1 **Title page**

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3 **Building on Margalef: Testing the links between landscape structure,**

4 **energy and information flows driven by farming and biodiversity**

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6 Joan Marull[a,*], Sergi Herrando[b,c], Lluís Brotons[b,c,d,e], Yolanda Melero[c,f], Joan Pino[c], Claudio Cattaneo[g],

7 Manel Pons[a], Jordi Llobet[a], Enric Tello[h]

8

9 [a] IERMB, Autonomous University of Barcelona, 08193 Cerdanyola del Vallès, Spain.

10 [b] Catalan Ornithological Institute, Natural History Museum of Barcelona, 08019 Barcelona, Spain.

11 [c] CREAF, Autonomous University of Barcelona, 08193 Cerdanyola del Vallès, Spain.

12 [d] InForest Jru (CTFC-CREAF), Crta. Antiga St Llorenç de Morunys km 2, 25280 Solsona, Spain.

13 [e] Spanish National Research Council (CSIC), 08193 Cerdanyola del Vallès, Spain.

14 [f] Ecology and Evolutionary Biology, School of Biological Sciences, University of Reading, RG6 6AS, UK.

15 [g] Department of Environmental Studies, Masaryk University, Jostova 10, 60200 Brno, Czech Republic.

16 [h] Department of Economic History and Institutions, Barcelona University, 08034 Barcelona, Spain.

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18 * Corresponding author: Tel: +34 93 5868880; Fax: +34 93 5814433; Email: joan.marull@uab.cat

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29   **Abstract**

30   The aim of this paper is to test two methodologies, applicable to different spatial scales (from regional

31   to local), to predict the capacity of agroecosystems to provide habitats for the species richness of

32   butterflies and birds, based on the ways their socio-metabolic flows change the ecological functionality

33   of bio-cultural landscapes. First, we use the more general Intermediate Disturbance–Complexity (*IDC*)

34   model to assess how different levels of human appropriation of photosynthetic production affect the

35   landscape functional structure that hosts biodiversity. Second, we apply a more detailed Energy–

36   Landscape Integrated Analysis (*ELIA*) model that focusses on the energy storage carried out by the

37   internal biomass loops, and the energy information held in the network of energy flows driven by

38   farmers, in order to correlate both (the energy reinvested and redistributed) with the energy imprinted in

39   the landscape patterns and processes that sustain biodiversity. The results obtained after applying both

40   models in the province and the metropolitan region of Barcelona support the Margalef's energy-

41   information-structure hypothesis by showing positive relations between butterflies' species richness,

42   *IDC* and *ELIA*, and between birds' species richness and energy information. Our findings support the

43   view that strong relationships between farming energy flows, agroecosystem functioning and

44   biodiversity can be detected, and highlight the importance of farmers' knowledge and labour to maintain

45   bio-cultural landscapes.

46

47   **Keywords**

48   Landscape Agro-ecology; Land-sharing debate; Intermediate disturbance hypothesis; Human

49   Appropriation of Net Primary Production; Energy Return on Energy Investment

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51 **Graphical abstract**

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53 Conceptual scheme of the energy-information-structure
hypothesis to explain biodiversity in cultural landscapes

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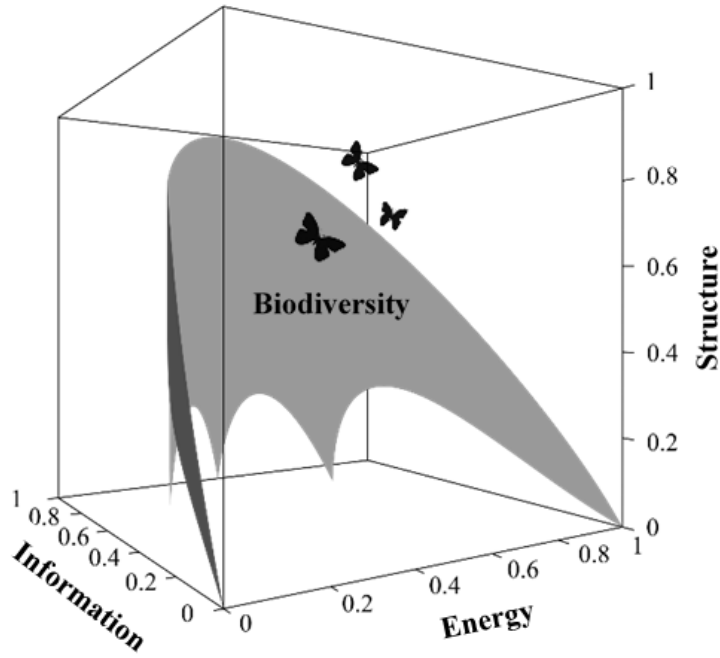
Highlights

- The energy-information-structure hypothesis of bio-cultural landscapes is tested

- Two models are applied at different scales and verified using biodiversity data

- The results obtained confirm the Margalef's hypothesis using butterflies and birds

- Importance of farmers' knowledge and labour to maintain bio-cultural landscapes

- Impact of land-use policies on ecological functioning in human-modified territories

Manuscript

1. Introduction

"Our civilization is constantly conducting large-scale experiments that could be used more often than they actually are to develop the foundations of a disturbance ecology. […] *Man creates systems to control and amplify flows of external energy that become more and more powerful.* […] *By looking at energy subsidies we can gain a better understanding of the role that external energy plays in ecosystems"* (Margalef 1991). Ramon Margalef (1919-2004) greatly contributed to clarify that sustainability of human development is a direct function of complexity and an inverse function of energy dissipation. These ideas are still in the cutting edge of Ecology in the centennial of his birthday; however, they have been rarely tested in a proper way (Gracia 2008). During this century, there has been an unprecedented growth in global food production and its associated socio-environmental impacts stemming from industrialised farming (Mayer et al. 2015). As a result of this socio-metabolic transition (Schaffartzik et al. 2014) –i.e. the change towards sustainability in the set of material and energy flows that occur between nature and society-, farm systems are facing the challenge posed by the simultaneous growing demands of food, energy and biodiversity maintenance (Tilman et al. 2009; Godfray et al. 2010). This requires halting and reversing the current loss of species richness derived from global change (Cardinale et al. 2012). Industrialisation of agriculture through the 'green revolution' has been a major cause of this biodiversity loss (Matson et al. 1997; Tilman et al. 2002).

As it is increasingly recognized, well-managed farm systems can also play a positive role in maintaining biodiversity (Tscharntke et al. 2005). From a land-sharing perspective on biological conservation (Perfecto and Vandermeer 2010), agroecosystems may either enhance or decrease biodiversity at landscape scale depending on land-use intensity (Swift et al. 2004). In turn, the environmental impacts of farming and agroforestry disturbances vary across species and biomes (Gabriel et al. 2013). Therefore, a heterogeneous and well-connected land matrix can maintain high species richness in human-transformed landscapes (Jackson et al. 2012). In order to solve the global energy-food-biodiversity challenge, trade-offs between species richness and land-use patterns need to be assessed by combining the levels and spatiotemporal patterns of ecological disturbances farmers exert

97   across the landscape (Fischer et al. 2008; Phalan et al. 2011). If society aims at maintaining ecosystem

98   services in the future, we need operative criteria, appropriate methods, and meaningful indicators to

99   assess when, where and why the matter-energy flows driven by farming increases or decreases the

100   capacity of landscapes to hold biodiversity (Gliessman 1990; Pierce 2014).

101   The aim of this paper is to test the hypothesis that the complexity and information of these farming-

102   driven energy flows can lay the foundations for sustainable land-use policy, by testing the linkages that

103   exist between social metabolism –i.e. the flows of materials and energy that occur between nature and

104   society-, landscape ecology and biodiversity. We carry out this test applying two complementary

105   methodologies aimed at describing how the socio-metabolic flows generated by human activity affect

106   the landscape functional structure which, in turn, maintains biodiversity. We adopt the Intermediate

107   Disturbance–Complexity model (*IDC*), a spatially explicit analysis only considering energy inputs and

108   outputs based on human appropriation of net primary production (Marull et al., 2016a); and the Energy–

109   Landscape Integrated Analysis (*ELIA*), an improved model that goes deeper in understanding how these

110   flows of materials and energy are reinvested and redistributed in the landscape (Marull et al., 2016b).

111   We then test both models with species richness of two main biodiversity components of cultural

112   landscapes, namely butterflies and birds.

113   **2. Methodology**

114   **2.1. Biodiversity components**

115   There could be many measures of efficiency of land management for biodiversity conservation.

116   Many Essential Biodiversity Variables (EBV) can be potentially used for such purpose (Pereira et al.

117   2013). In this context, local species richness and abundance can be considered as basic measures of

118   interaction of species since they describe how species live together in a given area. Functional type

119   composition of the ecosystem is often derived from species composition and abundance of observed

120   communities and richness may provide a first indication of these processes. To test the *IDC* and *ELIA*

121   models on real biodiversity data, we used the abundance and the species richness of two different

122   taxonomic groups (butterflies and birds) in different transects randomly distributed in the Barcelona

123   (Spain) province and metropolitan region (Figure 1). Both birds and butterflies are known to be

124   especially sensitive to global change drivers (Tucker and Heath 1994; Stefanescu et al. 2004; Aronson

125   et al. 2014; Melero et al. 2016), and they account for large datasets often produced by citizen science

126   initiatives.

127   These data were obtained during the period 2005-2015 by the Catalan Butterfly Monitoring Scheme

128   (http://www.catalanbms.org/), and by the Catalan Breeding and Wintering Bird Surveys

129   (http://www.ornitologia.org/ca/quefem/monitoratge/seguiment/socc/index.html). These biodiversity

130   programmes are based on walked transects repeated several times each year. For each breeding bird

131   species and each year, the maximum count recorded during these two censuses is retained as the best

132   estimation of its annual abundance. Butterfly censuses are carried out on 30 consecutive weeks from

133   March to September and the sum of the individuals recorded during the surveys for a species is retained

134   as the estimate of its annual abundance. In this study we used data consisting of: *i*) transects monitored

135   to get data of birds (linear buffer: 500 m) in the province (151 transects) and the region (91 transects) of

136   Barcelona (Figure 1); and *ii*) transects monitored to obtain data of butterflies (circular buffer: 750 m) in

137   the province (56 transects) and the region (41 transects) of Barcelona (Figure 1). We studied the

138   dynamics of abundance and species richness of the biodiversity components (Table 1) only using

139   transects with data for all the years considered in the period of analysis.

140   To analyse the spatial association between the values of *IDC* and *ELIA* models and these biodiversity

141   components, we performed lineal regression analyses for the observations (a proxy of abundance) and

142   species richness of butterflies, breeding and wintering birds, using transects with data of 2009 as

143   biodiversity data and buffers around them as models' data (34 and 23 butterfly transects, and 96 and 69

144   bird transects for the province and region of Barcelona, respectively). Both *IDC* and *ELIA* models are

145   calculated over the land-cover patches of transects' buffers. The province provides a gradient of

146   landscape transformation highly responsible for strong changes in biodiversity (Clotet et al 2016, Marull

147   et al. 2018). In the region, the focus is located in the metropolitan context where farming transformation

148   and its effects on biodiversity are especially intense (Guirado et al. 2007; Santos et al. 2008).

149   The regression analyses took into account all the variables included in the models: primary and

150   secondary energy variables; composition and configuration landscape variables; *ELIA* and *IDC*; and

biodiversity components (Table A1). Before doing any analysis, a non-parametric contrast was conducted for each of the endogenous variables to analyse their distributions (Normal, Exponential and Poisson, to assess if it was necessary to apply ordinary least-squares model –OLS, log model or Poisson model, respectively). We performed OLS to contrast normal endogenous variables (log-lin model was required in two specific cases; Table 3). VIF<5 ensured no multi-collinearity between the exogenous variables used in the regression analyses. T-student tests were applied in all cases (only significant variables are represented in Table 1, Table 2 and Table 3).

2.2. The Intermediate Disturbance–Complexity Model (*IDC*)

The *IDC* model analyses how the interplay between different farming disturbances exerted across different land-uses create diverse combinations of landscape heterogeneity and ecological connectivity, and they jointly become a key mechanism for biodiversity maintenance (Loreau et al. 2010), as well as the provision of ecosystem services to society (Tscharntke et al. 2005).

2.2.1. *Measuring landscape complexity*

Much of this farm-associated biodiversity is only perceived at scales larger than plot or farm level, because it depends on the landscape patterns and processes that take place in agroforest mosaics (Margalef 2006).

Landscape Heterogeneity (*L*) was calculated as a modification of the Shannon-Wiener Index, to capture the landscape patterns (richness and evenness) of habitats.

$$L = \left(-\sum_{i=1}^{k} p_i \log_k p_i \right)(1 - p_u)$$

Where k is the number of different land cover categories. The existence of built-up land cover p_u results in a loss of potential habitats. Thus, p_i is the proportion of non-urban land covers i.

The assessment of landscape processes is based on the ecological connectivity model proposed by Marull and Mallarach (2005). It relies on defining a set of *Ecological Functional Areas* (*EFA*; including forests, scrublands, croplands, pastures and agroforestry mosaics) of minimum size depending on each category and a cost distance model (based on an *ad-hoc* impedance matrix), which includes the effect of anthropogenic barriers (urban areas, road and rail networks), the range of distances and the involved

177 land cover categories. The assessment defines a basic *Ecological Connectivity Index* (ECI_b) in a

178 normalized scale from 0 to 10. This ECI_b emphasizes the functional role played by the land matrix:

179 $$ECI_b = 10 - 9 \left[ln \left(1 + x_i \right) / ln \left(1 + x_t \right)^3 \right]$$

180 Where x_i is the value of the sum of the cost distance by pixel and x_t the maximum theoretical cost

181 distance, then, ECI_a is the absolute *Ecological Connectivity Index*:

182 $$ECI_a = \sum_{m=1}^{m=n} ECI_b / m$$

183 Where *m* is the number of *EFA* considered. This index helps to emphasize the role played by all sorts

184 of *EFA* in keeping up ecological connectivity (Pino and Marull 2012).

185 We then obtain an indicator of landscape complexity, the *Landscape Ecology Metric* (*Le*) (Marull et

186 al. 2015); capturing landscape patterns (*L*, heterogeneity) and processes (ECI_a, connectivity).

187 $$Le = \frac{\left(L + \frac{ECIa}{10} \right)}{2}$$

188 The statistical test was based on biodiversity transects where locations of birds and butterflies have

189 been observed in 2009. The landscape composition and configuration of these transects was taken from

190 the 2009 Land Cover Map of Catalonia (www.creaf.uab.es/mcsc/) reclassified in eight land cover

191 categories: forest, scrubland, river corridor and wetlands, pasture, cropland, unproductive, road and rail

192 networks and urban areas (Figure 1).

193 *2.2.2. Measuring farming ecological disturbance*

194 In the *IDC* model, we use the *Human Appropriation of Net Primary Production* (*HANPP*) as a

195 measure of farming disturbance, where *NPP* is the net amount of phytomass produced annually by

196 autotrophic organisms that constitutes the nutritional basis for food chains. *HANPP* is calculated using

197 the following identities (Haberl et al. 2014):

198 $$HANPP = HANPP_{luc} + HANPP_{harv}$$

199 $$HANPP_{luc} = NPP_0 - NPP_{act}$$

200 Where $HANPP_{harv}$ is the *NPP* appropriated through harvest, and $HANPP_{luc}$ is the change of *NPP*

201 through farming-induced land conversions. $HANPP_{luc}$ is defined as the difference between the *NPP* of

202 the potential (NPP_0) and actual (NPP_{act}) vegetation. *HANPP* is calculated in each land unit of the study

203   area as the weighted sum of some fixed land unit coefficients (w_i) by the proportion of surface occupied

204   by each land unit within the sample cell:

205
$$HANPP = \sum_{i=1}^{k} w_i p_i$$

206   Where w_i denotes the weight of land unit i, and p_i the proportion of land unit i in the study area.

207   Variations in *HANPP* not only depend on the variations of p_i, but on the variations of w_i as well.

208   To estimate *HANPP* values in the same transects in which birds and butterflies were monitored, it

209   was necessary to assess different levels and amounts of *NPP* and harvests. Harvest ratios taken from

210   each land cover were transformed into the energy content of all biomass flows driven by farming.

211   Conversion factors such as the residue/product ratio and weed biomass (Guzmán et al. 2014) were

212   accounted for the harvested by-products and for the unharvested biomass left for all heterotrophic

213   organisms in each land cover category.

214   *2.2.3.   Calculating the IDC indicators*

215   The result is that we have one *Le* and *HANPP* value for each unit of analysis (Marull et al. 2016a).

216   *HANPP* expresses a *NPP* appropriation average number for each unit, but can be obtained with different

217   land cover combinations; and *L* (or *Le*) expresses a land cover pattern value (richness and evenness) for

218   each unit, but can be obtained with different *NPP* combinations. The *IDC* model combines the landscape

219   structure (*L*) with the biomass available to other species (*1-HANPP/100*) (Figure 2):

220   *IDC = L (1 – HANPP /100)*

221   Where *L* is the "energy imprint" in the landscape patterns (*L* can be substituted by *Le*, including the

222   landscape processes). *IDC* ranges from 0 to 1, even though its maximum value depends on where the

223   weights (w_i) of *HANPP* are displayed (Figure 2).

224   Figure 2 shows all the possible values for the theoretical relationship between human disturbance

225   and landscape complexity, wherever it is possible to represent the site-specific disturbance-complexity

226   (*IDC*) values of a given territory. *1-HANPP* expresses the average energy available for (butterflies or

227   birds) species in each transect (our unit of analysis), but the same *HANPP* value can be obtained with

228   different land cover combinations (having one or various habitats composition). Furthermore, the same

229   *L* value can also be obtained using different land cover categories, although the contribution of each

230   land cover to biodiversity may vary (due to the variable amount of energy available for the trophic

231   chains). Consequently, the combination of spatially uneven disturbances and land cover heterogeneity

232   in human-modified landscapes could greatly affect biodiversity maintenance.

233   *IDC* aims at improving our understanding of the functioning of agroecosystems, and the subsequent

234   effects on biodiversity on a regional scale (Marull et al. 2016a), by revealing how and why different

235   managements lead to turning points in the relationship between farming disturbance (*HANPP*) and the

236   landscape structure in terms of land cover heterogeneity and ecological connectivity. In order to go

237   deeper into the analysis at local level, we need to account the biomass flows moved by farming in the

238   more precise manner performed through the *ELIA* model by accounting how the energy is reinvested

239   and redistributed in the land matrix.

240   **2.3. The Energy-Landscape Integrated Analysis (*ELIA*)**

241   Through the *ELIA* model we can represent in more detail the energy flows in an agroecosystem.

242   Figure 3 shows how the biomass produced by solar radiation obtained from solar radiation, that accounts

243   for the *actual Net Primary Production* (NPP_{act}) is the energy source for consumers living there (Vitousek

244   et al. 1986), either domesticated or not. From this starting point, we analysed the pattern adopted by

245   energy flows subsequently carried out through the metabolic circulation of farming-driven biomass, the

246   internal loops generated, the final product extracted, and the external inputs introduced from outside the

247   agroecosystem. The graph shows the three subsystems of internal energy loops ("forestry" –green;

248   "farmland" –red; and "livestock" –purple) included in a mixed farming agroecosystem.

249   In all of the sub-processes identified (Figure 3), the energy flows are differentiated between those

250   that remain within the agroecosystem and those that go to other subsystems or out of the whole

251   agroecosystem. Accordingly, there is always a pair of incoming-outgoing energy flows for each sub-

252   process. Hence, we can account twelve coefficients (β_i) along all the edges of the graph. Then we can

253   differentiate between even and odd β_i's, where the even β_i's account for the energy flows looping inside

254   the agroecosystem, and the odd ones for those that are leaving it.

255   Based on these agroecosystem's energy flows (Figure 3) and its related land matrix, *ELIA* combines

256   the following three indicators (Marull et al., 2016b): the complexity attained through the energy storage

257   of internal loops in an agroecosystem (*E*); the information embedded in the energy network of flows (*I*);

258   and energy imprinted in the landscape functional structure (*L*).

259   The energy analysis is based on a flow-fund representation of agroecosystems (Tello et al. 2016;

260   Cattaneo et al. 2018), using data from the Spanish Ministry of Agriculture and the Catalan Statistics

261   Institute (2009) for the parameters calculation (Table A1). The landscape composition and configuration

262   of the biodiversity transects have been calculated from the 2009 Land Cover Map of Catalonia

263   (www.creaf.uab.es/mcsc/).

264   ### *2.3.1. Measuring the energy storage*

265   We understand agroecosystem complexity as the differentiation of dissipative structures (Gonzalez

266   de Molina and Toledo 2015). The more complex the space-time differentiation is, the more energy is

267   stored within a system (Ho and Ulanowicz 2005). Conversely, given that speciation is a result of this

268   space-time differentiation that gives rise to habitat diversity, the maintenance of biodiversity also

269   requires complex landscapes with different, intermingled land covers. In the *ELIA* model, higher mean

270   values of even β_i's entail that agroecosystems are increasing in complexity because the different cycles

271   are coupled together, and the residence time of the stored energy is higher thanks to a greater number of

272   interlinked transformations looping inside (Figure 3). Accordingly, our way of calculating the *Energy*

273   *Storage (E)* is as follows:

274
$$E = \frac{\beta_2 + \beta_4}{2} k_1 + \frac{\beta_6 + \beta_8}{2} k_2 + \frac{\beta_{10} + \beta_{12}}{2} k_3.$$

275
$$k_1 = \frac{UB}{UB + BR + LS}, k_2 = \frac{BR}{UB + BR + LS}, k_3 = \frac{LS}{UB + BR + LS},$$

276   Where the coefficients k_1, k_2, k_3 account for the share of reusing energy flows that are looping

277   through each of the three subsystems of the graph model (Figure 3).

278   *E* assesses the amount of all the energy flows that go inside the agroecosystem, relative to the total

279   amount of energy flowing across each one of the three subsystems of the network structure. Hence, *E*

280   measures the proportion of energy flows stored on the land matrix, and remains within the range [0,1].

281   *E* close to 0 implies low reuse of energy flows —usually corresponds to an agro-industrial management,

282   dependent on external inputs and with high levels of *HANPP*. *E* close to 1 implies more internal energy

283   loops, meaning that a high share of energy flows harvested are reused within the agroecosystem —

284   usually associated to organic farming with lower dependence on external inputs, lower biomass

285   extraction as final produce, and moderate *HANPP* levels.

286   ### 2.3.2.   *Comparing E and HANPP*

287   We compare *HANPP* and *E* (Marull and Font 2017) to analyse two important variables of both

288   models, *IDC* and *ELIA*. Expanding the formula of *E* and assuming the spatially explicit expression of

289   each β_i (that is, the energy flows specific for each land use), we have:

290
$$E = (\beta_2 + \beta_4)\frac{k_1}{2} + (\beta_6 + \beta_8)\frac{k_2}{2} + (\beta_{10} + \beta_{12})\frac{k_3}{2}$$

291
$$= \sum_{i=1}^{n} p_i \frac{1}{2}\left(k_1\beta_2^i + k_1\beta_4^i + k_2\beta_6^i + k_2\beta_8^i + k_3\beta_{10}^i + k_3\beta_{12}^i\right).$$

292   Now, we can call $\alpha_i = \frac{1}{2}\left(k_1\beta_2^i + k_1\beta_4^i + k_2\beta_6^i + k_2\beta_8^i + k_3\beta_{10}^i + k_3\beta_{12}^i\right)$, so we obtain:

293
$$E = \sum_{i=1}^{n} p_i \alpha_i.$$

294   This expression is similar to the *HANPP* formula; in fact, the two indicators have the same behaviour.

295   Given that $\sum_{i=1}^{n} p_i = 1$, in both cases we have a weighted sum of w_i and α_i, respectively.

296   According to the new expression of *E*, the difference between *HANPP* and *E* can be compared with

297   the values w_i and α_i. This is because α_i plays the same role as w_i in *HANPP*. However, we should

298   remember that *E* and *HANPP* have opposite meaning. High values of *HANPP* indicate more human-

299   appropriation and so less energy available for other species, while high *E* denotes just the contrary, more

300   internal energy processes within agroecosystems (and this means more energy available to sustain

301   biodiversity). For this reason, it is better to compare *E* and *1-HANPP* when it comes to assess the energy

302   carried through biomass flows that cycle within the land matrix and remain available to all heterotrophic

303   species for a while.

2.3.3. *Measuring the energy information*

Information can be interpreted as a measure of uncertainty, or the degree of freedom for the system to evolve (Prigogine 1996). This kind of information is often called structuring-information that registers the likelihood of the occurrence of a pair of events (Ulanowicz 2001). It differs from the meaningful content of the information farmers use to direct the energy flows they move according to a defined purpose. Accordingly, the *Energy Information* (*I*) shows whether the β_i's pairs are evenly distributed or not. This measure of *I* accounts for the equi-proportionality of pairwise energy flows that exit from each node in all the sub-processes of the graph (Figure 3) that represents the agroecosystem functioning:

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

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

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

Base 2 logarithms are applied as the probability is dichotomous. Sometimes some energy flows circulating inside the agroecosystem are turned into what Odum (1993) named a 'resource out of place' (i.e. waste, non-renewable). The introduction of the information-loss coefficients γ_F, γ_L ensures that *I* remains lower than 1 when the agroecosystem presents farm and/or livestock waste. The coefficients α_F, α_L penalize the use of non-renewable external inputs as a loss of information.

I values close to 1 are those with an equi-distribution of incoming and outgoing flows of the agroecosystem's network structure where the structuring information-message is high, whereas values close to 0 mean patterns of probability far from equi-distribution. *I* values close to 0 correspond to a low site-specific information content in agroecosystem functioning, which may be related to an industrialised farm system with high *HANPP* and low relevance of traditional peasant knowledge embedded in the landscape; or, by contrast, to an almost 'natural' turnover with slight *HANPP* that may also correspond at present to rural abandoned forest or pastoral areas. Pristine spaces, with high value for biodiversity conservation, can also have *I* values close to 0, but they are not included in the *ELIA*

328   agroecosystem's assessment. Conversely, agroecosystems with *I* equal to 1 are the ones with equi-

329   distributed incoming and outgoing energy flows in each sub-process, as well as with intermediate levels

330   of *HANPP*, that correspond to organic mixed farming (heterogeneous landscapes characterized by a set

331   of land-uses possessing contrasting disturbances and low no-renewable external inputs) deeply

332   embedded in local knowledge.

333   *2.3.4.   Calculating the indicators of the ELIA model*

334   After having defined all the *ELIA* indicators (*E*, *I* and *L*), we can analyse the relationship between

335   variables included in the model. We surmise that the interplay between *E* and *I* jointly leads to

336   complexity, understood as a balanced level of intermediate self-organisation (Gershenson and

337   Fernández 2012). We also assume that the complexity of interlinked energy flows (*E·I*) and *L* values of

338   landscape heterogeneity are related to landscape ecological processes and biodiversity. This *ELIA*

339   modelling enables us to test the relationship we deem to exist between the simultaneous loss in energy

340   throughput and landscape ecological efficiency (Marull et al. 2016b).

341   In order to go a step forward from previous explorations of the linkages between intermediate levels

342   of socio-metabolic ecological disturbance, as assessed with *HANPP,* and the ecological functioning of

343   cultural landscapes on a regional scale (Marull et al. 2018), we use *ELIA* as an operative model that

344   combines, the landscape functional structure with the complexity of the interlinking pattern of energy

345   flows and the information carried by them:

346
$$ELIA = \frac{(E \cdot I)\, L}{max\{EI\}e}$$

347   Where *E* is the energy storage, *I* is the information carried by the network of energy flows, and *L* is

348   the energy imprint in the landscape patterns (*L* can be substituted by *Le*; i.e. including landscape

349   processes). According to the assumptions of the *ELIA* model, we have that the equilibrated

350   $max\{EI\}e = 0.6169$ ($k_i = \frac{1}{3}$). Once we have the maximum $E \cdot I$ (energy reinvested and

351   redistributed), which corresponds to the highest farmer's capability to structure the land matrix, we can

352   add the landscape energy imprint (*L*). This synthetic expression of *ELIA* ranges from 0 to 1.

353   **3. Results and discussion**

3.1. Analysing birds' and butterflies' biodiversity dynamics

A preliminary analysis of the dynamics of the biodiversity indicators in the province of Barcelona showed that the number of bird observations (total breeding birds: mean = 13,852; standard deviation = 1,696) experienced a steep decrease between 2005 and 2015 (Figure A1). This decrease was especially stronger in species associated with agriculture (Santos et al. 2008; Vallecillo et al. 2008), for both breeding (mean = 3,210; standard deviation = 449) and wintering (mean = 3,167; standard deviation = 211) birds. This fits with the constant decrease in populations of common bird species related to open spaces reported at European level, which has been related to continental-wide long-term land use trends of agricultural and grassland surface reductions, while urban growth and forestland increase (Inger et al. 2014).

Regarding butterflies, while their populations showed evident fluctuations during the period of analysis (Figure A1), probably due to external factors –e.g. climate, we could see a declining trend in the number of species, mostly specialists –i.e., related to specific plants and habitats (mean = 19.6; standard deviation = 2.8) and those associated with open spaces –such as agriculture or pasture (mean = 68.1; standard deviation = 1.4). This is in concordance with the observed declines in butterfly species associated with species' degree of habitat specialisation (Melero et al. 2016). Many studies (Brückmann et al. 2010; Verdasca et al. 2012) have showed that butterflies are particularly sensitive to climate and habitat changes, such as those that the European rural landscapes have experienced in recent decades (Stefanescu et al. 2010).

3.2. Testing the *IDC* and *ELIA* models with birds' and butterflies' data

To test the social metabolism / landscape ecology models as predictors of biodiversity, energy and landscape components were set as independent variables (Table A1), and empirical data of biodiversity from transects of birds and butterflies as dependent variables, in the province (*IDC* model) and the region (*ELIA* model) of Barcelona. Our regression analyses showed a relationship between the energy and landscape variables with the number of observations and the species richness of butterflies, breeding birds and wintering birds (Table 1, Table 2 and Table 3, respectively).

380   In the province of Barcelona, *IDC* and Edge Density (a proxy of landscape ecotony) were positively

381   related (r^2=0.160) with the abundance of butterflies (Table 1); and *IDC* and Polygon Density (number

382   of land cover patches) with species richness (r^2=0.286). Therefore, we interpret this result as a support

383   to the intermediate disturbance of suitable habitats, with intermediate values of landscape complexity

384   contributing to species richness and abundance of butterflies. The results confirmed others obtained in

385   previous tests (Marull et al. 2018), relating *IDC* values with biodiversity of different taxa (vascular

386   plants, amphibians, reptiles and mammals) in Catalonia.

387   In the region of Barcelona (Table 1), only *ELIA* was positively related with the observations of

388   butterflies (r^2=0.266); Shannon and Ecological Connectivity (heterogeneous and well-connected

389   landscapes) and *I* (information-driven redistribution of biomass flows) were also positively correlated

390   with species richness (three of the *ELIA* components), while Grassland (pasture) and *FEInr* (non-

391   renewable external inputs –fertilizers, pesticides) correlated negatively (r^2=0.521).

392   Other regressions showed which energy and landscape variables have statistical relation with the

393   number of observations and species richness of breeding (Table 2) and wintering (Table 3) birds. The

394   case of birds was more complex because, in general, this group responds better to landscape

395   heterogeneity at larger spatial scales than butterflies. However, the results confirmed previous analyses

396   (Marull et al., 2018) that also supported *IDC* relation with vascular plants, amphibians, reptiles and

397   mammals, but not with birds. In this paper, we wanted further explore the specific response of birds' to

398   the *IDC*.

399   In the province of Barcelona, Cropland and Grassland cover positively affected the distribution of

400   breeding birds (Table 2), while Ecological Connectivity was negatively related (r^2=0.361). Largest Path

401   Index (size of land cover patches) increased species richness while Scrubland reduced it (r^2=0.206). In

402   the case of wintering birds (Table 3) *HANPP* (harvest), Cropland (arable crops) and Grove (fruit crops)

403   were positively related (r^2=0.380) with the abundance (birds are moving to these land-uses to find food),

404   as well as the percentage of Open Space and Shannon with species richness (r^2=0.301).

405   Finally, applying the *ELIA* model in the region of Barcelona, *I* (the biomass redistributed between

406   different land-uses) was the key explaining both the number of observations and the species richness of

407 breeding (r^2=0.500 and r^2=0.248, respectively) (Table 2) and wintering birds (r^2=0.543 and r^2=0.401,

408 respectively) (Table 3). This indicator penalizes the use of non-renewable inputs, such as pesticides and

409 synthetic fertilizers together with polluting waste.

410 **3.3. Using the *IDC* and *ELIA* models to test Margalef's hypothesis**

411 The combination of energy-flow pattern characterisation and information on the way energy is

412 redistributed in space appears as a good starting point to model the society-environment relationships.

413 According to Margalef (1991, 2001), to understand how human activities affect the organization of space

414 where ecosystem functioning takes place it is necessary to clarify conceptually and formulate

415 quantitatively *"the relationship between the external energy inputs and the dimensions that characterize*

416 *the spatial patterns of its distribution"* –i.e. the functional structure of the land matrix. The models

417 proposed in this paper allowed us to assess the relationships between landscape structure and energy

418 and information flows with biodiversity in human-transformed landscapes.

419 As previously shown in other studies (e.g. Tucker and Heath 1994), the biodiversity indicators

420 (butterflies and birds) used in statistical tests showed a special strong decrease in species associated with

421 agroforestry mosaics (Santos et al. 2008; Melero et al. 2016). These effects are added to those of climate

422 change (Stefanescu et al. 2010; Devictor et al. 2012). This study confirms the constant decrease in

423 populations of common bird species related to open spaces in the Barcelona Province. The decrease of

424 birds' populations is of increasing concern in Europe (Inger et al. 2014). The preservation of bio-cultural

425 landscapes and of traditional mixed farming are recognized as key elements to halt the serious decline

426 of butterfly populations in Europe (van Swaay et al. 2008). Moreover, butterflies are a proxy of

427 biodiversity (Thomas 2005). These troubling birds' and butterflies' population dynamics justify the need

428 for an integrated land-use planning, where organic mixed-farming agriculture may have a key role as

429 green infrastructure guaranteeing ecosystem services provisioning.

430 The *IDC* and *ELIA* models linking social metabolism with landscape ecology here tested at different

431 resolutions have demonstrated their capability as predictors of biodiversity locations using butterfly

432 empirical data either at regional (*IDC*) or at local (*ELIA*) levels. In the case of birds (also butterflies),

433 the information-driven redistribution of biomass flows within agroecosystems (*I*) appears to be a major

factor behind biodiversity patterns (Table 1, Table 2 and Table 3). This is an interesting result, because it points out to the role of farmers' knowledge and labour in maintaining the ecological functionality of bio-cultural landscapes by means of a subtle and historically changing human-nature dynamics (Marull et al. 2018). This is good news for addressing the energy-food-biodiversity trilemma currently posed at global scale (Tilman et al. 2009).

The combination of spatially and temporarily uneven disturbances with increased landscape complexity can be capable to offer more habitats and available energy resources for different species and ecological communities within and agro-ecological land matrix. As a result of this combination of intermediate disturbances in heterogeneous bio-cultural landscapes, beta-diversity (at landscape scale) increased, and overrode the inevitable fall in alpha-diversity (at plot level) in cropland, which is the typical local impact of organic farm system functioning on biodiversity (Gliessmann 1990). As long as this newly introduced farm-associated biodiversity (Altieri 1999) did not preclude the survival of former species richness, which would be sheltered in more undisturbed land-units, the whole process could even entail an increase in gamma-diversity (on a regional scale).

In summary, the relationship between biodiversity and agrarian metabolism shows that abundance and species richness are positively related to non-intensive farming (*IDC* and *ELIA* models with butterflies; Table 1) and the heterogeneous distribution of energy flows across the landscape with minimum use of industrial inputs (*I* with butterflies and birds; Table 1, Table 2 and Table 3). These findings are in line with a recent comprehensive review in conservation biology (Sanchez-Bayo and Wyckhuys 2019) for what concerns the worldwide decline of entomofauna.

4. Conclusion

This paper has been the first attempt to check the Margalef's energy-information-structure hypothesis testing the links of landscape patterns and energy and information flows with biodiversity in human-transformed landscapes. We used an Intermediate Disturbance–Complexity (*IDC*) model to assess how different levels of human appropriation of photosynthetic capacity affect the landscape structure that hosts biodiversity on a regional scale (Marull et al. 2016a). We also applied an Energy–Landscape Integrated Analysis (*ELIA*) of agroecosystems to measure the "energy storage" (*E*) and "energy

461   information" (*I*) held in the whole network of agricultural socio-metabolic flows, to correlate both

462   variables (*E·I*) with the "energy imprint" in the landscape patterns and processes that sustain biodiversity

463   on a local scale (Marull et al. 2016b).

464   Both models can increase our capability to understand the ultimate factors that determine different

465   components of biodiversity location (butterflies and birds) in human-transformed landscapes. The *IDC*

466   is an energy-space input-output model (based on the human appropriation of net primary production),

467   while *ELIA* goes deeper in opening the black box on how energy is reinvested (*E*) and redistributed (*I*)

468   in the land matrix (assessing the complexity of the internal energy loops at local scales). As Margalef

469   suggested (Margalef 1991), *"the patterns of energy distribution"*–in terms of inputs, outputs, and

470   internal flows- have been determinant to understand species richness and abundance in Mediterranean

471   human-transformed landscapes.

472   Confirming or rejecting the Margalef's hypothesis requires further research applying *IDC* and *ELIA*

473   to different case studies in diverse bioregions, and using larger biodiversity datasets in order to find out

474   the critical thresholds in the interplay among energy throughputs and information-complexity landscape

475   patterns. This research agenda would help to reveal how and why different agroecosystem managements

476   can lead to key turning points in the relationship of the network of socio-metabolic energy flows of

477   farming with landscape ecological functioning and biodiversity (Agnoletti 2014).

478   Testing these linkages between social metabolism, landscape ecology and biodiversity may also

479   assist to appraise the wider impact of land-use policies on ecological functioning in human-modified

480   territories (*IDC* and *ELIA* models can be potentially regionalized), thus helping to resolve the global

481   energy-food-biodiversity trilemma (Tilman et al. 2009). The traditional sectorial policies have to be

482   overcome by a new systemic vision of the agricultural, forestry and livestock metabolic circulation

483   within the landscape functional structure of green infrastructures (Marull et al. 2019). This requires

484   going ahead in an agro-ecology research useful for designing more sustainable human-transformed

485   landscapes worldwide in the future.

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639 Table 1 Linear regression analysis taking into account all the predictor variables (energy and landscape;
640 Table 1) and the dependent variables of biodiversity components (total butterfly species richness and
641 abundance), applying the Intermediate Disturbance–Complexity (*IDC*) and the Energy–Landscape
642 Integrated Analysis *(ELIA)* models at the Barcelona province and region, respectively

Total Butterflies – Abundance (*Province*)			
	Coef.	t	VIF
(constant)	18,724.647	0.607	
IDC	221,202.465	2.730	1.201
Edge Density	97.207	1.938	1.201
	Adj. R^2	F	Sig
Statistics	0.160	4.132	,026(b)
a) Dependent variable: TB-AB			
b) Predictor variables: (constant), IDC, Edge Density			
Only significative variables are represented			
Total Butterflies – Species Richness (*Province*)			
	Coef.	t	VIF
(constant)	23.778	2.754	
IDC	102.183	3.830	1.066
Polygon Density	0.078	1.658	1.066
	Adj. R^2	F	Sig
Statistics	0.286	7.596	,002(b)
a) Dependent variable: TB-SR			
b) Predictor variables: (constant), IDC, Polygon Density			
Only significative variables are represented			
Total Butterflies – Abundance (*Region*)			
	Coef.	t	VIF
(constant)	41,293.408	2.109	
ELIA	527,216.781	2.824	1.000
	Adj. R^2	F	Sig
Statistics	0.266	7.978	,010(b)
a) Dependent variable: TB-AB			
b) Predictor variables: (constant), ELIA			
Only significative variables are represented			
Total Butterflies – Species Richness (*Region*)			
	Coef.	t	VIF
(constant)	7.623	0.561	
Ecological Connectivity	4.032	2.405	1.386
FEInr	-0.307	-4.062	1.553
I	92.206	2.758	1.314
Grassland	-189.150	-3.022	1.758
Shannon	48.194	2.493	2.003
	Adj. R^2	F	Sig
Statistics	0.521	6.005	,002(b)
a) Dependent variable: TB-SR			
b) Predictor variables: (constant), Ecological Connectivity, FEInr, I, Grassland, Shannon			
Only significative variables are represented			

643 Note: Farmland External Input no-renewable (FEInr); Energy Information (I). See Table A1.

644 Table 2 Linear regression analysis taking into account all the predictor variables (energy and landscape;

645 Table 1) and the dependent variables of biodiversity components (breeding birds species richness and

646 abundance), applying the Intermediate Disturbance–Complexity (*IDC*) and the Energy–Landscape

647 Integrated Analysis (*ELIA*) models at the Barcelona province and region, respectively

| Total Breeding Birds – Abundance (*Province*)			
	Coef.	t	VIF
(constant)	502.910	10.661	
Ecological Connectivity	-56.406	-6.753	1.009
Cropland	166.904	1.863	1.075
Grassland	779.270	1.735	1.067
	Adj. R^2	F	Sig
Statistics	0.361	19.070	,000(b)
a) Dependent variable: TBB-AB			
b) Predictor variables: (constant), Ecological Connectivity, Cropland, Grassland			
Only significative variables are represented			
Total Breeding Birds – Species Richness (*Province*)			
	Coef.	t	VIF
(constant)	113.412	16.681	
Largest Path Index	$-1.251 \cdot 10^{-5}$	-4.700	1.116
Scrubland	-39.183	-3.597	1.116
	Adj. R^2	F	Sig
Statistics	0.206	13.459	,000(b)
a) Dependent variable: TBB-SR			
b) Predictor variables: (constant), Largest Path Index, Scrubland			
Only significative variables are represented			
Total Breeding Birds – Abundance (*Region*)			
	Coef.	t	VIF
(constant)	526.167	7.576	
Grassland	2,134.082	3.029	1.262
E	-316.791	-4.063	1.142
Le	-446.136	-3.676	1.231
I	523.249	2.125	1.353
	Adj. R^2	F	Sig
Statistics	0.500	17.273	,000(b)
a) Dependent variable: TBB-AB			
b) Predictor variables: (constant), Grassland, E, Le, I			
Only significative variables are represented			
Total Breeding Birds – Species Richness (*Region*)			
	Coef.	t	VIF
(constant)	70.962	9.144	
BEROI	-15.720	-2.060	1.090
I	69.576	2.440	1.217
Grassland	158.545	1.773	1.291
	Adj. R^2	F	Sig
Statistics	0.248	8.257	,000(b)
a) Dependent variable: TBB-SR			
b) Predictor variables: (constant), BEROI, I, Grassland			
Only significative variables are represented			

648 Note: Energy Storage (E); Energy Information (I); Landscape Complexity (Le); Biodiversity Energy Return of Investment
649 (BEROI). See Table A1.

650　Table 3 Linear regression analysis taking into account all the predictor variables (energy and landscape;

651　Table 1) and the dependent variables of biodiversity components (wintering bird species richness and

652　abundance), applying the Intermediate Disturbance–Complexity (*IDC*) and the Energy–Landscape

653　Integrated Analysis (*ELIA*) models at the Barcelona province and region, respectively

Total Wintering Birds – Abundance (*Province*)			
	Coef.	t	VIF
(constant)	3.485	6.815	
HANPP	2.732	6.329	2.233
Scrubland	-2.262	-5.067	1.273
Open Space (%)	1.200	2.909	2.386
	Adj. R^2	F	Sig
Statistics	0.406	20.139	,000(b)
a) Dependent variable: ln(TWB-AB)			
b) Predictor variables: (constant), HANPP, Scrubland, Open Space			
Only significative variables are represented			
Total Wintering Birds – Species Richness (*Province*)			
	Coef.	t	VIF
(constant)	75.439	11.161	
Ecological Connectivity	-11.614	-4.839	4.311
Open Space (%)	40.571	2.385	4.496
Shannon	50.302	3.304	1.568
Scrubland	-21.032	-1.640	1.163
	Adj. R^2	F	Sig
Statistics	0.301	10.052	,000(b)
a) Dependent variable: TWB-SR			
b) Predictor variables: (constant), Ecological Connectivity, Open Space, Shannon, Scrubland			
Only significative variables are represented			
Total Wintering Birds – Abundance (*Region*)			
	Coef.	t	VIF
(constant)	5.981	14.292	
Grassland	7.808	2.568	1.267
E	-1.694	-4.264	1.235
I	3.057	2.725	1.212
	Adj. R^2	F	Sig
Statistics	0.543	22.015	,000(b)
a) Dependent variable: ln(TWB-AB)			
b) Predictor variables: (constant), Grassland, E, I			
Only significative variables are represented			
Total Wintering Birds – Species Richness (*Region*)			
	Coef.	t	VIF
(constant)	80.723	5.558	
BEROI	-24.532	-2.213	1.509
I	114.948	2.745	1.449
Ecological Connectivity	-3.950	-2.607	1.058
	Adj. R^2	F	Sig
Statistics	0.401	12.811	,000(b)
a) Dependent variable: TWB-SR			
b) Predictor variables: (constant), BEROI, I, Ecological Connectivity			
Only significative variables are represented			

654　Note: Human Appropriation of Net Primary Production (HANPP); Energy Storage (E); Energy Information (I); Biodiversity
655　Energy Return of Investment (BEROI). See Table A1.
656

657 Figure 1 Butterfly transects (circular buffer: 750m)* and bird transects (longitudinal buffer: 500m)**

658 monitored in the Barcelona province and region (RMB), represented over a land cover map (2009)

659
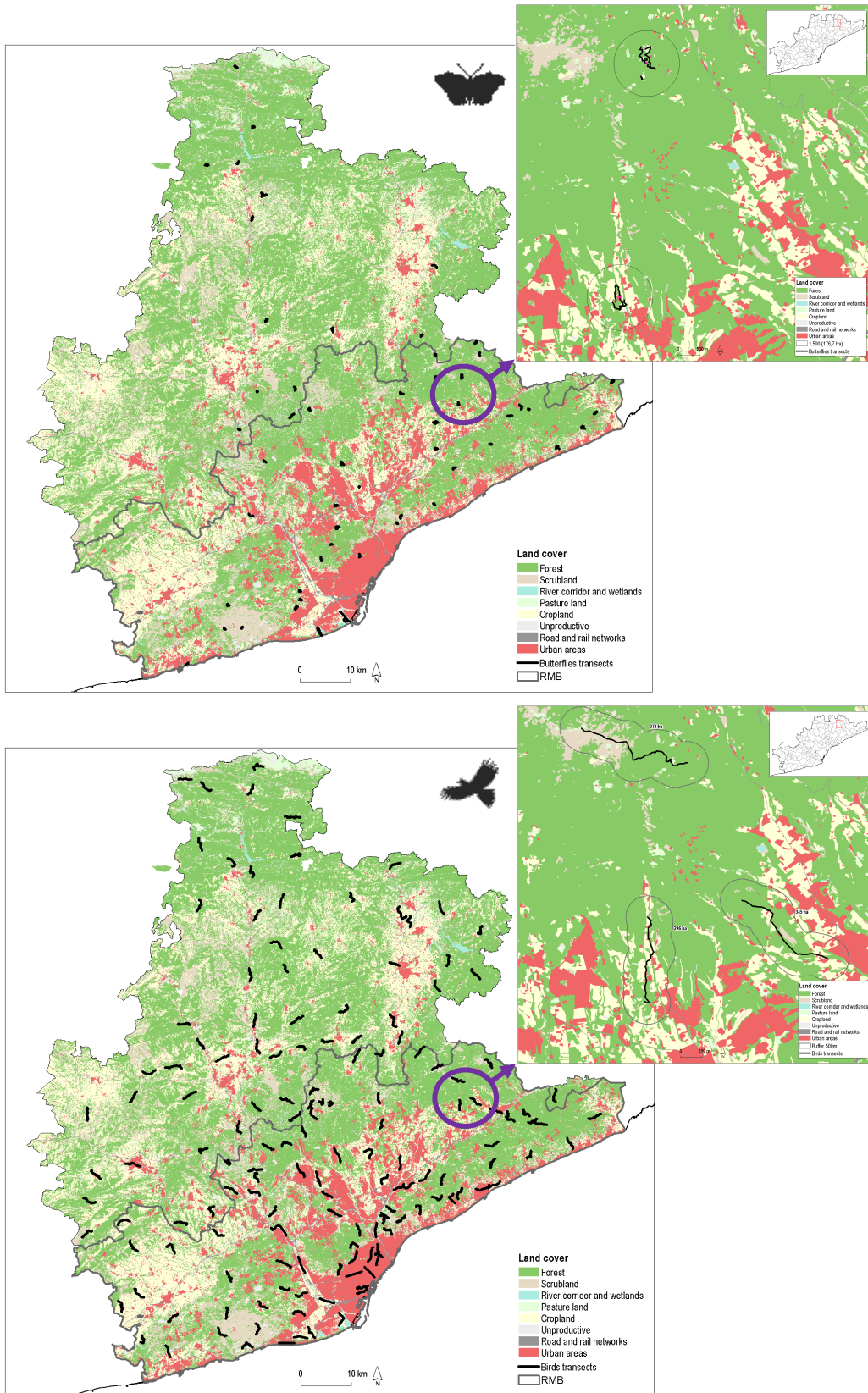
684 Source: * Catalan Butterfly Monitoring Scheme (CBMS); ** Institut Català d'Ornitologia (ICO).

685   Figure 2 Theoretical values of the Intermediate Disturbance–Complexity (*IDC*) model. Relationship

686   between Landscape Heterogeneity (*L*) and Human Appropriation of Net Primary Production (*HANPP*)

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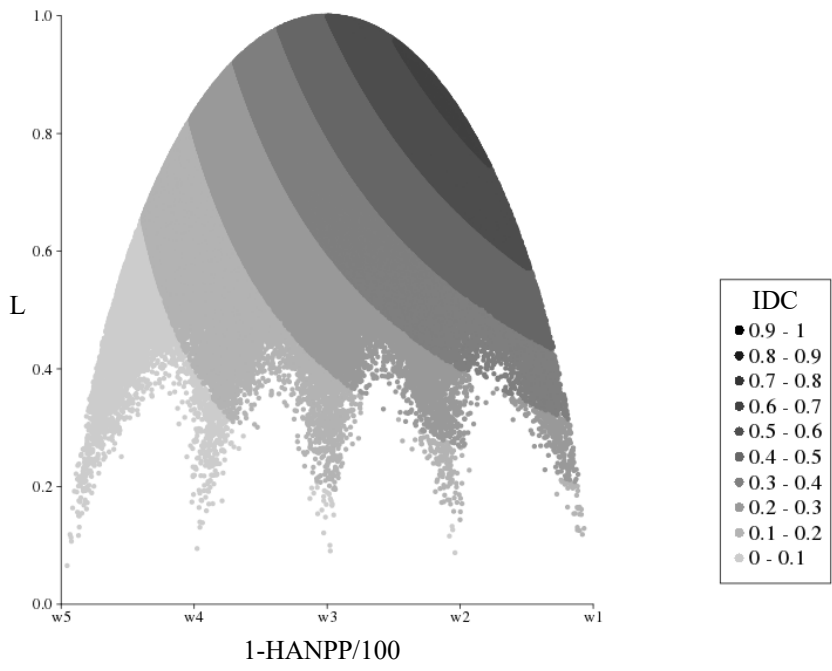
697   Note: *IDC = L (1- HANPP/100)*

698   Source: Marull et al. 2016a.

699

700 Figure 3 Graph model of the energy carriers used in the Energy–Landscape Integrated Analysis (*ELIA*)

701
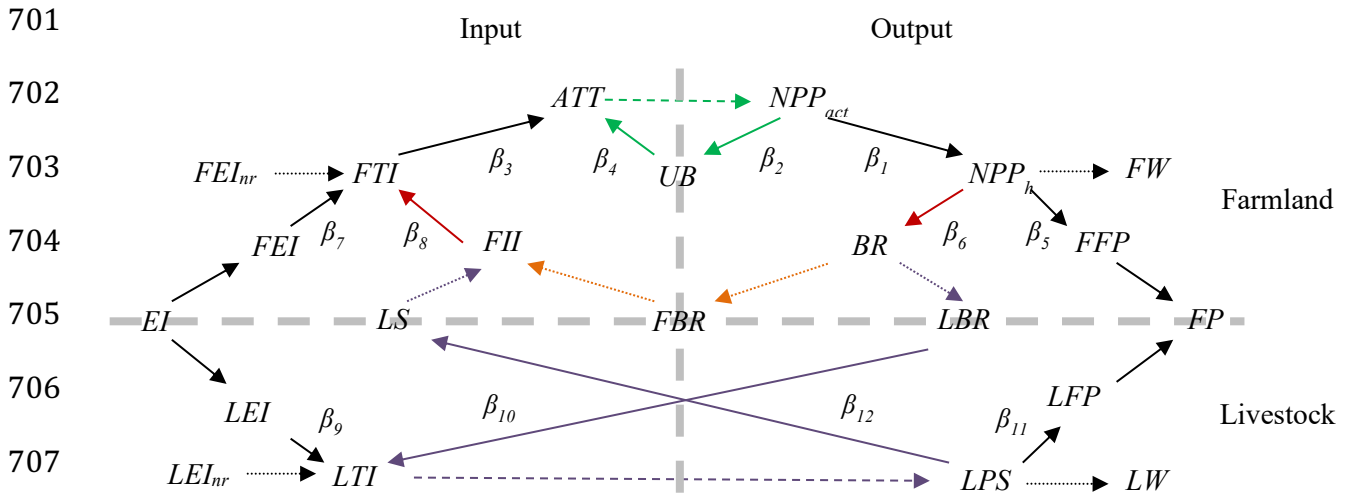
708 Variables: Actual Net Primary Production (*NPP$_{act}$*); Unharvested Biomass (*UB*); Harvested Net Primary Production (*NPP$_h$*);
709 Biomass Reused (*BR*); Farmland Biomass Reused (*FBR*); Livestock Biomass Reused (*LBR*); Farmland Final Produce (*FFP*);
710 External Input (*EI*); Farmland External Input (*FEI*); Livestock External Input (*LEI*); Livestock Total Input (*LTI*); Livestock
711 Produce and Services (*LPS*); Livestock Final Produce (*LFP*); Livestock Services (*LS*); Final Produce (*FP*); Agroecosystem
712 Total Turnover (*ATT*); Farmland Total Input (*FTI*); Farmland Internal Input (*FII*); Farmland Waste (*FW*): Livestock Waste
713 (*LW*). *nr* means no-renewable. β_i's are the incoming-outgoing coefficients.

714 Relationships between variables: $NPP_{act} = UB + LP$; $NPP_h = BR + FFP$; $BR = FBR + LBR$; $EI = FEI + LEI$; $LTI = LEI +$
715 LBR; $LPS = LP + LS$; $FP = FFP + LFP$; $ATT = FTI + UB$; $FTI = FII + FEI$; $FII = FBR + LS$.

716
717 Note: The colours of the arrows represent the 'forestry' (green), 'farmland' (red) or 'livestock' (purple) subsystems.

718 Source: Marull et al. 2016b.

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720

Appendix A

Figure A1 Butterfly species richness and abundance (represented as generalist / specialist, open-space / close-space species) and bird species richness and abundance (represented as total or farmland breeding / wintering species) in the Barcelona province, from 2005 to 2015

756   Table A1 Variables used in the Intermediate Disturbance–Complexity (*IDC*) and the Energy–Landscape

757   Integrated Analysis (*ELIA*) models at the Barcelona region and province (RMB & PROV, respectively)

Typology		Code	Name	RMB	PROV
Energy	Primary Energy Variables	FEI r	Farmland External Input renewable	*	
		FEI nr	Farmland External Input no-renewable	*	
		FEI	Farmland External Input	*	
		UB	Unharvested Biomass	*	
		FW	Farmland Waste	*	
		FBR	Farmland Biomass Reused	*	
		LBR	Livestock Biomass Reused	*	
		FFP	Farmland Final Produce	*	
		LEI R	Livestock External Input	*	
		LEI nr	Livestock External Input renewable	*	
		LEI	Livestock External Input no-renewable	*	
		LW	Livestock Waste	*	
		LS	Livestock Services	*	
		LFP	Livestock Final Produce	*	
	Secondary Energy Variables	NPPact	Actual Net Primary Production	*	
		NPPh	Harvested Net Primary Production	*	
		ATT	Agroecosystem Total Turnover	*	
		LTI	Livestock Total Input	*	
		LPS	Livestock Produce and Services	*	
		FTI	Farmland Total Input	*	
		FII	Farmland Internal Input	*	
	Socio-economic Indicators	EF-EROI	External - Energy Return of Investment	*	
		IF-EROI	Internal - Energy Return of Investment	*	
		F-EROI	Final - Energy Return of Investment	*	
	Agro-ecological Indicators	NPP-EROI	Net Primary Production - Energy Return of Investment	*	
		AF-EROI	Agro-ecological - Energy Return of Investment	*	
		B-EROI	Biodiversity - Energy Return of Investment	*	
	Energy Indicators	E	Energy Storage	*	
		I	Energy Information	*	
		HANPP	Human Appropriation of Net Primary Production	*	*
Landscape	Landscape Composition	CR-LC	Cropland	*	*
		GR-LC	Grove	*	*
		VN-LC	Vineyard	*	*
		GS-LC	Grassland	*	*
		SC-LC	Scrubland	*	*
		FR-LC	Forest	*	*
		WT-LC	Wetland	*	*
		UN-LC	Unproductive	*	*
		UR-LC	Urban	*	*
	Landscape Configuration	LPI	Largest Path Index	*	*
		PD	Polygon Density	*	*
		ED	Edge Density	*	*
		EMS	Effective Mesh Size	*	*
		L	Landscape Heterogeneity	*	*
		ECI	Landscape Connectivity	*	*
		Le	Landscape Complexity	*	*
Energy - Landscape	ELIA / IDC	ELIA	Energy - Landscape Integrated Analysis	*	
		IDC	Intermediate Disturbance Complexity		*
Biodiversity (transects)	Birds	TBB-SR	Total Breeding Bird Species Richness	69	96
		FBB-SR	Farmland Breeding Bird Species Richness		
		TBB-AB	Total Breeding Bird Abundance		
		FBB-AB	Farmland Breeding Bird Abundance		
		TWB-SR	Total Wintering Bird Species Richness		
		FWB-SR	Farmland Wintering Bird Species Richness		
		TWB-AB	Total Wintering Bird Abundance		
		FWB-AB	Farmland Wintering Birds Abundance		
	Butterflies	TB-SR	Total Butterfly Species Richness	23	34
		TB-AB	Total Butterfly Abundance		
		OPE-SR	Open-space Butterfly Species Richness		
		OPE-AB	Open-space Butterfly Species Abundance		
		CLOS-SR	Close-space Butterfly Species Richness		
		CLOS-AB	Close-space Butterfly Species Abundance		
		GEN-SR	Generalist Butterfly Species Richness		
		GEN-AB	Generalist Butterfly Species Abundance		
		SPE-SR	Specialist Butterfly Species Richness		
		SPE-AB	Specialist Butterfly Species Abundance		

758