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1 Unpacking ecosystem service bundles: towards predictive 2 mapping of synergies and trade-offs between ecosystem 3 services

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37 **Unpacking ecosystem service bundles: towards predictive** 38 **mapping of synergies and trade-offs between ecosystem** 39 **services**

40

41 **Abstract**

42 Multiple ecosystem services (ES) can respond similarly to social and ecological factors to form
43 bundles. Identifying key social-ecological variables and understanding how they co-vary to produce
44 these consistent sets of ES may ultimately allow the prediction and modelling of ES bundles, and
45 thus, help us understand critical synergies and trade-offs across landscapes. Such an understanding is
46 essential for informing better management of multi-functional landscapes and minimising costly
47 trade-offs. However, the relative importance of different social and biophysical drivers of ES bundles
48 in different types of social-ecological systems remains unclear. As such, a bottom-up understanding of
49 the determinants of ES bundles is a critical research gap in ES and sustainability science.

50 Here, we evaluate the current methods used in ES bundle science and synthesize these into four steps
51 that capture the plurality of methods used to examine predictors of ES bundles. We then apply these
52 four steps to a cross-study comparison (North and South French Alps) of relationships between social-
53 ecological variables and ES bundles, as it is widely advocated that cross-study comparisons are
54 necessary for achieving a general understanding of predictors of ES associations. We use the results
55 of this case study to assess the strengths and limitations of current approaches for understanding
56 distributions of ES bundles. We conclude that inconsistency of spatial scale remains the primary
57 barrier for understanding and predicting ES bundles. We suggest a hypothesis-driven approach is
58 required to predict relationships between ES, and we outline the research required for such an
59 understanding to emerge.

60 **Keywords:** cross-study comparison, ecosystem services, French Alps, land use, social-ecological
61 systems, trade-off, natural capital, biodiversity.

62 **1. Introduction**

63 Current understanding of how multiple ecosystems services (ES) are associated across heterogeneous
64 landscapes remains limited (Bennett et al. 2009; Qui & Turner et al. 2013; Bennett et al. 2015). This
65 understanding is essential for informing better management of multi-functional landscapes. Although
66 the idea that the spatial distribution of ES and their associations are driven by the interplay between
67 social and ecological variables is well-established (Reyers et al. 2013), the relative importance of
68 different social and biophysical drivers of sets of ES and how these change across different socio-

69 ecological systems remains unclear (Bennett et al. 2015). Consequently, there have been calls to
70 achieve a greater understanding of the drivers of ES distributions and associations (Bennett et al.
71 2009, Howe et al. 2014, Bennett et al. 2015).

72 Associations among ES are understood to occur when multiple services respond to the same driver of
73 change or ecological process, or when interactions among the services themselves cause changes in
74 one service to alter the provision of another (Bennett et al. 2009). Such associations are commonly
75 referred to as ES interactions (Raudsepp-Hearne et al. 2010), with synergies and trade-offs being
76 routinely explored in multi-ES assessments (Howe et al. 2014). Synergies arise when multiple
77 services are enhanced simultaneously, while trade-offs occur when the provision of one service is
78 reduced due to increased use of another. While ES associations can be highly context-specific (Howe
79 et al. 2014), there have been calls for the development of general rules about the relationships among
80 ES (Bennett et al. 2009; Raudsepp-Hearne et al. 2010). In attempting to distinguish ES associations
81 that are context-specific from those that are universal, several authors have emphasised the need for
82 cross-study comparisons (e.g. Bennett et al. 2009; Raudsepp-Hearne et al. 2014, Meacham et al.
83 2015). However, cross-study comparisons are hampered by differences in approaches, the services
84 covered, spatial scale, how ES are modelled and what drivers are used (Grêt-Regamey et al., 2014;
85 Queiroz et al. 2015).

86 The concept of 'ecosystem service bundles' has been operationalised to help in the search for general
87 rules determining ES associations (Bennett et al. 2009; Raudsepp-Hearne et al. 2010). While rather
88 confusingly the use of the term varies in the literature, with bundles and synergies used
89 interchangeably (Berry et al 2015; see Box 1 for definitions used here), the term has been widely used
90 in conjunction with the application of a spatially explicit framework developed by Raudsepp-Hearne
91 et al. (2010) for identifying and mapping ES associations based on cluster analysis. Raudsepp-Hearne
92 et al. (2010) defined ES bundles as coherent sets of ES repeatable in space or time. This clustering
93 approach has been applied across the world to facilitate cross-study comparisons of ES associations
94 and their drivers (Table 1; Fig 1). Maps of ES bundles delineated with this approach can indicate what
95 services can be expected to associate based on where we find services repeatedly occurring together
96 across a landscape (Raudsepp-Hearne et al. 2010). Their distributions have been typically interpreted
97 with regards to known distributions of principal human activities or land use within the region (Table
98 1), and are therefore considered useful for communicating the potential impact of management
99 decisions to policy-makers (Crouzat et al. 2015). This qualitative interpretation of ES bundle
100 distribution provides some information about the drivers of ES associations and whether different
101 social-ecological systems have particular sets of ES associated with them (Bennett et al 2009).

102 In addition to qualitative interpretation of ES bundles, recent studies have attempted a more
103 mechanistic approach to understanding ES bundle distribution, based on the relative roles of different
104 social-ecological drivers, with multi-variate approaches being increasingly used (Mouchet et al. 2014)

105 reviewed the quantitative methods that are available for such analyses. Raudsepp-Hearne et al. (2010)
106 suggested that spatially explicit analyses of the social-ecological variables driving ES bundles could
107 ultimately allow for the prediction and modelling of ES bundles and thus, critical trade-offs and
108 synergies across regions (Raudsepp-Hearne et al. 2010). Studies that aim to achieve such an
109 understanding typically infer ES associations from the analysis of spatial trends in the distribution of
110 two or more ES, and relate these to underlying social-ecological determinants (Mouchet et al. 2014).
111 Further, if widely accessible data on social-ecological drivers (such as land use and population
112 density) can predict ES bundles, this could potentially overcome problems associated with complex
113 and data-intensive models that are required to produce ES maps (Meacham et al. 2015). Indeed, an
114 ability to use limited variables to inform about the ES context is particularly important in data scarce
115 regions (Meacham et al. 2016).

116 Here, we critically assess the strengths and limitations of current approaches for explaining and/or
117 predicting the distribution of spatial associations between multiple ES. Most studies of this type to
118 date follow the spatially explicit ES bundle approach first outlined by Raudsepp-Hearne et al. (2010)
119 (Table 1). We first review studies that have applied this approach (Table 1; Fig. 1) and synthesise the
120 application of it into four steps (Fig. 2), that capture the plurality of methods currently used, and
121 illustrate them with a case study – a cross-study comparison of the North and South regions of the
122 French Alps. We then use the outcomes of this case study to assess the strengths and limitations of
123 current approaches for linking social ecological drivers to ES bundles. . Finally, we outline a roadmap
124 for research required to enable a general understanding of ES associations.

Box 1. Definitions of key concepts surrounding ecosystem services (ES) used in this article

ES associations	Arise when two or more services respond to the same driver of change or ecological process or when true interactions among the services themselves cause changes in one service to alter the provision of another (Bennett et al. 2009). Commonly referred to as ES interactions (Mouchet et al. 2014) and are inferred from spatial overlaps or lack thereof.
ES bundle	“Sets of ES that appear together repeatedly across space or time” (Raudsepp-Hearne et al., 2010). Have been delineated and mapped using cluster analysis following Raudsepp-Hearne et al. 2010 (Table 1). In a bundle, ES can be positively (synergy) or negatively (trade-off) associated (Mouchet et al. 2014).
ES demand	“the amount of a service required or desired by society” (Villamagna et al., 2013). Different sectors of society can have different, and even conflicting demands.
ES flow	“the service actually received by people, which can be measured directly as the amount of a service delivered, or indirectly as the number of beneficiaries served” (Villamagna et al., 2013).
ES supply	The capacity of the structures and processes of a particular ecosystem to provide ES within a given time period (modified from Burkhard et al., 2012).
ES use	Refers to an ecosystem being accessed/altered/managed/protected due to ES demand (Turkelboom et al. 2015).
ES indicator	Proxy measures derived from empirical data or modelled estimates of ES.
Realised ES	By definition, an ES is only realised if there is a human benefit. Without human beneficiaries and demand for an ES, ecosystem functions and processes are not services (Fisher et al., 2009).
Social-ecological system	A set of social and ecological components that interact in a constantly evolving and interdependent manner (Berkes and Folke, 1998).
Synergy	Arises when multiple services are enhanced simultaneously by the use of an ES. Typically inferred from positive spatial overlaps.
Trade-off	When the provision of one service is reduced as a consequence of increased use of another, such as the case of crop production diminishing water quality. Inferred from negative spatial overlaps.
Win-win	A situation (or area) where a synergy occurs.

126 Table 1. Examples of studies that have assessed social-ecological drivers of spatially explicit ES bundles. The studies included here identified and
 127 produced maps of bundles of ecosystem services derived from spatially explicit multivariate analyses of ES*.

Study	Region	Service categories (total number of variables)#	Grain	Method used to obtain bundles	Interpretation of ES bundles
Raudsepp-Hearne (2010)	Quebec, Canada	P,C,R(12)	Municipality	<i>k</i> -means clustering	Qualitatively interpreted with regards to coincidence with social-ecological systems as defined by dominant land uses.
Haines-Young et al. (2011)	Part of Europe	P,C,R(15) (Not just ES)	NUTS-2 regions	Unknown	Mean service loadings and marginal impacts of land use and cover change for four services across two time periods were clustered to define groupings of NUTS-2 regions with similar change trajectories.
Martin-Lopez et al. (2012)	Iberian Peninsula, Spain	P,C,R(14)	Respondents	Hierarchical clustering	Used redundancy analysis to analyse associations between the relative importance of ecosystem services perceived by people and three types of explanatory variables: stakeholders' characteristics (e.g. education, income), land management strategy (e.g. protection level) and ecosystem type (e.g. presence of mountains). First three axes of the RDA were clustered to obtain bundles.
Qiu and Turner (2013)*	Yahara Watershed southern Wisconsin (USA)	P, C, R (10)	30-m grid cells (within 1,336 km ² watershed)	Factor analysis	Identified three orthogonal axes that represented synergies as well as trade-offs for ES supply. Interpreted interactions by mapping factor scores that represented synergies and trade-offs in ES.
Hanspach et al. (2014)	Southern Transylvania, Romania	P, C,R,B(9)	Village	Hierarchical clustering	Qualitatively interpreted with regards to spatial coincidence with socio-demographic data, derived from commune level statistics, including e.g. total population size, proportions of the main ethnic groups, unemployment, migration levels.

Plieninger et al. (2014)	Gutttau, Germany	C(11) (includes disservices)	'land cover unit'	Hierarchical clustering of PCA scores	Bundles in the perception of cultural services obtained by clustering PCA axes of ES variables by land cover units. Qualitatively interpreted with regards to land cover type of the land cover unit.
Turner et al. (2014)	Denmark	P,C,R (11)	10 km × 10 km	<i>k</i> -means clustering of PCA scores	Qualitatively interpreted with regards to overlap with social-ecological systems as defined by dominant land uses.
Derkzen et al. (2015)	Rotterdam, Netherlands	R,C(6)	Neighbourhood District	<i>k</i> -means clustering	Qualitatively interpreted with regards to overlap with water bodies and urban green spaces.
Renard et al. (2015)	Quebec, Canada	P,C,R(9)	Municipality	<i>k</i> -means clustering	Used redundancy analysis to analyse the relationship between the provision of ES and socioeconomic (population density, distance from urban center) and biophysical (agricultural land capability) variables.
Crouzat et al. (2015)	French Alps, France	P,C,R,B(18)	1 km × 1 km	Self-organizing map	Qualitatively analysed the geographical distributions, elevation and land cover patterns of different ES bundles.
Hamann et al. (2015)	South Africa	P(6)	Municipality	<i>k</i> -means clustering	Multinomial logistic regression used to identify the most important social-ecological predictors of the spatial pattern observed in the distribution of ES bundle types.
Quiroz et al. (2015)	Sweden	P,C,R(16)	Municipality	<i>k</i> -means clustering	Qualitatively interpreted with regards to overlap with social-ecological systems as defined by dominant land uses, management intensity and soil types.
Yang et al. (2015)	Yangtze River Delta, China	P,C,R(12)	"Urban-rural complexes" as defined by city boundaries	Hierarchical clustering	Qualitatively interpreted with regards to overlap with social-ecological systems as defined by dominant land uses and human activities.
Meacham et al. (2016)	Sweden	P,C,R(16)	Municipality	Bundles identified by Quiroz et al. (2015)	Used random forest analysis to identify best combinations of social-ecological variables to best predict ES bundle types.
Schulze et al. (2016)	Germany	P, R, B(6)	500 m × 500 m	<i>k</i> -means clustering	Binomial logistic regression used to assess relative importance of variables in determining the occurrence of different bundles

Raudsepp-Hearne & Peterson (2016)	Quebec, Canada	P,C,R (12)	1 km × 1 km 3 km × 3 km Municipality	<i>k</i> -means clustering	Assessed how interactions among ES as characterised using correlation and cluster analysis varied across three grain sizes
Hamann et al. (2016)	South Africa	P(6)	Municipality	Bundles identified by Hamann et al. (2015)	Assessed spatial overlap with 'well-being bundles', as identified using cluster analysis of social and demographic factors such as income and education.
Lamy et al. (2016)	Quebec, Canada	P,C,R(10)	Municipality	Multivariate regression tree (MRT)	Used eight landscape variables (composition and configuration metrics) as a constraint in the clustering. Performed an RDA analysis to explore relationship between ES covariation and landscape structural variables.
Depellegrin et al. (2016)	Lithuania	P,C,R(31)	100 m × 100 m	PCA	Identified five orthogonal axes that represented synergies as well as trade-offs for ES potential (ES were derived using a look-up table and a land cover map). Interpreted interactions by mapping factor scores that represented synergies and trade-offs in ES.
Yao et al. (2016)	Liaoning Province, China	P,R(11)	Watershed	Cluster analysis	Qualitatively interpreted with regards to dominant land uses.
Mouchet et al. (2017)	Europe	P, C, R(11)	1 km × 1 km	Self-organizing map	Used redundancy analysis to identify combinations of social-ecological variables that explained the co-variation of ES indicators within each cluster.

128 * These are studies that have delineated and mapped ES bundles using cluster analysis or PCA/factor analysis. Studies were identified by a key word search
129 in the ISI Web of Science ("ecosystem service*" AND bundle*), followed by a 'snowballing' approach, searching for references within retrieved articles and
130 pertinent reviews e.g. Lee and Lautenbach (2016).

131 # Ecosystem service categories: P, provisioning; C, cultural; R, regulating; B, biodiversity.



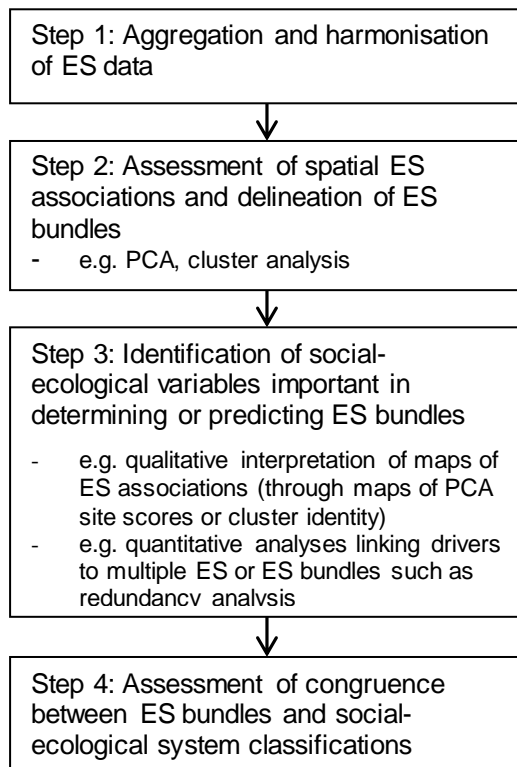
132

133 Figure 1. Distribution of 21 case studies that have mapped ES bundles based on cluster
 134 analysis. Three studies at the European scale (extent) are not plotted. See Table 1.

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2. Current approaches to understanding spatially explicit ES associations



138

139 Figure 2. Approach of the spatially explicit analyses of ES associations, organized into four
140 conceptual steps.

141 2.1 Step 1: Assessment, aggregation and harmonisation of ecosystem service indicators

142 Studies that have examined drivers of spatial ES bundles exhibit considerable variation regarding the
143 number and types of ES considered, and in how individual ES are quantified (Table 1). Studies have
144 typically considered a relatively large number of ES (averaging ~12 ES), encompassing a range of
145 provisioning, regulating and cultural ES, and also biodiversity metrics (Table 1). Contrasting large
146 numbers of ES within different ES categories can contribute to a better understanding of ES trade-offs
147 (Raudsepp-Hearne et al. 2010; Crossman et al. 2013).

148 ES maps often vary in the units, range of output values, and spatial resolution. To enable bivariate or
149 multivariate analyses, ES datasets have been aggregated to a common resolution. While studies have
150 mapped ES at scales ranging from local to global (see Crossman et al. 2013 and Malinga et al. 2015
151 for recent reviews), studies mapping ES bundles tend to be conducted for parts of countries at the
152 spatial resolution of administrative boundaries, typically the smallest political units such as
153 municipalities (Table 1). The use of administrative boundaries has been advocated as relevant for
154 multi-ES studies (Raudsepp-Hearne et al. 2010), as municipalities represent the smallest scale of

155 governance (in most areas of Europe) where many decisions regarding planning and landscape
156 management are taken (Hamann et al. 2015; Queiroz et al. 2015). The selected grain for multi-ES
157 research is also likely to have been driven by data availability; municipalities often are the finest scale
158 at which some ES (such as provisioning ES) and potential social data are available (e.g. census data).
159 We consider the potential limitations of municipality-level analyses in the discussion.

160 Following collation and aggregation of multi-ES datasets, data are usually harmonised to a common
161 range and unit to allow for comparison prior to data analysis. The methods used such as
162 standardisation (transformation to z -scores by centring and scaling), serve to adjust the magnitude and
163 variability of the variables to make them compatible for analysis (Legendre & Legendre 2012).

164 ***Application of step 1 to French Alps case study***

165 The French Alps represent a relatively large, highly socially and ecologically diverse region
166 characterized by excellent ES data over this large extent (e.g. Crouzat et al. 2015). Within the region,
167 elevation, climate and vegetation gradients have had historical influenced social dynamics and
168 economic activities, resulting in the conventional separation into the North and the South Alps
169 (Crouzat et al. 2015; a detailed description of study system is given in SI). This social-ecological
170 divide is also recognised by an administrative boundary at the NUTS II level (Nomenclature of
171 Territorial Units For Statistics by Eurostat [<http://ec.europa.eu/Eurostat>], basic regions for the
172 application of regional policies).

173 We selected nine ES that have been quantified and mapped in the French Alps previously by Crouzat
174 et al. (2015). These services were deemed socially, ecologically, and economically relevant to the
175 region following consultation with scientists and local collaborators (Crouzat et al. 2015), and
176 included three provisioning (crop [crop], fodder [fodd] and wood [wood] production) three cultural
177 (hunting [hunt], recreation [rec] and tourism [tour]) and three regulating ES (water quantity regulation
178 [wqt], carbon storage [cstock], erosion mitigation [eros]; see Table S1. These ES are mixed indicators,
179 ranging from potential capacity to actual use values, as is the case in the majority of ES bundle
180 analyses (Raudsepp-Hearne et al. 2010; Crouzat et al. 2015; Queiroz et al. 2015; Meacham et al.
181 2016). By using the same ES for both the North and South Alps we were able to control for the effect
182 of choice of the ES selected in our bundles in our cross-study comparison. All ES were based on
183 either primary data or bespoke modelled surfaces of ES based on primary data. Full details of these
184 ES are in Crouzat et al. 2015 and Appendix S1. Our analyses were conducted at the municipality scale
185 (a total of 2336 municipalities; 1498 in North Alps and 838 in the South, ranging in area from 0.52 to
186 246.20 km², averaging 22.19 km² (SD 23.98km²)). To minimise skew and make the ES variables
187 dimensionless and comparable in terms of their magnitudes and variability, Box-Cox transformation
188 (Box & Cox, 1964), centring and scaling was applied.

189 **2.2 Step 2: Assessment of ecosystem service associations and delineation of ES bundles**

190 ES associations have typically been assessed by mapping multiple ES across broad regions, and any
191 spatial overlaps (or absence of overlaps) are assumed to signify a particular type of ES association;
192 positively correlated ES are assumed to be synergistic, while negative correlations infer trade-offs
193 (Tomscha & Gergel, 2016). Spatial overlaps between multiple ES have been most commonly
194 quantified through assessments of pairwise correlations or PCA (Mouchet et al. 2014); a correlation
195 biplot from a PCA (scaling type 2; Borcard et al. 2011) is considered a useful way to visualise the
196 strength of correlations between multiple ES indicators (e.g. Maes et al. 2012; Turner et al. 2014).

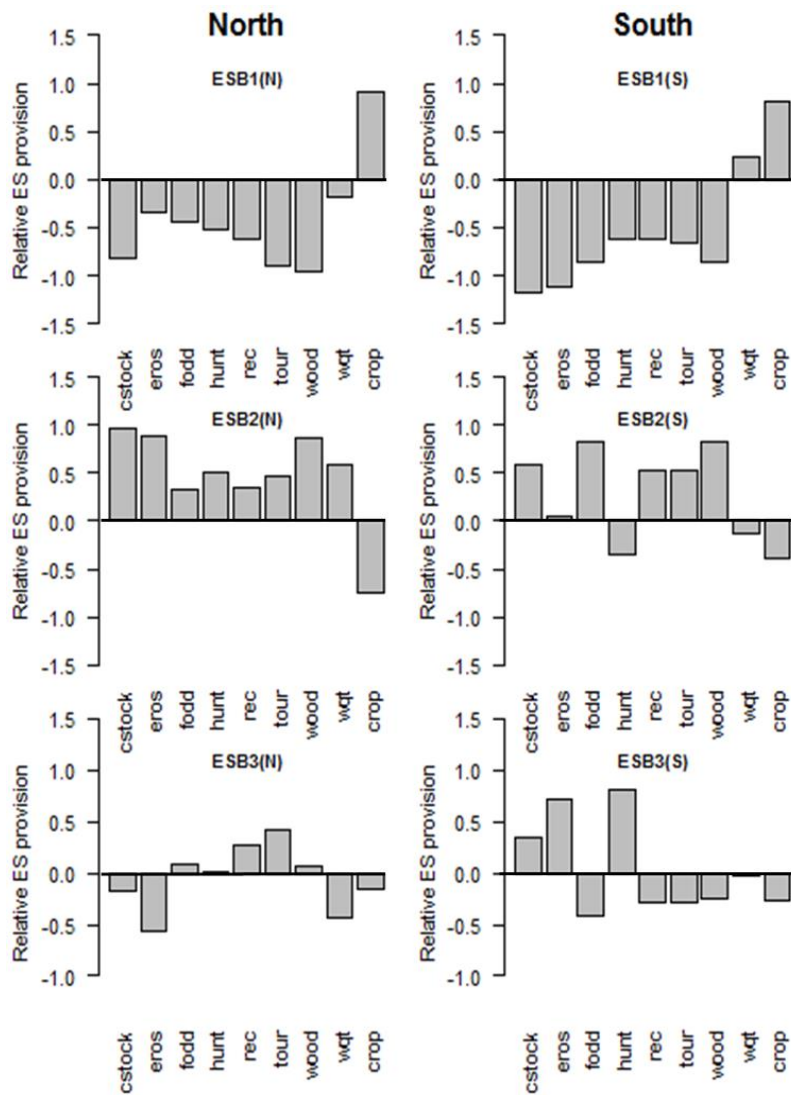
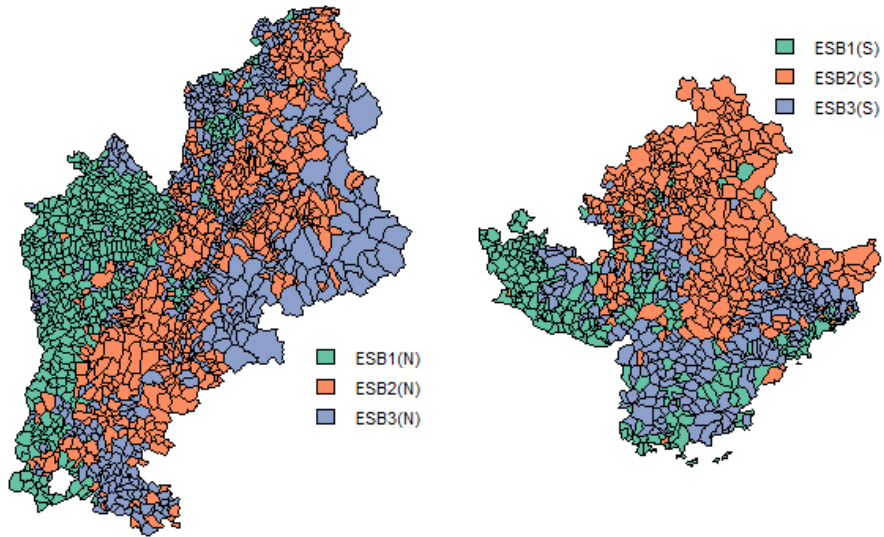
197 Raudsepp-Hearne et al. (2010) developed an approach for identifying ES bundles based on cluster
198 analysis, which has since been widely applied to social-ecological systems across the world (Table 1;
199 Fig 1). In this approach, clustering algorithms (e.g. *k*-means, self-organizing maps) have been applied
200 to define groups of ES that are associated in space by delineating spatial units supplying the same
201 magnitude and types of ES (Raudsepp-Hearne et al. 2010; Mouchet et al. 2014). As such, ES bundles
202 as defined by cluster analysis are emergent properties of the maps of different ES that are used in the
203 cluster analysis and will often result from the distribution of underlying driver variables that drive
204 more than one ES. Following clustering, ES associations have frequently been visualized using star
205 diagrams (Mouchet et al. 2014), showing the relative delivery of different ES within each bundle.
206 Clustering approaches also underpin many current methodologies for mapping social-ecological
207 systems (Ellis and Ramankutty 2008; Asselan and Verburg 2012; Levers et al. 2015), by identifying
208 localities that have similar sets of multiple social-ecological variables.

209 ***Application of step 2 to French Alps case study***

210 Following the spatially explicit ES bundle approach of Raudsepp-Hearne et al. (2010) we used *k*-
211 means cluster analysis to delineate ES bundles across the N and S French Alps separately (Full
212 Methods in Appendix S2). Briefly, for both the North and South regions, a two step clustering
213 approach was adopted (Turner et al. 2014). A PCA was firstly used to quantify the main multivariate
214 relationships between the ES variables to assess whether ES co-occur in spatial bundles. As a
215 precursor to cluster analysis, PCA can serve to separate signal from noise and lead to a more stable
216 clustering solution (Husson et al. 2010). We applied *k*-means clustering to the relevant PCA axes
217 (selected according to the Kaiser-Guttman criterion; Legendre and Legendre, 2012; Turner et al.
218 2014), to delineate ES bundles with 1000 random starts and 10,000 iterations to find a solution with
219 the lowest within-cluster sum of squares according to the relevant PCA axes. *K*-means clusters
220 municipalities so that the composition of ES values are more alike within than between clusters.
221 Following Renard et al. (2015), we quantified the effective number of ES provided in each bundle
222 using a transformation (*H*) of the Gini–Simpson's index (*S*): $H = 1/(1 - S)$, (Jost, 2006; Appendix S2).

223 In both the North and South Alps, three ecosystem service bundles (ESBs) were identified. In both
224 regions, bundles were identified that were characterized by high crop production and far below
225 average levels of most other services (ESB1(N) and ESB1(S)). Crop production was negatively
226 correlated with most services across both study regions, except for water quantity regulation in the
227 south (Appendix S2). In both the north and south, these crop-dominated bundles had the lowest
228 diversity ($H=2.8$ for the north Alps and 1.8 for the south Alps). In the north and south regions,
229 bundles were identified that were characterised by a high delivery of forest ecosystem services
230 (carbon storage, wood production), and relatively high provision of other services but a complete lack
231 of crop production (ESB2(N) and ESB2(S)). These forest ES-dominated bundles had the highest
232 diversity in both the North and South regions. In the North Alps, multifunctionality was higher
233 ($H=9.0$) than in the South Alps ($H=6.0$). A third ESB had a more intermediate mix of ecosystem
234 services in the north and South Alps. In the north, ESB3(N) exhibited intermediate levels of crop
235 production while remaining relatively multi-functional, delivering other services including high levels
236 of tourism and intermediate hunting and recreation (Fig. 3; $H = 6.9$). In the South, ESB3(S) was
237 dominated by delivery of hunting, erosion mitigation, and carbon storage ($H=5.9$; Fig. 3).
238

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240

241 Figure 3. Distributions of ecosystem service bundles (ESBs) for the North and South French
 242 Alps. Barplots indicate the relative provision of ES within each bundle type. Values are ES z-scores
 243 averaged across all municipalities belonging to a specific bundle. Positive z-scores refer to above-
 244 average, negative z-scores to below- average values regarding the ES for the regions.

245 **2.3 Step 3: Identification of social-ecological determinants of ES bundles**

246 Understanding the spatial distribution of ES associations means identifying key drivers and their
247 interactions that produce coherent sets of ES across landscapes (Raudsepp-Hearne et al. 2010;
248 Meacham et al. 2016). Several studies have mapped ES associations to allow for their qualitative
249 interpretation by association with broad social-ecological systems (Table 1). The results of cluster
250 analysis are made spatially explicit when the spatial units (typically administrative units or grid cells,
251 Table 1) are classified into groups (bundles) and projected onto maps (Fig 3), allowing the researcher
252 to identify which localities exhibit similar ES associations (Raudsepp-Hearne et al. 2010; Mouchet et
253 al. 2014). ES interactions have also been visualised by mapping the site scores of factor analysis and
254 PCA of multiple ES (Qiu & Turner, 2013; Turner et al. 2014). This approach has allowed for the
255 identification of where trade-offs and synergies are the most pronounced in the landscape. Mapping
256 ES associations in these ways has enabled qualitative interpretation of mapped bundles with respect to
257 known distributions of dominant land uses or principal human activities within regions (e.g.
258 Raudsepp-Hearne et al. 2010; Quieroz et al. 2015; Turner et al. 2014; Crouzat et al. 2015).

259 In addition to qualitative interpretation, several quantitative methods are available for analysing ES
260 bundles in relation to potential social-ecological determinants or predictors (Mouchet et al. 2014).
261 Widely used methods include those frequently used in community ecology to study the relationships
262 between ecological communities and the environment, through the coupling of two data tables, a site
263 \times environmental variable table and a site \times species table (Doledec & Chessel, 1994). Studies are
264 increasingly applying these techniques in ES research to determine how drivers and ES are related to
265 one another, by replacing the latter table with a site \times ES table (Mouchet et al. 2014; Meacham et al.
266 2016), including, for example, redundancy analysis and canonical correspondence analysis. Other
267 approaches have used regression-based or machine-learning methods with a single response variable,
268 such as ES bundle type (e.g. Hamann et al. 2015; Meacham et al. 2016; Schulze et al. 2016), or
269 whether a locality represents a win-win or not (Qui & Turner et al. 2013).

270 Whichever quantitative method is used, a critical step is the identification of candidate social-
271 ecological variables that are important in explaining or predicting different ES bundles. This initial
272 selection is based either on relationships demonstrated in the primary literature or on expert
273 knowledge, and of course depends on the ES considered in the study. Meacham et al. (2016) explored
274 four theories of the driving forces behind human impact on ecosystems and tested their relative ability
275 to predict ES bundles. The four models were created by distilling the different driver variables that
276 each theory emphasises. Using random forest analysis, they found that models based on
277 socioeconomic variables performed better than those based on land use. Hamann et al. (2015) used
278 multiple logistic regression to predict the distribution of three ES bundles characterised by low,
279 medium and high levels of direct ES use across South Africa. Drivers were chosen based on variables
280 thought to contribute to the use of natural resources at the household level. They found bundle

281 distribution was determined by social factors, such as household income, gender of the household
282 head, and land tenure, and only partly determined by the supply of natural resources. Qui and Turner
283 (2013) used logistic regression to determine social-ecological determinants of win-win areas, with
284 candidate variables including land use, population density, slope and soil properties. See Mouchet et
285 al. (2014) and Table 1 for a review of quantitative methods for identifying drivers of ES associations.

286 ***Application of step 3 to the French Alps case study***

287 In our case study, potential social-ecological drivers included social and ecological components used
288 in the modelling or quantification of the ES in question (including land cover, elevation, climatic
289 factors), in addition to variables that directly or indirectly drive individual ES and their associations as
290 identified in the literature (biodiversity, NPP) (Table S1). Land cover variables and population density
291 are frequently cited drivers of ES magnitude and distribution (Kienast et al. 2009), including
292 mountainous regions (Grêt-Regamey et al. 2012) and have been widely used as a proxy of ES demand
293 and supply in ES assessments (e.g. Burkhard et al. 2012). Protected area coverage relates to an
294 ecosystem's governance and accessibility, has been used as a proxy for spiritual, aesthetic and
295 recreational services (van Jaarsveld et al. 2005) and has been shown to be positively correlated with
296 measures of aggregated ecosystem service supply across Europe (Maes et al. 2012). Full details are
297 given in Appendix S3.

298 To identify candidate variables significantly affecting the co-variation of multiple ES, we performed a
299 preliminary redundancy analysis (RDA) with all potential social-ecological driver variables followed
300 by forward stepwise selection to select the model with the combination of variables with the highest
301 R^2 and p -value (Legendre and Legendre, 2012). This stepwise procedure defined which variables are
302 relevant in exploring relationships among ES. RDA and the stepwise selection of variables were
303 performed using the “vegan” and “packfor” R packages (Oksanen et al., 2013; Dray et al. 2011).

304 RDA revealed that the combinations of the following variables significantly explained the co-
305 variation of ES indicators within the North and South Alps ($p \leq 0.001$): the coverage of grassland,
306 forest, semi-natural, urban land area, protected area coverage, elevation, NPP, plant species richness
307 and population density. The adjusted R^2 values, representing the amount of variance of ES indicators
308 explained by the social-ecological variables were 0.46 for the north and 0.42 for the south. Full
309 methodological details and results are in Appendix S3.

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312 **2.4 Step 4: Assessing whether ES bundles are associated with different social-ecological** 313 **systems**

314 In a call to develop general rules about ES relationships and their implications for management of ES,
315 Bennett et al. (2009) asked whether there exist consistent sets of ES associated with particular social-
316 ecological systems. As these systems are not only defined by land cover type, Bennett et al. (2009)
317 suggested that the ‘anthrome’ approach of Ellis and Ramankutty (2008) might be useful for
318 identifying a social-ecological system classifications, with distinct systems derived from overlays of
319 social and land use/land cover (LULC) data. Hamann et al. (2015) tested this assertion and quantified
320 the percentage of land area occupied by different anthrome types (derived from overlays of population
321 and LULC data) and bundles of locally derived provisioning ES across South Africa. Hamann et al.
322 (2016) also assessed the spatial overlap with ‘well-being bundles’, as identified using cluster analysis
323 of social and demographic factors such as income and education. We include this last step, as it
324 represents a logical progression from testing the relative predictive power of individual social-
325 ecological variables.

326 ***Application of step 4 to the French Alps case study***

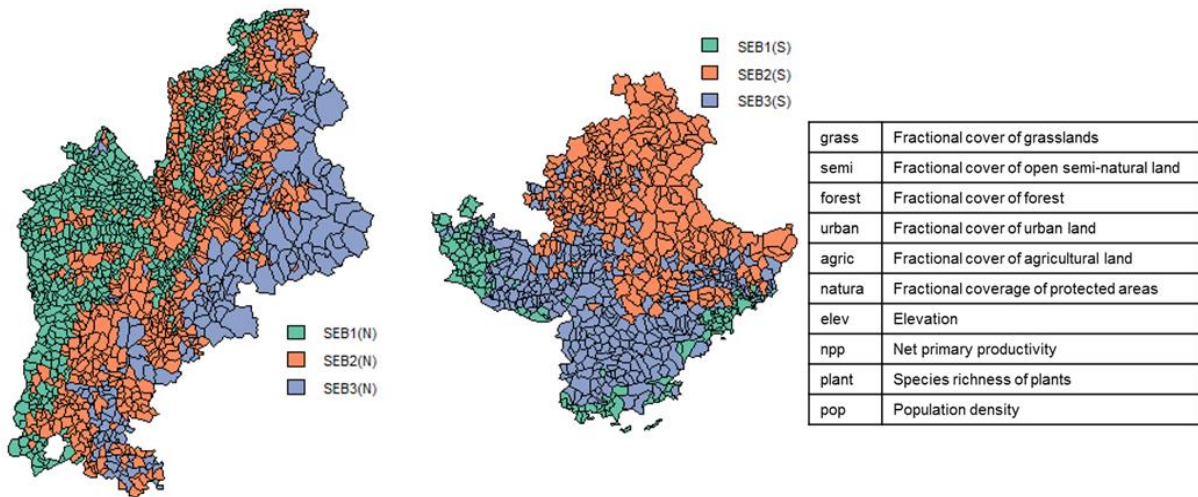
327 We followed the approach of Hamann et al. (2015, 2016) to ascertain whether ES bundles were
328 congruent with social-ecological systems. Having identified the most important social-ecological
329 determinants of ES bundles in step 3 using RDA, we used the *k*-means algorithm to cluster these
330 variables into social-ecological bundles (SEBs). SEBs delineate spatial units supplying the same
331 magnitude and types of social-ecological variables. Hamann et al. (2015) found that anthromes
332 offered little predictive power for provisioning service bundles in South Africa. We therefore used the
333 variables deemed important from the RDA to delineate SEBs, as opposed to those used in the original
334 construction of anthromes (Ellis & Ramankutty, 2008).

335 To assess whether particular ES bundles are associated with SEBs, or whether SEBs can act as
336 proxies for ES bundles, the spatial congruence between SEBs and ES bundles was assessed using
337 overlap analysis, a simple and intuitive way to run a spatially explicit detection of possible
338 associations (Mouchet et al. 2014). We calculated overlap as the percentage of municipalities of a
339 particular bundle category that overlapped with each SEB category.

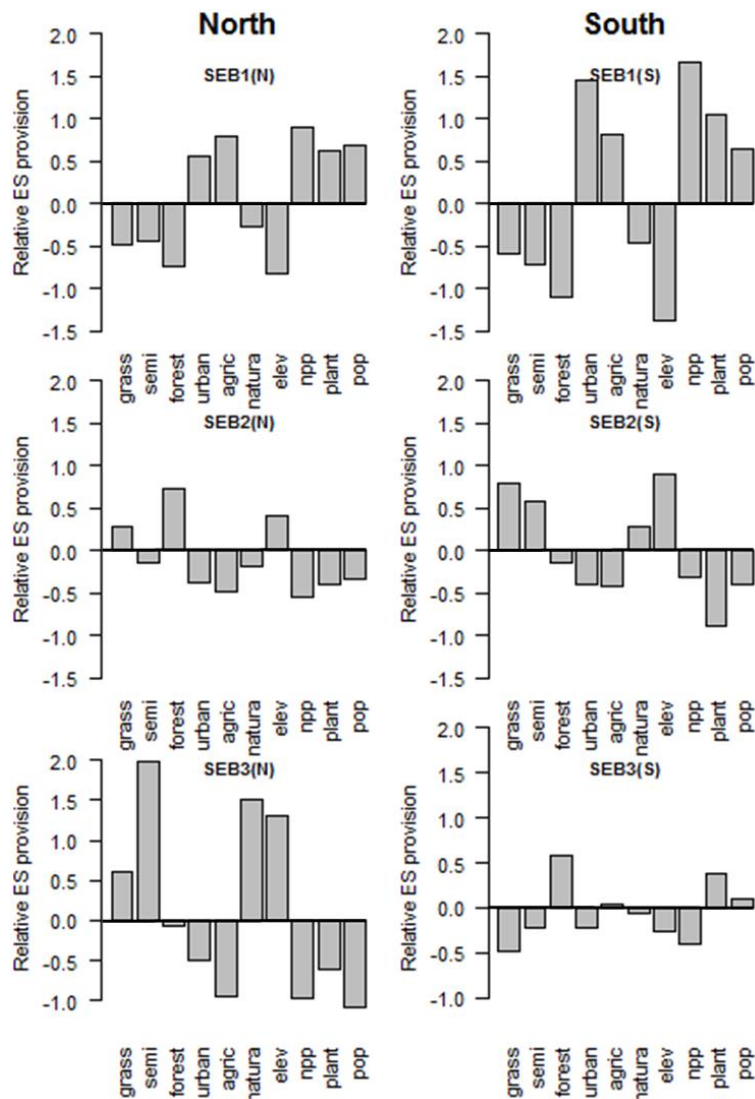
340 The crop-dominated bundles in the North and South (ESB1(N) and ESB1(S)) overlapped with SEBs
341 characterised by agricultural land coverage at low elevation and low to intermediate cover of other
342 land uses (Figs. 4 and 5; SEB1(N) and SEB1(S)). In the north, the bundle characterised by high
343 provision of forest services (ESB2(N)) broadly overlapped with a bundle characterised by high forest
344 cover (SEB2(N)). The North ES bundle dominated by tourism (ESB3N) did not overlap neatly with
345 any SEB (Fig. 5), except in the north-east of the region (Fig. 4), dominated by high elevation
346 grasslands and semi-natural areas with high levels of protected area coverage. However, in the South,

347 the forest bundle (high wood production and carbon storage) (ESB2(S)) does not overlap with forest
348 cover, but with high elevation areas with grassland and semi-natural coverage).

349

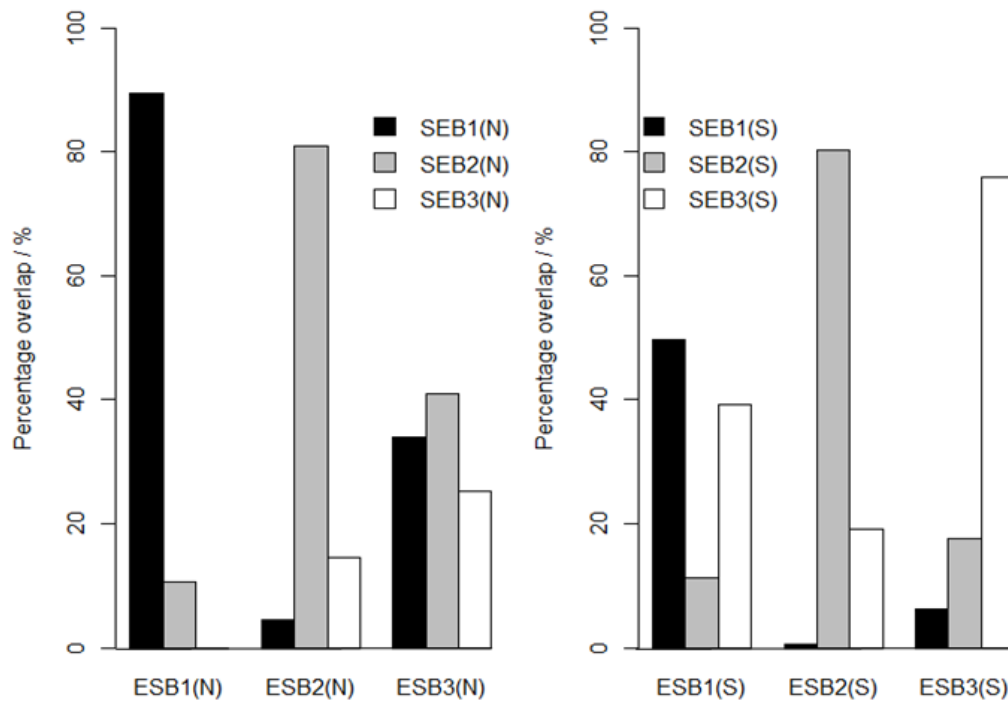


350



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352 Figure 4. Distributions of SEBs for the North and South French Alps. Barplots indicate the
 353 relative magnitude of social-ecological variables within each bundle type. Values are variable z-scores
 354 averaged across all municipalities belonging to a specific SEB. Positive z-scores refer to above-
 355 average, negative z-scores to below- average values regarding the variables for the region. See
 356 appendix S2 for variable descriptions).



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358 Figure 5. Overlap between ES bundle and SEBs for the north (left) and south (right) of the
 359 French Alps, expressed as a percentage of municipalities.

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3. Discussion

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A multitude of methods are available to analyse and explore ES associations relative to possible social-ecological predictors (Mouchet et al. 2014). Here, we have reviewed the application of a widely (Fig 1) and increasingly used (Table 1) method that analyses the spatial distribution of ES bundles, delineated by cluster analysis, in relation to possible socio-ecological predictors. A common theme across all such studies is the reliance on the spatial coincidence of ES and driver variables (Crouzat et al. 2015), assuming that consistency in the spatial congruency between ES likely emerges from common social-ecological drivers. While comparison among multiple studies, such as cross-site comparisons, could help disentangle the effect of context-dependent drivers from interactions between services within bundles (Queiroz et al. 2015), such comparisons are made difficult by study differences in scale (i.e. grain and extent), and methodology, in terms of how ES are modelled and what drivers are used (Grêt-Regamey et al., 2014; Queiroz et al. 2015). It is also widely acknowledged that which ES are selected is critical because conclusions are highly influenced by which indicators are considered in a decision making context (Rodríguez-Loinaz et al. 2012). Therefore, studies that have bundled different ES, or measured or modelled ES in different ways, are not straightforward to compare, or necessarily generalisable to other regions. We attempted to overcome both issues in our French Alps case study by comparing two regions using the same ES and social-ecological datasets, and do so using a widely used method to analyse ES bundles. However, we show that even within the French Alps, there is enormous variation in the degree to which different

379 social-ecological variables can explain the distributions of ES bundles (See Appendix S4 for more
380 discussion on the findings from the case study).

381 Importantly, our case study – which is based on the current state of the science – does not enable us to
382 identify why the explanatory power of different social and ecological variables considered here differs
383 so much between our two regions. As such, current approaches based on readily available data that
384 may have little relationship to underpinning mechanisms may not provide an effective basis for
385 predicting ES bundles across space or time, as is required for effective sustainable management of ES.
386 Here we discuss why current approaches for analysing ES bundles are poorly suited to enabling sound
387 understanding and prediction of ES bundles and propose a roadmap to guide future studies aimed at
388 understanding, mapping or predicting ES associations.

389 ***3.1 Issues of scale in understanding determinants of ES associations***

390 Here we detail issues of scale related to the ES bundle approach. We address two key components of
391 scale: i) grain, the size of the spatial unit of analysis; and ii) extent, the size of the study area.

392 **3.1.1 Spatial unit and grain**

393 ES associations are often analysed using municipalities or similar administrative spatial units (e.g.
394 Raudsepp-Hearne et al. 2010; Table 1), justified by the fact that municipalities are expected to be a
395 grain at which synergies and trade-offs between ES are observed (Rodríguez-Loínaz et al. 2012), and
396 as while ES synergies and trade-offs can be causally linked, they do not necessarily occur in close
397 proximity (Berry et al. 2015). However, municipality boundaries could be relevant for some ES, such
398 as cultural ES, but arbitrary for others in management terms, such as for managing water quality.
399 Boundaries may often dissect ecologically meaningful units, such as watersheds, that could be
400 appropriate for measuring and managing some ES.

401 The choice of municipality-level analysis is also often driven by data availability; municipalities often
402 are the finest scale at which some ES (namely provisioning ES) and social variables are available
403 (census data). Despite some good reasons for municipality-scale analyses, several considerations must
404 inform their interpretation. At such coarse scales, the identification of ES bundles relies on spatial
405 coincidence (Crouzat et al. 2015), and cannot show direct causal relationships between ES and social-
406 ecological variables. This is a key assumption with the approach; that consistency in the spatial
407 congruency between ES likely emerges from common social-ecological drivers. In actuality, the fine-
408 scale processes that some ES respond to might not be represented at this scale.

409 As one moves across different grain sizes, different processes are responsible for apparent synergies
410 and trade-offs between ES and relationships to social-ecological drivers. At coarse grains such as
411 municipalities, spatial units are highly heterogeneous, encompassing multiple LULC types. ES
412 relationships are likely to be largely driven by fractional land cover of the large spatial units, due to its

413 representation of i) natural conditions; e.g. natural land cover and soil conditions as well as ii) human
414 impacts; mainly via land use (Burkhard et al. 2012). ES relationships will, therefore, principally
415 reflect land use distribution. For example, ES may trade-off against each other simply because they
416 compete for space (e.g. a negative relationship between timber and crop production; Lautenbach et al.
417 2010). At smaller grain sizes, where individual spatial units are less heterogeneous and likely to
418 comprise a principal land cover type, the main drivers of ES variation are still likely to be land use. If
419 ES within a single land cover type are analysed at small grains, however, such as individual forest
420 plots or stands, then it is possible that a more useful understanding might be obtained. By analysing a
421 single land cover type, one can understand drivers of ES variation in relation to land use activities that
422 result in ‘land modifications’, changes that occur *within* the same LULC type (e.g. Lavorel et al.
423 2011). These remain much less studied than multi-ES relationships to LULC, but data are becoming
424 increasingly available (Erb et al. 2016).

425 Another well-documented scale effect related to spatial unit is the modifiable area unit problem, in
426 which statistical results can depend on the size and shape of spatial units in which a variable is
427 aggregated (Openshaw & Taylor, 1979). Grain size-dependence in the direction of correlations of ES
428 has been demonstrated in several studies (e.g. Naidoo et al., 2008; Anderson et al. 2009). Various
429 processes can cause this phenomenon. Aggregation obscures ES trade-offs particularly when ES
430 compete for space. For example, different crop competing for productive floodplain soils could be
431 seen as spatially concurrent in aggregated datasets, thereby suggesting a synergistic relationship
432 (Tomscha & Gergel, 2016).

433 When administrative units are used, the degree of variation in the grain size among units is likely to
434 be an issue for the interpretation of relationships, as the mechanisms essential to an ES at one grain
435 can be less important or absent at another. Significant variation in areal size could then reduce the
436 specificity of the measured associations, and also decrease their strength (Arsenault et al. 2013). Such
437 a phenomenon could affect the apparent relationships between ES or social-ecological variables, e.g.
438 population density could appear to be inversely related to landscape multi-functionality, but in
439 actuality, this could be a function of municipality size, as densely populated areas often divided into
440 smaller administrative units for health care and mail delivery (Arsenault et al. 2013). Raudsepp-
441 Hearne & Peterson (2016) showed that bundles delineated at three grain sizes (1×1 km, 3×3 km and
442 municipality) exhibited contrasting patterns across the study area and varied in their composition in
443 terms of the magnitude and types of ES. They concluded that individual ES that exhibit strongly
444 clumped or sparse distributions are likely to vary significantly as one moves from smaller to larger
445 grain sizes, and therefore are more likely to influence bundling in a larger study area if they are
446 present in multiple areas, which is more likely at a larger scale of observation (Raudsepp-Hearne &
447 Peterson (2016).

448 **3.1.2 Study spatial extent and context-dependency**

449 The spatial extent of the study region can impact ES relationships. At present, most studies have
450 delineated ES bundles at regional scale (Table 1), likely due to data availability, but also due to the
451 relevance to management of considering variation in ES bundles across municipalities within a
452 region. However, regions will differ in the variability of both the ES and social-ecological drivers that
453 may underpin these ES, as seen, for example in our case study, confusing our results. The relative
454 importance of social-ecological variables in driving ES variation can change across regions, and
455 therefore study extent. For example, Holland et al., (2011) found a negative relationship between
456 agricultural production and river habitat quality at the extent of Britain, due to the negative effects of
457 agriculture on aquatic ecosystems. However, within some heavily urbanized sub-regions of Britain, a
458 positive relationship was observed; this was attributed to urban land cover having a larger negative
459 effect on aquatic ecosystems than agricultural land. Variability of predictor and response variables
460 also affects the degree of statistical power that is available to detect relationships between spatial
461 variables (Eigenbrod et al. 2011). Moreover, the types of social-ecological driver variables considered
462 will likely vary with spatial extent. For example, over larger study regions, it is possible to analyse the
463 effect of slow variables, that exhibit variation at larger extents, but remain homogeneous across
464 spatial units at small extents. Given these issues, cross-study comparisons will not necessarily enable
465 meaningful comparisons of the relative explanatory power of different drivers between regions, even
466 when the same ES and the same explanatory variables are considered (as in this study).

467 ***3.2 Careful selection of ES indicators in multi-ES analyses is critical for interpretation***

468 The studies that have delineated ES bundles based on spatial associations in Table 1 exhibit
469 considerable variation in the number (mean ~12 ES) and types of ES considered, and in how
470 individual ES are quantified. It is important to distinguish what aspect of a service is being measured
471 by an ES indicator; the potential value provided by an ecosystem, or the service that is actually
472 realised by humans (Jones et al. 2016). Most previous ES bundle analyses, including this study, have
473 mixed indicators ranging from potential supply to actual use values. Two key problems with mixing
474 indicators make attribution and prediction difficult. Firstly, because the ES indicators may be
475 anywhere along a spectrum from ecological stocks to flows to benefits in support of human well-
476 being, some ES indicators may not respond to the influence of social factors (Hamann et al. 2015).
477 Indeed, supply and demand bundles are likely to exhibit very different dynamics and respond to
478 different drivers, potentially making mixed-indicator bundles more difficult to interpret or predict, as
479 in this and previous studies (Hamann et al. 2015; Meacham et al. 2016). Hamann et al. (2015) focused
480 on bundles of one type of ES, direct use of locally available ES in South Africa (e.g. wood for
481 heating), potentially allowing for a deeper understanding of linkages between ES use and human well-
482 being. There is a second difficulty of interpreting bundles of mixed ES indicators: Crouzat et al.

483 (2015) highlighted that positive associations between ES that are actual or potential do not necessarily
484 reflect synergies and can even represent conflicts once the ES are utilised.

485 The selection of which ES are analysed jointly is particularly critical to cross-study comparisons;
486 studies that have analysed associations of different ES, or ES measured or modelled in different ways,
487 are not straightforward to compare. Ultimately, ES bundles delineated by cluster analysis are not
488 generalizable to other regions because a clustering solution is entirely dependent upon the variables
489 used. This issue is already recognised as a limitation for the use of composite indicators of ES
490 (Rodríguez-Loinaz et al. 2012). Raudsepp-Hearne & Peterson (2016) demonstrated that ES bundle
491 spatial patterns were highly dependent on the numbers and types of ES included in the cluster
492 analysis.

493 ***3.3 Careful selection of social-ecological variables in multi-ES analyses is critical for*** 494 ***attribution***

495 There have been several calls for ES analysts to improve understanding of ES associations, to allow
496 for knowledge of how to minimize trade-offs and enhance synergies (Bennett et al. 2009; Bennett et
497 al. 2015). This understanding requires identifying key social-ecological variables that determine the
498 co-variation in ES. Other authors have suggested the potential benefit of predicting ES associations
499 from widely available social-ecological datasets, that are not necessarily causal (Meacham et al.
500 2015). If widely accessible data on social-ecological drivers (such as land use and population density)
501 can predict ES associations, this may overcome problems associated with complex and data-intensive
502 models that are required to produce ES maps in data scarce regions (Meacham et al. 2016). While
503 causal relationships are predictive (within similar contexts), prediction of ES associations does not
504 necessarily require causative links. We emphasise that causal social-ecological predictors for multi-
505 ES analysis are likely to be more robust and less-context dependent (see also Mouchet et al. 2014).

506 Land-use change is a management intervention that can drive demand and supply in one or more ES
507 (Bennett et al. 2009), and therefore land use/land cover (LULC) has been considered as a determinant
508 of individual ES or ES bundles in this study and many others (e.g. Hamann et al. 2015; Meacham et
509 al. 2016; Schulze et al. 2016). There are several issues with using LULC as a determinant in multi-ES
510 analyses. In this study and others, land cover categories were treated as homogeneous across study
511 regions, ignoring significant variations due to management and biophysical gradients (e.g. tree species
512 and age structure in forests). In our study, forest cover was correlated with forest services (wood
513 production, carbon storage) in the North (Figs 3 and S6), but not in the South (Figs 4 and S7). This is
514 because the French South Alps experienced extensive afforestation during the last century due to both
515 natural regeneration and deliberate planting on abandoned agricultural land. The secondary forests are
516 not widely harvested because their uniform and dense structure makes cutting expensive, and because
517 local populations are concerned for their conservation (Douguédroit, 1981). By using forest cover as a

518 driver, we gained no fine understanding of ecological processes and interactions. We only considered
519 variables for which continuous spatial data were available in the French Alps, but other unmeasured
520 factors or practices (relating to management history, age of abandonment, or forest age structure)
521 could affect synergies and trade-offs among ES in the regions. This emphasises the need for careful
522 consideration of what actually constitutes a driver of individual ES and ES bundles. Bennett et al.
523 (2009) considered many drivers as finer scale management interventions; for example, exogenous
524 drivers (e.g. industrial production) causing environmental change in the social-ecological system, and
525 pressures (e.g. use of fertilizers) quantifying the effect of exogenous drivers on a given social-
526 ecological system (Mouchet et al. 2014). By using LULC as a determinant, much ES research states
527 the obvious about LULC-ES relationships. A danger of circularity exists in such associations, as when
528 crop yield is necessarily associated with agricultural lands, and forest-based recreational services can
529 only be provided by forests.

530 ***3.4 Issues relevant to using cluster analysis for modelling ES associations***

531 Cluster analysis is considered a useful first step when no prior knowledge about existing relationships
532 in a multivariate dataset exists (Bennett et al. 2009; Dheng et al. 2016). However, its exploratory
533 nature makes it unsuitable for understanding causality in ES associations. Cluster analysis requires
534 somewhat subjective decisions including the clustering algorithm and the number of clusters, which is
535 not straightforward (Legendre & Legendre 2012). The clustering solution is also entirely dependent
536 on the input variables, rendering the results ungeneralizable to other regions. In summary, the
537 subjectivity of cluster analysis makes it poorly suited to cross-study comparisons that are required for
538 understanding general socio-ecological causes of ES associations. This will likely have led to the poor
539 congruence between ES-bundles and social-ecological bundles as found in this study (Fig. 5). Maps
540 produced in this way should therefore be used with caution when presented to stakeholders. The ‘air
541 of authority’ (Hauck et al. 2013) imparted by these maps and their associated star diagrams
542 completely mask any uncertainty and could lead to erroneous management decisions.

543 ***3.5 Summary: ES bundles display pattern-based multifunctionality, but not process-based*** 544 ***multifunctionality***

545 The visualisation of relationships among multiple ES is considered a challenge to ES analysts
546 (Birkhofer et al., 2015) and for effectively communicating with policy makers (Crouzat et al. 2015).
547 Maps of ES bundles are therefore useful for visualising the joint spatial distributions of multiple ES.
548 They can be used to identify ‘pattern-based multifunctionality’, the joint supply of multiple ES in
549 space, without regard for the ecological processes underlying the pattern (Mastrangelo et al. 2014),
550 and help guide land management decisions, such as where to allocate urban development or prioritise
551 conservation efforts. This is possible when the scale of analysis (spatial unit type, grain and extent)
552 are close to the desired scale required by key stakeholders (Scholes, et al. 2013). We suggest that

553 analyses that wish to map ES bundles compare multiple scales corresponding to a portfolio of
554 management policies (Qiu et al. 2017), focussing for example on biophysically bounded spatial units
555 such as watersheds of different size (e.g., Qiu and Turner 2013).

556 However, while such correlational analysis is a logical first step in assessing ES associations, it cannot
557 allow for a mechanistic understanding (Bennett et al. 2009). When ES bundles are delineated using
558 correlation at coarse resolutions, with spatial units exhibiting high within-unit heterogeneity in land
559 cover and thus ES, and with each ES mapped at the same resolution and extent, the approach cannot
560 help ES analysts understand general rules of mechanistic relationships between key drivers and ES.
561 They therefore cannot provide ‘process-based multifunctionality’, the joint supply of ES in space
562 caused by well-understood relationships (Mastrangelo et al. 2014). Such a mechanistic understanding
563 of relationships between ES and management will allow the transferral of management
564 recommendations outside the context where data were collected (Birkhofer et al., 2015).

565 **4. A roadmap for predictive mapping of bundles of ecosystem** 566 **services**

567 Determining the cause of a relationship among ES based on studies that track only their spatial
568 concordance is difficult (Bennett et al. 2009). Here, we outline three key requirements for
569 improvements to current approaches to understanding and predicting ES associations. The theme that
570 underlies all these requirements is that studies that aim to explain or predict associations between ES
571 must be designed to have a clear mechanistic basis in order to be confident about any relationships
572 found.

573 **4.1 Requirement 1: Design studies to test specific hypotheses about specific predictors of** 574 **key relationships between key ES of interest.**

575 The quantification and mapping of associations between a wide range of ES including provisioning,
576 cultural, and regulating services, is thought to enable the identification of a diverse range of trade-offs
577 and synergies that might be missed if only individual ES, or a few more commonly quantified ES are
578 considered (Lee & Lautenbach 2016). However, as outlined earlier, differences in the distributions
579 and types of ES found in different regions mean that determining causal drivers of bundles of all
580 available ES is likely impossible.

581 Given the diversity and complexity of drivers that affect different ES, a promising approach for
582 understanding the degree of generality of different predictors of relationships between ES may be to
583 test specific predictions about the importance of specific drivers of relationships of key policy-
584 relevant ES, based on putative mechanistic relationships. For example, a study might set out to test the
585 relative importance of forest management history and forest age in determining the value of multiple
586 ES across heterogeneous stands (as in Sutherland et al. 2016). Such ‘unpacking’ of ES bundles into

587 series of specific, focused studies should enable a bottom-up understanding of ES bundles in a way
588 that studies that consider all ES simultaneously – like this case study – cannot. Mitchell et al's (2015)
589 recent framework and set of specific predictions about how habitat fragmentation will affect ES
590 provides an excellent example of the types of clearly defined questions that are required for a
591 predictive science for ES. The need for formulating specific questions and hypotheses in ES research
592 is also relevant to the generation of policy-relevant knowledge. Indeed, designing problem-oriented
593 ES assessments, which focus on the information demands of decision-makers, can help make ES
594 studies more decision relevant (Förster et al. 2015; Willcock et al. 2016).

595 **4.2 Requirement 2: The testing of specific research questions requires bespoke study** 596 **designs**

597 Observational studies of the relationships between ES and their drivers are unlike experimental
598 studies in that the identity, crossing, replication and interspersions of variables are, by definition,
599 outside the control of the observer (Smart et al. 2012). Careful study designs can help to deal with
600 these challenges and generate meaningful tests of very specific and focused predictions about
601 relationships between ES. Here, ES science should build on the large literature examining the effects
602 of habitat loss and fragmentation on biodiversity (Fahrig, 2003; McGarigal and Cushman's 2002). Of
603 key importance is the need to account for habitat amount before considering effects of habitat
604 configuration when attributing effects. For example, Qiu & Turner (2015) examined whether adding
605 configuration variables could significantly improve the explanatory power of models explaining water
606 quality after accounting for the effect of composition. Using this two-step procedure, they found
607 forests to be more effective at retaining nutrients when more dispersed across subwatersheds.

608 One major consideration in designing studies to test predictors of relationships between ES is the
609 issue of scale (section 3.1). Multi-scale assessments of social-ecological relationships with individual
610 ES are vital to understanding scale-dependent social and ecological processes and causality (Scholes
611 et al. 2013; Eigenbrod, 2016). Multi-scale assessments may not be possible, for example when the
612 highest spatial resolution of the data is the municipality as with census-derived socioeconomic
613 variables (Raudsepp-Hearne et al. 2010, Hamann et al. 2015, Queiroz et al. 2015). Recent
614 developments in downscaling or disaggregating datasets hold promise for higher resolution analyses
615 with available datasets (e.g. Keil & Jetz 2014; Lamboni et al. 2016).

616 **4.3 Requirement 3: Utilize a wider range of statistical and modelling approaches**

617 While statistical techniques cannot compensate for poor study design (e.g. Hurlbert 1984), taking
618 advantage of the best statistical approaches will maximize the inferential strength of a given study
619 design. As such, a predictive science for ES should take advantage of recent advances from ecological
620 modelling including models that take account of biases in data, confounding variables, and
621 mechanistic relationships (e.g. Sugihara et al. 2012; Warton et al. 2015).

622 One approach with potential to provide major insights in refining our hypotheses about how different
623 predictor variables may affect relationships between ES is simulation modelling. For example, the
624 creation of artificial landscapes could enable researchers to control and tease apart variables that are
625 inherently confounded in real landscapes. Such studies have led to major insights in landscape
626 ecology (e.g. With and King 1997; Gardner et al. 1989), macroecology (e.g. Lennon, 2000), but also
627 in our understanding of how landscape structure might affect ES at different spatial scales (Mitchell et
628 al. 2015). Simulation models can also be linked with future scenarios in which effects of changing
629 drivers, such as land-use patterns and climate, on spatial dynamics of ecosystem services are explored
630 (e.g., Carpenter et al. 2015).

631 ***4.4 The use of primary data or process models rather than land cover based proxies***

632 A major issue for understanding causal drivers of relationships between ES is that most available
633 maps of ES are themselves modelled rather than measured. For example, regulating services such as
634 pollination and erosion mitigation are typically and necessarily quantified using models that
635 incorporate causal relationships between social–ecological variables (Martínez-Harms & Balvanera,
636 2012). An element of circularity therefore exists in ours and most other studies from having assessed
637 the relationship between social-ecological variables and modelled surfaces of ES derived from exactly
638 such variables. As such, a true understanding of determinant predictors of ES will only come through
639 increased availability of primary data on actual services rather than LULC surrogates, including from
640 remote sensing (Ayanu et al. 2012) and field studies that measure ES indicators such as water quality
641 and carbon storage. That said, understanding the degree to which widely accessible social-ecological
642 data can be used to predict ES associations, composed of ES that are either data-intensive or complex
643 to model is still useful (Meacham et al. 2016), as it facilitates modelling of such ES associations in
644 data-poor regions.

645 **The consideration of temporal changes in ES and drivers**

646 Inferring interactions from spatial co-occurrence is loosely analogous to a space-for-time substitution in
647 that spatial relationships are used to infer dynamics over time (Tomscha & Gergel, 2016). A major
648 limitation of this approach is that most spatial studies use ES snapshot data to assess ES associations
649 and relationships with drivers. Mismatches in the timing between change in a driver (including
650 demand) and the supply of an ES may cause relationships to be misinterpreted or overlooked,
651 particularly in transitioning landscapes. This can also be due to mismatches in the time series of
652 available datasets. ES are not static but spatially and temporally dynamic in terms of their delivery
653 and associations with other services.; Municipalities have been found to change in the bundles of
654 services they provide over time raising concerns about using snapshots of ES provision to build
655 understanding of ES relationships in complex and dynamic social-ecological systems (Renard et al.
656 2015). Long-term monitoring studies could potentially capture complex long-term ES interactions

657 and help us avoid or minimize trade-offs and adequately track synergies that simultaneously support
658 multiple ES (Tomscha & Gergel, 2016).

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676

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861

862 **Supplementary Information**

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875 **Appendix S1. Ecosystem service data and spatial characteristics of the case study area**

876 The French Alps study region (Figure S1) covers a total of 52,149 km² (SPCA 1991) and is
877 characterised by high variation in biodiversity, ecosystems and ES provision relative to European
878 averages (Tappeiner et al. 2008, Crouzat et al. 2015), typical of mountain regions (Grêt-Regamey et
879 al. 2012). The region is dominated by forests and semi-natural areas (67% of the region), with arable
880 lands mainly concentrated in the western broad valleys and piedmonts (27% of the region), while
881 artificial areas cover only 5% of the region. This leads to a clear distinction, typical for mountain
882 regions, of low elevation high-density urban areas surrounded by intensive agriculture in the valleys,
883 and more isolated rural areas (Tappeiner et al. 2008, Crouzat et al. 2015).



884

885 Figure S1. Location of the French Alps study region in France.

886 We selected nine ES that have been quantified and mapped in the French Alps previously by Crouzat
887 et al. (2015). These are services that were deemed socially, ecologically and economically relevant to
888 the region following consultation with scientists and local collaborators (Crouzat et al. 2015), and
889 include three provisioning (crop, food, wood) three cultural (hunt, rec, tour) and three regulating ES
890 (wqt, cstock, eros; see Table 1 for variable codes). All ES are based on either primary data or bespoke
891 modelled surfaces of ES. Full details of these ES are in Crouzat et al. 2015 and Appendix S1.

892 Within the region, elevation, climate and vegetation gradients have had historical consequences on
893 social dynamics and economic activities, resulting in the common separation into the North (Rhône-
894 Alpes) and the South Alps (Provence-Alps-Côte d'Azur; Crouzat et al. 2015). The social-ecological
895 north-south divide is also recognised by an administrative boundary at the NUTS II level, providing a

896 spatial context that is relevant for decision making. The North and South Alps therefore lend
 897 themselves well to a cross-study comparison.

898 Table S1. Details of ecosystem services modelled in the French Alps case study

ES category	ES	Code	Description	Aggregation to municipality-level
P	Agricultural production	crop	Yields for annual crops, vineyards and orchards (kg ha ⁻¹ year ⁻¹)	Median
P	Forage production	fodd	Yields of pastures, meadows and mountain grasslands (kg dry matter ha ⁻¹ year ⁻¹)	Median
P	Wood production	wood	Potential woody biomass supply for stemwood and logging residues (Gg dry matter km ⁻² year ⁻¹)	Median
C	Recreation potential	rec	Recreation potential for daily recreation (index)	Median
C	Tourism	tour	Territorial capital of rural tourism involving overnight stays (index)	Median
C	Leisure hunting	hunt	Density of shot wild ungulates (number of animals km ⁻² year ⁻¹)	Median
R	Erosion mitigation	eros	Biotic contribution to erosion risk mitigation (classes)	Majority
R	Physical water quantity regulation (wqt)	wqt	Relative water retention enabling flood regulation (index)	Median
R	Carbon storage	csto	Sum of carbon stocks from above-ground and below-ground biomass, dead organic matter and soils (tC km ⁻²)	Median

899

900 **Appendix S2. Delineation of ES bundles across the study regions**

901 ***Methods used to delineate ES bundles***

902 Associations among individual ES were quantified using pairwise correlation coefficients based on
903 Spearman's rho (Fig. S2), as is frequently used to inder relationships between ES (Mouchet et al.
904 2014). We adopted the spatially explicit ES-bundle approach of Raudsepp-Hearne et al. (2010) and
905 used cluster analysis to delineate ES bundles across the N and S of the French Alps. A two step
906 clustering approach was adopted (Turner et al. 2015). To minimise skew and make the ES variables
907 dimensionless and comparable in terms of their magnitudes and variability, Box-Cox transformation
908 (Box & Cox, 1964), centring and scaling was applied. First, a PCA was used to quantify the main
909 multivariate relationships between the ES variables to assess whether ES co-occur in spatial bundles.
910 The number of PCA axes deemed sufficient to characterize the non-random structure in the data in
911 both the N and S ES datasets was selected according to the Kaiser-Guttman criterion, which selects
912 the axes whose eigenvalues are greater than the mean of all eigenvalues (Legendre and Legendre,
913 1998; Turner et al. 2015). For both regions, the first three components were selected and accounted
914 for 61% and 57% of the total variation in ES in the N and S, respectively. As a precursor to cluster
915 analysis, PCA can serve to separate signal from noise and lead to a more stable clustering solution,
916 with the first axes extracting the essential information while the latter are restricted to noise (Husson
917 et al. 2010). Clustering of PCA axes i.e. uncorrelated components also means that correlated services
918 are not counted more than once or more heavily weighted (Turner et al. 2015). We applied *k*-means
919 clustering to the relevant PCA axes to delineate ES bundles with 1000 random starts and 10,000
920 iterations to find a solution with the lowest within-cluster sum of squares according to the relevant
921 PCA axes. *K*-means clusters municipalities so that the composition of ES values are more alike within
922 than between clusters. Three clusters was deemed appropriate for both the N and S datasets according
923 to a hierarchical cluster analysis using Ward's method and squared euclidean distance (with the
924 FactoMineR package; Lê et al. 2008) and qualitative assessment of ES bundles. Following Renard et
925 al. (2015), we quantified the effective number of ES provided in each bundle using a transformation
926 (*H*) of the Gini-Simpson's index (*S*): $H = 1/(1 - S)$, where

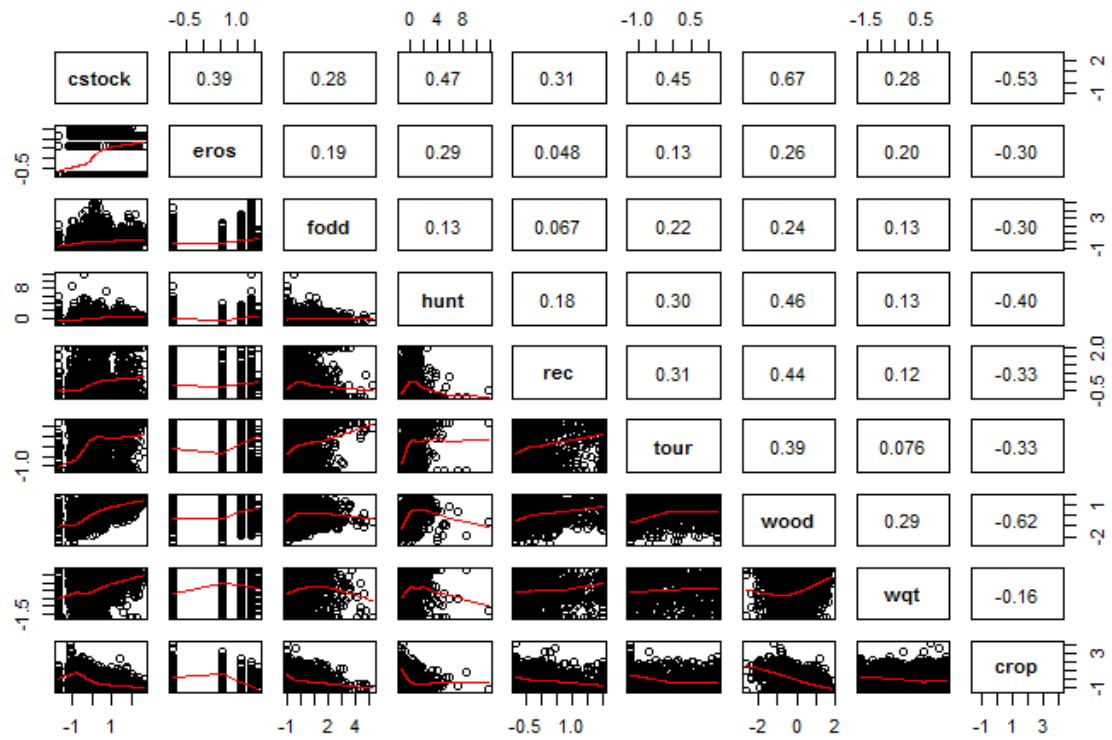
$$927 \quad S = 1 - \sum_{i=1}^N p_i^2$$

928 for a bundle with *N* ES with varying proportions *p* of each service (*i*).

929

930 *Results of correlation and PCA analyses for the North and South Alps*

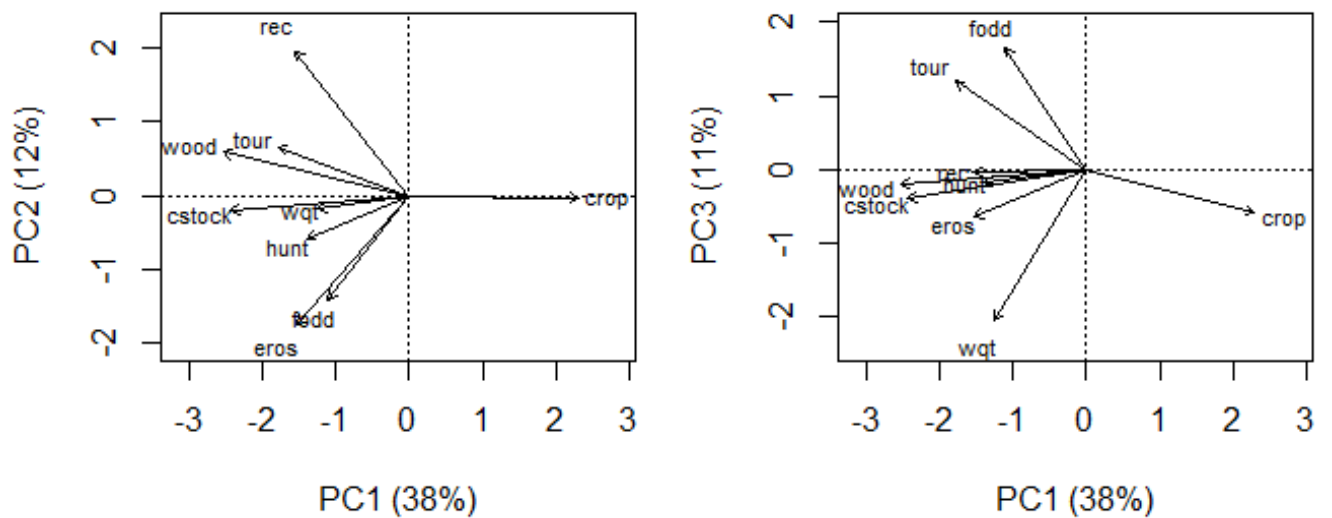
931 *North French Alps*



932

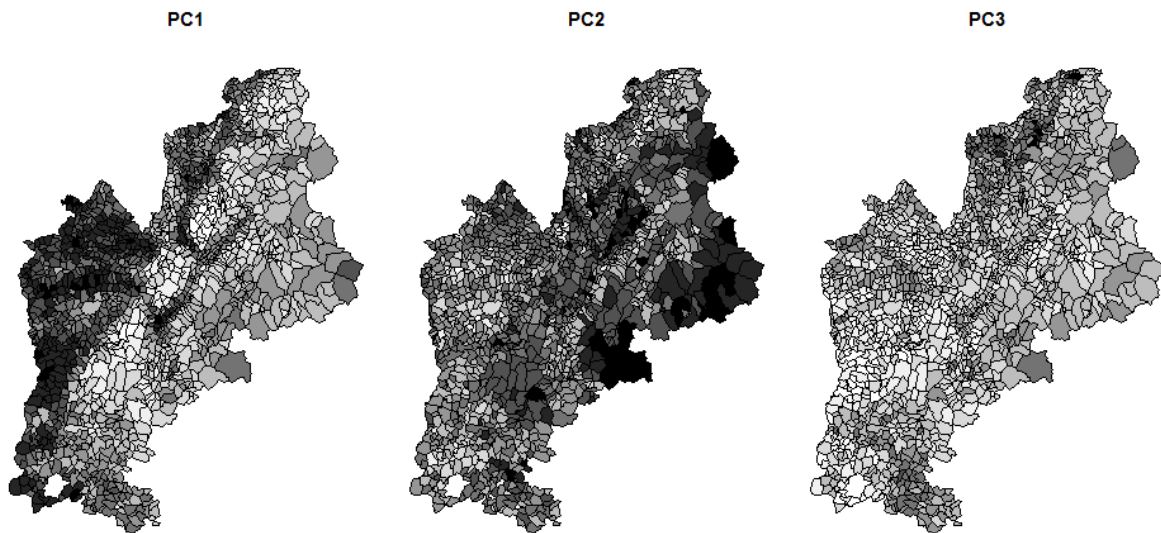
933 Figure S2. Spearman's rank correlation coefficients of pairs of ES across the North French Alps

934



935

936



937

938 Figure S3. Principal component analysis biplot for ES in the North French Alps. The first axis (PC1)
 939 represents a spatial trade-off between crop and most other services, most strongly with wood and
 940 cstock. The second axis (PC2) represents a synergy between high food and eros services, and their
 941 trade-off with rec. The third axis (PC3) represents a synergy between food and tourism, trade-off with
 942 wqt. The angles between ES represent the strength of their correlations. The first three components
 943 accounted for 61% of the total variation in ES.

944

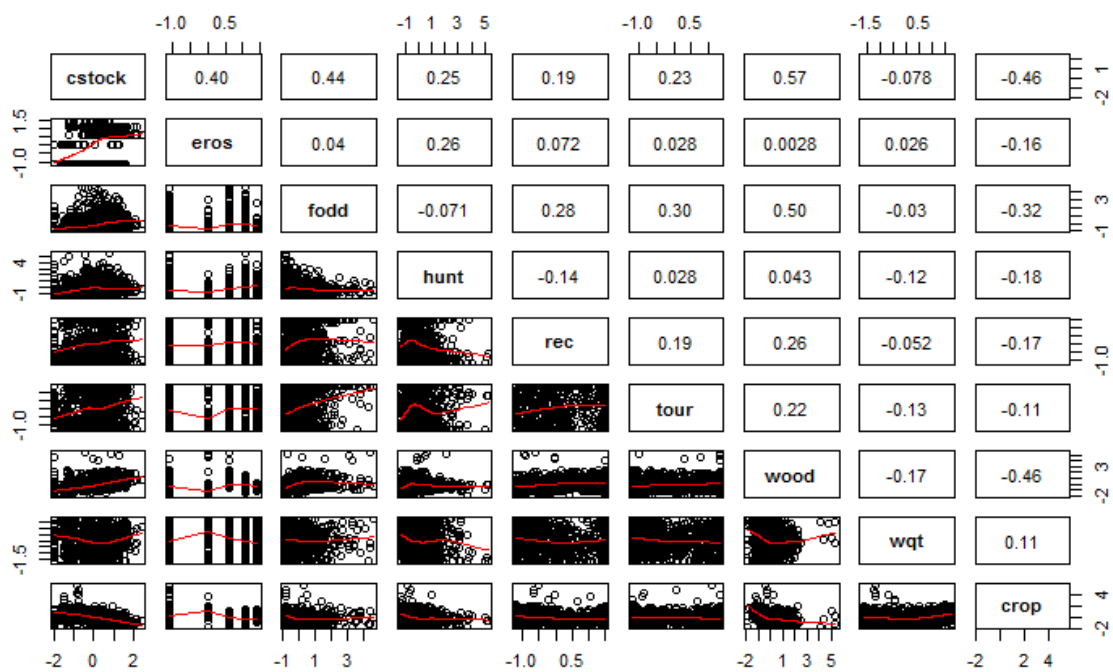
945

946 Table S3. Loadings of ES onto each principal component.

	PC1	PC2	PC3
cstock	-0.44	-0.06	-0.13
eros	-0.28	-0.55	-0.21
fodd	-0.2	-0.44	0.54
hunt	-0.25	-0.18	-0.05
rec	-0.28	0.62	-0.01
tour	-0.33	0.21	0.39
wood	-0.46	0.18	-0.06
wqt	-0.23	-0.06	-0.67
crop	0.42	-0.01	-0.19

947

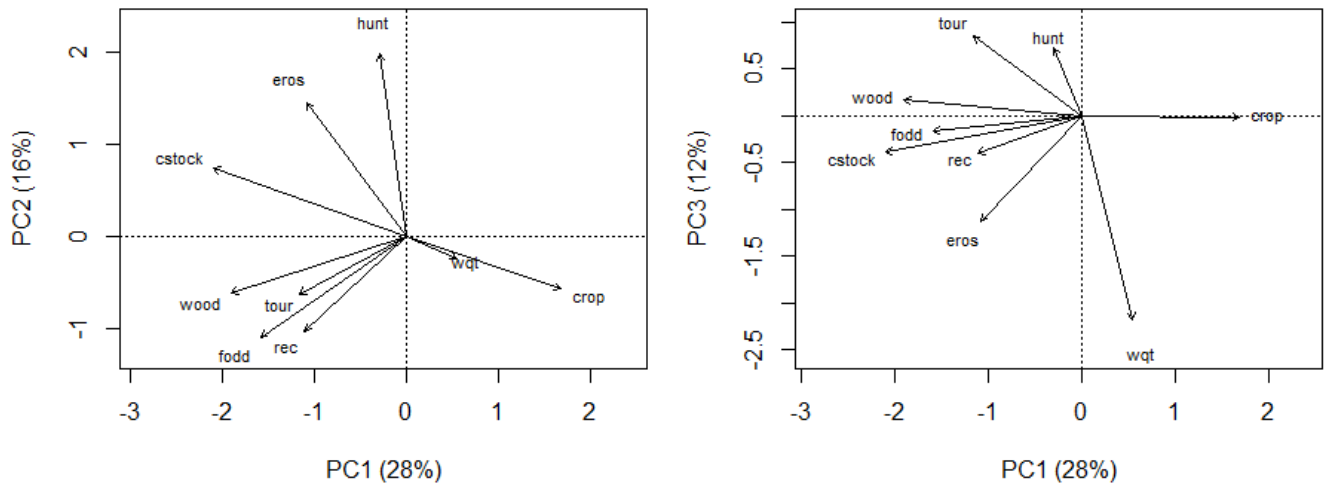
948 **South French Alps**



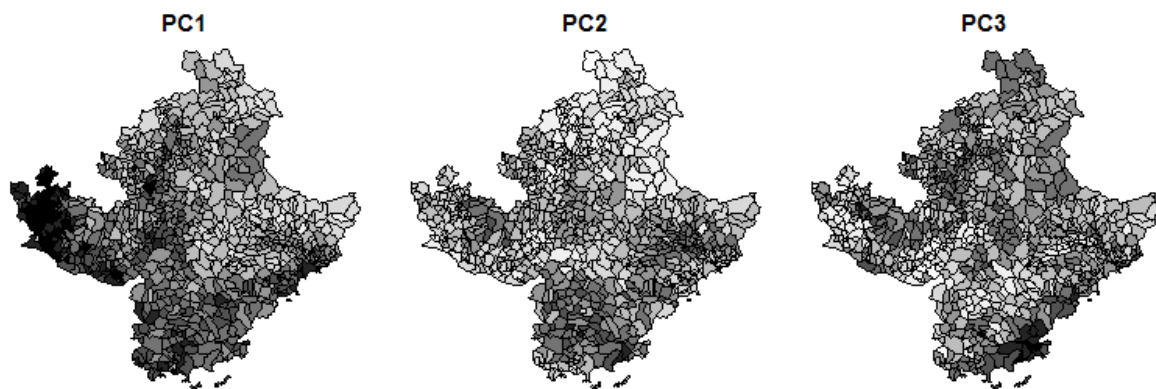
949

950 Figure S4. Spearman's rank correlation coefficients of pairs of ES across the South French Alps

951



952



953

954 Figure S5. Principal component analysis biplot for ES in the South French Alps. The first axis (PC1)
 955 represents a spatial trade-off between crop and most other services, most strongly with wood, fodd
 956 and cstock. The second axis (PC2) is highly descriptive of the distribution of hunt, and its synergy with
 957 eros. The third axis (PC3) represents a synergy between hunt and tourism, trade-off with wqt. The
 958 angles between ES represent the strength of their correlations. The first three components accounted
 959 for 57% of the total variation in ES.

960 Table S4. Loadings of ES onto each principal component.

	PC1	PC2	PC3
cstock	-0.50	0.23	-0.14
eros	-0.26	0.46	-0.41
fodd	-0.38	-0.35	-0.06
hunt	-0.07	0.63	0.26
rec	-0.27	-0.33	-0.15
tour	-0.28	-0.20	0.31
wood	-0.45	-0.20	0.06
wqt	0.13	-0.08	-0.79
crop	0.40	-0.18	-0.01

961 **Appendix S3. Identification of social-ecological variables important in discriminating**
 962 **between ES bundles**

963 Table S2 gives the initial list of candidate variables deemed important for explaining ES co-variation,
 964 after consulting with the literature.

965 Table S2. Details of social-ecological variables that are potentially important in distinguishing
 966 amongst ES bundles in the French Alps.

Social-ecological variable	Code	Description	Unit	Source
Agricultural land	agric	Municipality land area occupied by area classed as agricultural	%	CORINE
Grazing land	grass	Municipality land area occupied by area classed as grassland and pastures	%	CORINE
Forest land	forest	Municipality land area occupied by area classed as forest	%	CORINE
Urban land	urban	Municipality land area occupied by area classed as urban	%	CORINE
Open semi-natural land	semi	Municipality land area occupied by area classed as semi-natural, other than forest	%	CORINE
Protected area coverage	natura	The percentage of area covered by Natura 2000 sites designated by EU Member States under the Birds Directive (79/409/EEC) and the Habitats Directive (92/43/EEC)	%	EEA database
Elevation	elev	Derived from ASTER global digital elevation model	m	Global digital elevation model (DEM) derived from GTOPO30.
NPP	npp	Potential NPP	tC/m ² /yr	Haberl et al., 2007
Biodiversity	plant	Species richness of plants	Species richness	Maiorano et al., 2013
Annual mean temperature	bio1	Annual mean temperature for the 1950-2000 period	°C	WorldClim Global Climate Data Hijmans et al., 2005
Annual precipitation	bio12	Annual trends of precipitation for the 1950-2000 period	mm	WorldClim Global Climate Data Hijmans et al., 2005

Population density	Population density per square kilometre obtained by dividing the municipality population size by its area	Inhabitants/km ² INSEE
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967 ***Protected area coverage (natura)***

968 Protected area coverage was calculated by taking the percentage of total land area of each
969 municipality occupied by Natura 2000 sites. Natura 2000 is an ecological network composed of sites
970 designated under the Birds Directive (Special Protection Areas, SPAs) and the Habitats Directive
971 (Sites of Community Importance, SCIs, and Special Areas of Conservation, SACs). Shapefiles for the
972 most recently available year (2014) were used (available from [http://www.eea.europa.eu/data-and-](http://www.eea.europa.eu/data-and-maps/data/natura-6)
973 [maps/data/natura-6](http://www.eea.europa.eu/data-and-maps/data/natura-6)).

974 ***Agricultural land (agric)***

975 Agricultural land was calculated by taking the percentage of total land area of each municipality
976 occupied by area classed as agricultural by CORINE.

977 ***Grazing land (grass)***

978 Grazing land was calculated by taking the percentage of total land area of each municipality occupied
979 by area classed as grasslands or pastures by CORINE.

980 ***Forested land (forest)***

981 Forest land was calculated by taking the percentage of total land area of each municipality occupied
982 by area classed as forest by CORINE.

983 ***Urban land (urban)***

984 Urban land was calculated by taking the percentage of total land area of each municipality occupied
985 by area classed as urban by CORINE.

986 ***Open semi-natural (semi)***

987 Open semi-natural land was calculated by taking the percentage of total land area of each municipality
988 occupied by area classed as semi-natural, other than forest by CORINE.

989 ***Elevation (elev)***

990 Elevation values at 30-m resolution were taken from ASTER global digital elevation model raster
991 files (GTOPO30; available at <https://asterweb.jpl.nasa.gov/gdem.asp>). The median value for each
992 municipality was used.

993 ***Mean annual temperature (bio1)***

994 We used the mean annual mean temperature (°C) for the 1950-2000 period using the variable ‘bio1’
995 from WorldClim Global Climate Data (Hijmans et al., 2005). The median value for each municipality
996 was used.

997 ***Annual precipitation (bio12)***

998 Annual trends of precipitation for the 1950-2000 period in mm. ‘bio12’ from the WorldClim Global
999 Climate Data (Hijmans et al., 2005). The median value for each municipality was used.

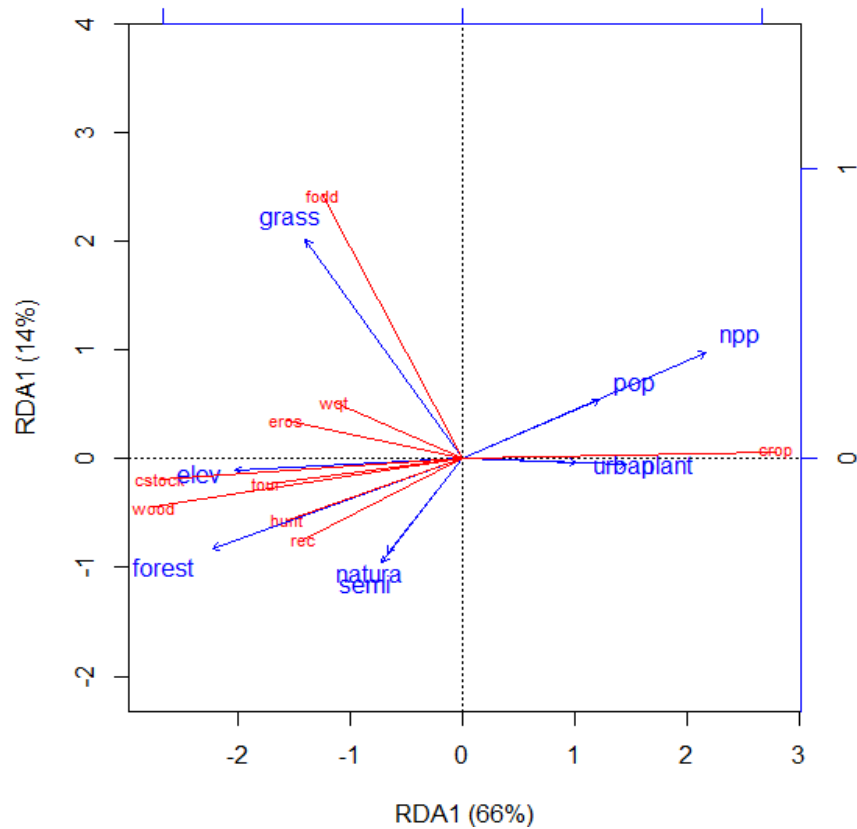
1000 ***Population density (pop)***

1001 We used the log of population density per square kilometre, obtained by dividing the municipality
1002 population size by its area. Data were compiled for the most recently available year (2007) (INSEE).

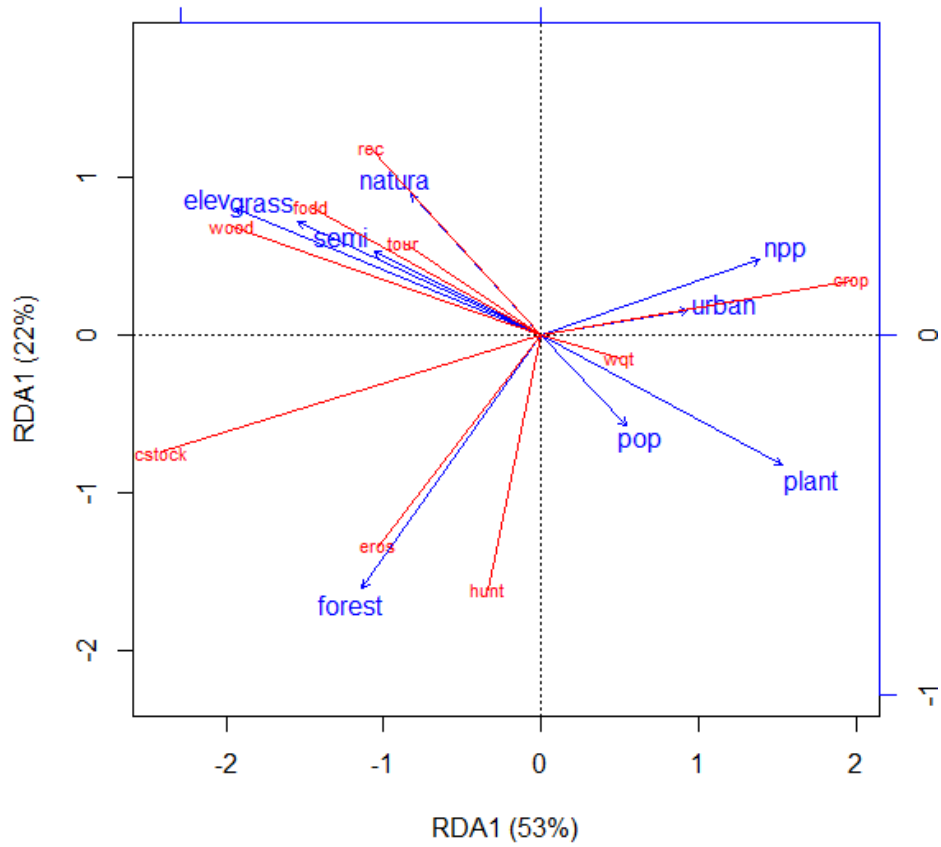
1003 ***Details of redundancy analysis used to select social-ecological variables important in***
1004 ***explaining covariation of ES***

1005 We initially considered all of the variables included in Table S2 for explaining covariation in ES. We
1006 inspected pairwise correlations between the variables and removed variables with correlation
1007 coefficients of >0.80 to reduce multicollinearity (bio1 and bio12). We then computed a global RDA
1008 with the remaining potential candidate variables: agric, forest, grass, semi, urban, pop, elev, natura
1009 and plant (see above for variables codes). Linear dependencies were further explored by computing
1010 variables’ variance inflation factors (VIF) for the global model. For both the North and South
1011 analyses, the variable agric (proportion of land area covered by agriculture) was not included in the
1012 global models to reduce variance inflation factors (all below 5 for the global models without agric).
1013 Forward selection using the packfor package (Dray et al. 2007) was run on the global model to select
1014 social-ecological variables important in explaining variation in ES. This procedure selects the model
1015 with the combination of variables with the highest R^2 and p -value (Legendre and Legendre, 2012).

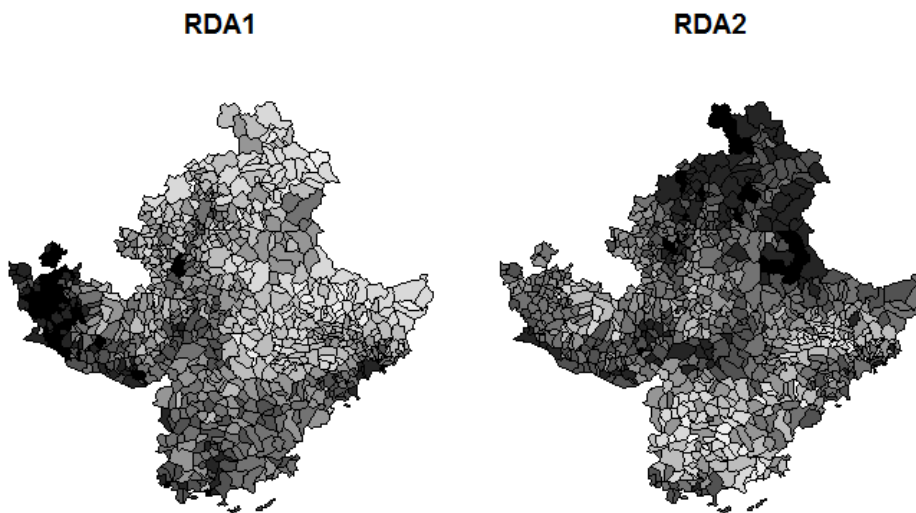
1016



1020 Figure S6. Redundancy analysis triplot of nine ES (red) constrained by the social-ecological variables
 1021 (blue) across the North French Alps, scaling 2. The bottom and left-hand scales are for the ES, the
 1022 top and right-hand scales are for the social-ecological drivers. The angles in the plot between ES and
 1023 social-ecological variables, and between ES themselves, represent the strength of their correlations.



1025



1026

1027 Figure S7. Redundancy analysis triplot of nine ES (red) constrained by the social-ecological variables
 1028 (blue) across the southern French Alps, scaling 2. The bottom and left-hand scales are for the ES, the
 1029 top and right-hand scales are for the social-ecological drivers. The angles in the plot between ES and
 1030 social-ecological variables, and between ES themselves represent the strength of their correlations.

1031

1032 **Appendix S4. Supplementary discussion of case study results**

1033 Here we discuss the correspondence between bundles of social-ecological variables and ES bundles, as
1034 revealed by RDA and cluster analysis, in order to test the extent to which social-ecological variables
1035 could be relevantly used in the French Alps to explain and predict ES bundles. Based on the qualitative
1036 interpretation of RDA site scores and cluster distribution, and expert knowledge, we show that results
1037 of cluster analysis are contrasted when comparing North to Southern Alps.

1038 In the North Alps, ESB1(N) is characterised by a high level of crop production and a below-average
1039 level of supply for all other ES (Fig. 2). Spatially, this bundle is clustered over the broadest lowland
1040 valleys and the fringe of the external Alps (Figures 2 and S6). This appears very consistent with its
1041 broad overlap with SEB1(N) (Fig. 5), where agricultural and artificial areas are overrepresented (Fig.
1042 4). ESB2(N) presents opposite patterns, as all ES are supplied at above-average levels except crop
1043 production which is supplied far below-average (Fig. 2). In particular, this bundle supplies the highest
1044 regional levels of forest-related ES (carbon stocks, erosion mitigation and wood stocks). This is
1045 coherent with its large overlap with SEB2(N) (Fig. 4), where forested areas are overrepresented
1046 compared to the two others (Fig. 4). In between, ESB3(N) supplies an average level of most ES except
1047 those specific to bundles ESB1(N) and ESB3(N) (Fig. 2). ESB3(N) is essentially concentrated over
1048 areas of intermediate altitude of the external Alps (e.g., the Chartreuse range), which can be captured
1049 at municipal scale as mosaic areas containing a mix of forests, grasslands, built-up and semi-natural
1050 open areas. This could explain the mixed overlap of ESB3(N) with the three SEB identified for the
1051 North Alps (Fig. 4).

1052 In the Southern Alps, ESB2(S) is characteristic of rural mosaic landscapes of the internal Alps,
1053 comprising forested and open areas at generally high altitudes (Figs 2 and S6). It supplies the highest
1054 regional levels of numerous ES, in particular fodder production and wood production, recreation and
1055 tourism, and carbon stocks (Fig. 2). This is consistent with its large overlap with SEB2(S) (Fig. 4),
1056 which over-represents high altitude grasslands and also contains a regional average level of forested
1057 areas (Fig. 4). ESB3(S) is a rich and diverse bundle as it supplies an average level of most ES, and the
1058 highest regional levels of erosion mitigation and leisure hunting in particular (Fig. 2). This high
1059 multifunctionality could be related to its heterogeneous spatial patterns, as inferred by the large
1060 combined overlaps of ESB3(S) with both SEB1(S) and SEB2(S) (Fig. 5), i.e. with areas of low to
1061 average elevations with contrasting land use features (Fig. 4). ESB1(S) echoes ESB1(N) in the North
1062 Alps and is characterised by a high level of crop production and an under-average level of supply for
1063 all other ES (Fig. 2). This mono-functional bundle is broadly located in the main intensive agricultural
1064 and urbanized valleys (Rhône and Durance rivers) but poorly overlaps with the Southern SEBs (Fig. 4).

1065 Overall, we highlight a discrepancy in our ability to understand, and further predict, ESBs from SEBs
1066 in comparing the results from the North versus the Southern Alps. We hypothesize that this could be

1067 linked to discrepancies in the clustering patterns between ES and social-ecological variables in these
1068 two regions, as captured at municipal scale. The North Alps can be characterised with easily
1069 distinguishable entities in terms of ES and ecological variables at the municipal scale, relying on
1070 aggregated land use and biophysical patterns (e.g., internal versus external Alps, large contrasts in terms
1071 of elevation and land uses). In contrast, the Southern Alps, and in particular the Southern pre-Alps, have
1072 more heterogeneous landscapes. Such landscapes are composed by a fine-grained mosaic of open spaces
1073 (pastures) and secondary forests, related to ecological secondary succession after agricultural
1074 abandonment (post World War II) (Hinojosa et al. 2016). We hypothesize that SEBs at municipal scale
1075 are too coarse in these heterogeneous landscapes for being predictive of aggregated ES. SEBs in the
1076 Southern Alps can be considered as a typology of land cover types, combined with elevation, and these
1077 appear not sufficient for predicting ES bundles in municipalities characterized by a high landscape
1078 heterogeneity – especially in the southern Pre-Alps (northwestern part of the map). ES were initially
1079 modelled at a finer resolution (1-km) and then aggregated at municipal scale to be coherent and
1080 comparable with SE variables. But in heterogeneous landscapes, the effect of fine landscape patterns
1081 on ES supply might not be negligible (Mitchell et al. 2015), explaining why SEBs at municipal scale
1082 cannot be good predictors of ESB. These results point to a discrepancy between the municipal scale
1083 required for many SE variables (in particular social ones), and the finer scale required for understanding
1084 ecological processes and ES patterns. As a conclusion, while the SEBs identified could be relevant
1085 predictors of ESBs at municipal scale in aggregated and contrasted landscape types as in the North Alps,
1086 they appear insufficiently comprehensive for heterogeneous areas as in the Southern Alps.

1087

1088