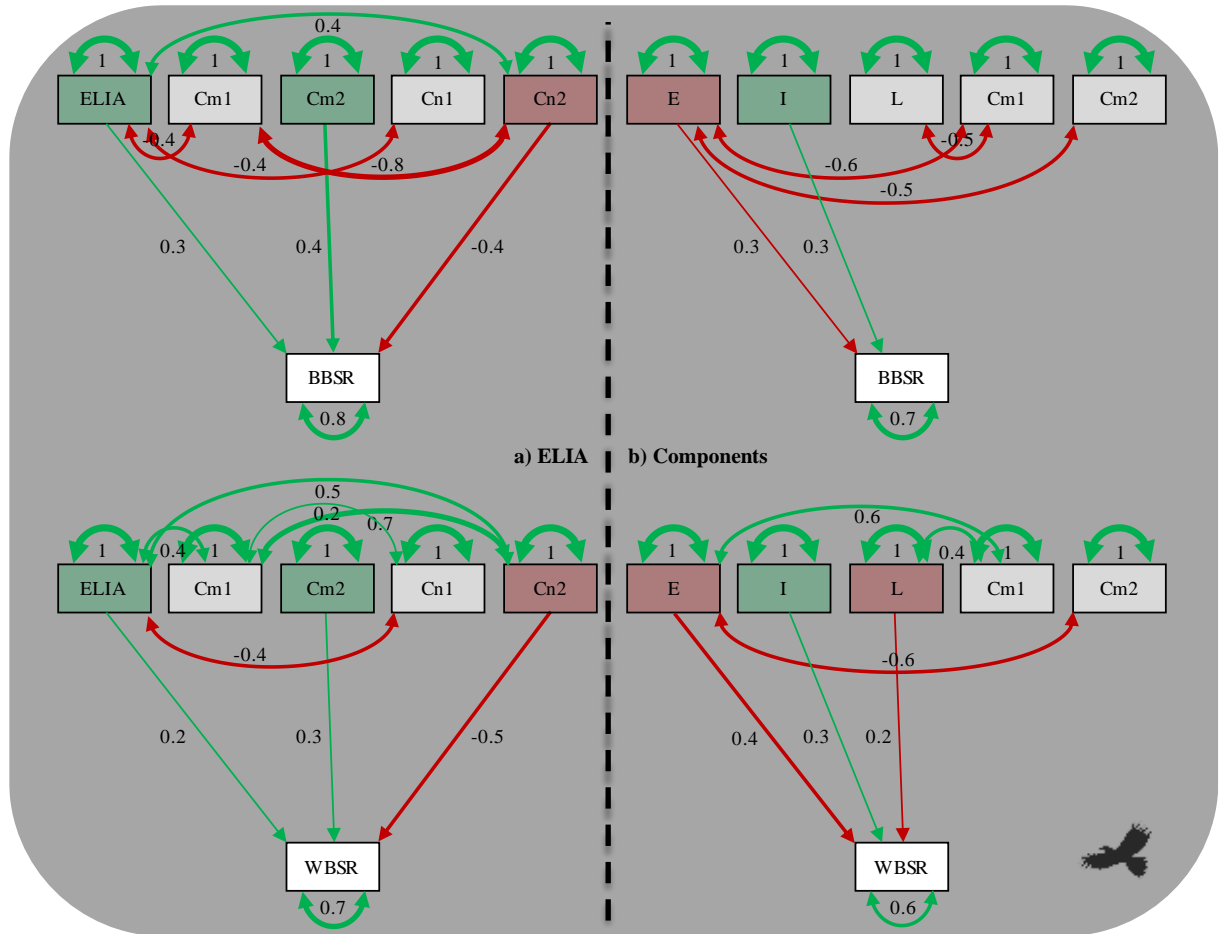


Figure 5. Structural Equation Model (SEM; see Supplemental Material) applied to the variables Breeding Bird Species Richness (BBSR) and Wintering Bird Species Richness (WBSR), taking into account: a) the Energy-Landscape Integrated Analysis (ELIA), and b) the ELIA components (Energy Storage, *E*; Energy Information, *I*, and Landscape Complexity, *L*). We have included Landscape Composition (*Cm*; in a and b) and Landscape Configuration (*Cn*; only in a, because in b we have included *L* using Principal Component Analysis (Table 1).

| Landscape Composition | | | | |
|------------------------|----------------------------|--------|-----------------------|--------|
| Land Cover | <i>Butterfly transects</i> | | <i>Bird transects</i> | |
| | Cm1 | Cm2 | Cm1 | Cm2 |
| Cropland | 0.169 | -0.651 | 0.359 | 0.571 |
| Scrubland | 0.549 | 0.561 | -0.208 | -0.721 |
| Forestland | -0.744 | 0.031 | -0.681 | 0.319 |
| Urban area | 0.342 | -0.511 | 0.603 | -0.229 |
| Standard deviation | 1.325 | 1.192 | 1.253 | 1.127 |
| Proportion of variance | 0.439 | 0.355 | 0.393 | 0.318 |
| Cumulative Proportion | 0.439 | 0.794 | 0.393 | 0.710 |

| Landscape Configuration | | | | |
|-------------------------|----------------------------|--------|-----------------------|--------|
| Land Metric | <i>Butterfly transects</i> | | <i>Bird transects</i> | |
| | Cn1 | Cn2 | Cn1 | Cn2 |
| Heterogeneity | -0.406 | 0.341 | -0.503 | -0.083 |
| Edge Density | -0.434 | 0.244 | -0.522 | 0.059 |
| Polygon Density | -0.421 | 0.331 | -0.490 | -0.005 |
| Largest Path Index | 0.458 | -0.097 | 0.433 | -0.308 |
| Effective Mesh Size | 0.354 | 0.611 | 0.027 | -0.696 |
| Connectivity | 0.367 | 0.577 | -0.216 | -0.641 |
| Standard deviation | 2.084 | 0.857 | 1.794 | 1.280 |
| Proportion of variance | 0.724 | 0.122 | 0.536 | 0.273 |
| Cumulative Proportion | 0.724 | 0.846 | 0.536 | 0.809 |

Table 1. Principal Component Analysis (PCA) applied to the Landscape Composition (Cm) and the Landscape Configuration (Cn) variables used in the Structural Equation Model (SEM; see Supplemental Material) for the butterfly and the bird transects observed in the Barcelona Metropolitan Region.