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Emilie Crouzat, M. Mouchet, F. Turkelboom, Coline Byczek, Jeroen Meersmans, F. Berger, P.J. Verkerk, S. Lavorel

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AUTHORS

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1 **Assessing bundles of ecosystem services from regional to landscape scale: insights from**
2 **the French Alps**

3 *Authors:*

4 - Emilie Crouzat^{1*} (emiliecrouzat@gmail.com)

5 - Maud Mouchet^{1,2} (maud.mouchet@mnhn.fr)

6 - Francis Turkelboom³ (Francis.TURKELBOOM@inbo.be)

7 - Coline Byczek¹ (coline.byczek@gmail.com)

8 - Jeroen Meersmans⁴ (J.Meersmans@exeter.ac.uk)

9 - Frederic Berger⁵ (Frederic.Berger@irstea.fr)

10 - Pieter Johannes Verkerk⁶ (hans.verkerk@efi.int)

11 - Sandra Lavorel¹ (sandra.lavorel@ujf-grenoble.fr)

12 ¹ Laboratoire d'Ecologie Alpine, CNRS, Université Grenoble Alpes, Grenoble, France

13 ² UMR 7204 MNHN-UPMC-CNRS Conservation des Espèces, Restauration et Suivi des
14 Populations, Paris, France

15 ³ Research Institute for Nature and Forest (INBO), Brussels, Belgium

16 ⁴ Department of Geography - College of Life and Environmental Sciences - University of
17 Exeter, UK

18 ⁵ Irstea, National Research Institute of Science and Technology for Environment and Agri-
19 culture, Grenoble, France

20 ⁶ European Forest Institute, Sustainability and Climate Change Programme, Yliopistokatu 6,
21 80100 Joensuu, Finland

22 * Corresponding author

23 Emilie CROUZAT

24 LECA – BP 53, 2233 rue de la Piscine, 38041 Grenoble Cedex 9, France

25 emiliecrouzat@gmail.com

26 tel: +33 4 76 63 54 38 / fax: +33 4 76 51 42 79

27 *Running title:* Multi-scale ecosystem service assessment

28

29 **Summary**

- 30 1. Assessments of ecosystem services (ES) and biodiversity (hereafter ecological
31 parameters) provide a comprehensive view of the links between landscapes,
32 ecosystem functioning and human well-being. The investigation of consistent
33 associations between ecological parameters, called bundles, and of their links to
34 landscape composition and structure is essential to inform management and policy, yet
35 it is still in its infancy.
- 36 2. We mapped over the French Alps an unprecedented array of 18 ecological parameters
37 (16 ES and two biodiversity parameters) and explored their co-occurrence patterns
38 underpinning the supply of multiple ecosystem services in landscapes. We followed a
39 three-step analytical framework to: i) detect ES and biodiversity associations relevant
40 at regional scale; ii) identify clusters supplying consistent bundles of ES at sub-
41 regional scale and iii) explore the links between landscape heterogeneity and
42 ecological parameter associations at landscape scale.
- 43 3. We used successive correlation coefficients, overlap values and self-organizing maps
44 to characterize ecological bundles specific to given land cover types and geographic
45 areas of varying biophysical characteristics and human uses at nested scales from
46 regional to local.
- 47 4. The joint analysis of land cover richness and ES gamma diversity demonstrated that
48 local landscape heterogeneity alone did not imply compatibility across multiple
49 ecosystem services, as some homogeneous landscape could supply multiple ecosystem
50 services.
- 51 5. *Synthesis and applications.* Bundles of ecosystem services and biodiversity parameters
52 are shaped by the joint effects of biophysical characteristics and of human history. Due
53 to spatial congruence and to underlying functional interdependencies, ecological

54 parameters should be managed as bundles even when management targets specific
55 objectives. Moreover depending on the abiotic context the supply of multiple
56 ecosystem services can arise either from deliberate management in homogeneous
57 landscapes or from spatial heterogeneity.

58

59 **Keywords**

60 Biodiversity, biophysical assessment, ecosystem service association, synergy and trade-off,
61 landscape heterogeneity, natural resources policy, multi-scale assessment

62 **Introduction**

63 The links between landscapes, ecosystem functioning and human well-being, as captured by
64 the ecosystem service concept, have emerged as a powerful bridge between science and
65 policy (Perrings *et al.* 2011). Relationships between ecosystem services (hereafter ES), as
66 well as between ES and biodiversity, can be understood by identifying which co-vary
67 positively or negatively. Evaluating their repeated associations goes beyond the assessment of
68 a static snapshot and enables assessment of “synergies”, that can be actively stimulated, and
69 “trade-offs”, that should be anticipated and limited, respectively (Raudsepp-Hearne, Peterson
70 & Bennett 2010, Mouchet *et al.* 2014; Verkerk *et al.* 2014). In particular, the consistent
71 associations in time and/or space between multiple services, known as “bundles” of ES
72 (Raudsepp-Hearne, Peterson & Bennett 2010), differentiate areas supplying the same
73 magnitude and types of ES as a result of a shared socio-ecological profile. Considering ES
74 bundles in natural resources management is thus ecologically relevant and should facilitate
75 the communication of the complexity of ecological interactions to stakeholders (Van der Biest
76 *et al.* 2014).

77 ES assessments increasingly use the concept of so-called “landscape multifunctionality”,
78 understood as “the capacity of a landscape to simultaneously support multiple benefits to
79 society from its interacting ecosystems”, relying on the “joint supply of multiple ES at the
80 landscape level” (Mastrangelo *et al.* 2014). Landscape heterogeneity closely links to supply of
81 multiple ecosystem services (Brandt 2003) and appears ‘easy to access’ for scientists and
82 ‘easy to grasp’ for stakeholders (Latterra, Orúe & Booman 2012). Yet, the extent and
83 generality of spatial or functional associations between landscape heterogeneity and multiple
84 ecosystem services are still debated (Anderson *et al.* 2009; Mastrangelo *et al.* 2014). In this
85 context, a better understanding of associations among ES and of their relationship to spatial

86 patterns of underlying biophysical variables is needed for more effective land allocation and
87 management (Briner *et al.* 2013).

88 To progress in this endeavour, Mastrangelo *et al.* (2014) proposed two alternative perspectives
89 on “landscape multifunctionality”. First, spatial approaches can detect pattern-based
90 multifunctionality. Often focusing on land cover, they identify bundles from spatial
91 coincidence and can guide spatial planning and priority setting. However, no fine
92 understanding of ecological processes and interactions is gained. Second, functional and
93 spatio-functional approaches can detect process-based multifunctionality. Both approaches are
94 explicit model drivers of individual ES, the latter being additionally spatially explicit. They
95 increase the ecological understanding of relationships between ES and can support optimal
96 management solutions balancing their supply levels. The availability of ecological data and
97 models guides the choice between these three approaches. Other approaches exist but require
98 stakeholder involvement, which was beyond the scope of this study.

99 In this study in the French Alps, we applied a spatial approach for a pattern-based assessment
100 of the supply of multiple ecosystem services at regional scale. Of the several ES assessments
101 in mountain regions (reviewed by Grêt-Regamey, Brunner & Kienast 2012), several have
102 highlighted the role of spatial heterogeneity resulting from natural and human factors (Briner
103 *et al.* 2013) for supporting multiple ecosystem services (Grêt-Regamey, Brunner & Kienast
104 2012). The European Alps encompass a high diversity of ecosystems, species and landscapes,
105 due to broad and often steep gradients of topography, soils, altitude and climate (Tappeiner,
106 Borsdorf and Tasser 2008). Within their range, a long history of human–nature interactions
107 has shaped cultural landscapes (EEA 2010), and so influenced ecological functioning. This
108 directly affects the many ES supplied to their population and to many living beyond them
109 (EEA 2010). Yet, in-depth joint biophysical assessments of ES and biodiversity are still scarce
110 (Grêt-Regamey, Brunner & Kienast 2012).

111 To address this need, we explored the following hypotheses: i) different bundles of ecological
112 parameters can be identified and linked both to diverse biophysical conditions and to land
113 allocation and management choices, and ii) heterogeneous landscapes provide richer sets of
114 ES than homogeneous ones. For this, we mapped an unprecedented array of 16 ES and two
115 biodiversity parameters (regrouped as ecological parameters henceforth) using ecological
116 models. We then analysed their joint variations as an expression of the supply of multiple
117 ecosystem services, and lastly explored and characterized their spatial patterns at various
118 scales from the entire region to the landscape.

119 Figure 1 summarizes our research questions and analytical framework following the three-
120 step framework by Mouchet *et al.* (2014) to: i) detect ES and biodiversity associations
121 relevant at regional scale; ii) identify clusters supplying similar bundles at sub-regional scale
122 and iii) explore the links between landscape heterogeneity and ecological parameter
123 associations at landscape scale. This third step analysed both how ecological bundles overlap
124 with dominant land cover types, and how ES diversity relates to landscape heterogeneity. We
125 explicitly related all analyses to potential application by discussing their scale-specific
126 relevance to stakeholders concerned with natural assets in the French Alps.

127 **Materials and methods**

128 **Study region**

129 Our analysis focused on the French Alps as defined by the Alpine Convention (SPCA 1991)
130 covering 52 149 km² over the western part of the Alpine arc. The complex topography formed
131 by Tertiary tectonic activity followed by glaciations encompasses elevations from below 100
132 m to 4810 m (Mont Blanc). Latitudinal climate and vegetation gradients have had historical
133 consequences on social dynamics and economic activities, resulting in the common separation
134 into the northern and the southern Alps. A secondary longitudinal climatic and geological
135 gradient runs from the western Atlantic influence, known as the Prealps, to continental
136 climate in the inner Alps. This geographic diversity is responsible for the high variety of
137 biodiversity, ecosystems and ES across the entire area compared to European averages
138 (Tappeiner, Borsdorf & Tasser 2008).

139 Based on Corine Land Cover 2006 Level 1 categories (EEA 2012), the French Alps are
140 dominated by forests and semi-natural areas (67% of the region). Arable lands are mainly
141 concentrated in the western broad valleys and piedmonts (27% of the region), while artificial
142 areas cover only 5% of the region. This leads to a clear distinction between high-density
143 urban areas surrounded by intensive agriculture in the valleys and more isolated or higher
144 rural areas (Tappeiner, Borsdorf & Tasser 2008).

145 **Modelling and mapping ecological parameters**

146 **Selection of ecological parameters: ES and biodiversity**

147 Following consultation with scientists and local collaborators, we selected four provisioning,
148 five cultural and seven regulating ES, and two biodiversity parameters (plant and vertebrate
149 diversity), encompassing most services relevant to the region from ecological, social and
150 economic points of view (Table 1).

151 **Modelling ecological parameters**

152 Depending on model and data availability, the 18 ecological parameters were modelled using
153 methods ranging from disaggregation of public statistics (e.g. hunting statistics) to process-
154 based models (e.g. STREAM for hydrological properties; Stürck, Poortinga & Verburg 2014)
155 and analytical models (e.g. RUSLE for erosion losses; Bosco *et al.* 2009) (Table 1). To allow
156 joint analysis, all ecological parameters were rescaled to a 1km × 1km resolution, through
157 aggregation of finer-scale process information (e.g. protection against gravitational hazards)
158 or downscaling of coarser statistical information (e.g. leisure hunting). Appendix S1.A in
159 Supporting Information provides standardized descriptions for all ecological parameters
160 (Crossman *et al.* 2013), with additional information on methods and data sources following
161 Martínez-Harms & Balvanera (2011).

162 Our selection comprised both potential values for ecosystem parameters, based on the natural
163 capacity of ecosystems, and actual values, considering the actual benefits to society (Van der
164 Biest *et al.* 2014). The observed association between parameters does not necessarily imply
165 that they are actually supplied jointly, but merely that the ecosystem has the potential for
166 supplying both. For instance, an association between potential plant habitat and actual crop
167 production would not mean that croplands host a high biodiversity, but only that natural
168 conditions suitable for growing crops are also conducive to plant diversity, whether
169 agricultural practices support their actual coexistence or not. Additionally, three types of
170 parameters were combined depending on their nature and data availability: stock (e.g. number
171 of species km⁻²), flow (e.g. tons of wood harvested year⁻¹) or status (e.g. relative capacity to
172 buffer floods).

173 Land cover categories used to analyse the joint occurrence of ecological parameters were
174 those of Corine Land Cover 2006 (CLC 2006) aggregated at 1km × 1km to match the
175 resolution of ES data. For altitude we used the 50-m French digital elevation model BD-

176 ALTI[®] IGN.

177 **Statistical analyses**

178 Spatial data processing was done using ArcGIS 10.0 and statistical calculations were carried
179 out using the statistical software R 2.15.

180 After an initial standardization and normalization phase, data analyses followed three
181 successive steps aiming to: i) detect consistent associations between ecological parameters at
182 regional scale, ii) identify clusters at sub-regional scale and describe their spatial patterns and
183 geographical determinants, and iii) explore the links between landscape and ecological
184 parameter local associations. Two points need attention for the interpretation of results. First,
185 we insist that the bundles we detected rely on spatial coincidence rather than on identification
186 of common functional drivers. Second, as we considered jointly potential and actual ES
187 parameters, associations do not necessarily reflect synergies and can even relate to conflicts as
188 further discussed below.

189 **Data transformation**

190 As ecological parameters had different units and scales (Table 1), we made the range and the
191 variability of values comparable across variables by rescaling each data set to a common,
192 unitless [0–1] interval by subtracting from each value the minimum value observed for the
193 data set and then dividing by the difference between the observed maximum and minimum
194 values (Paracchini *et al.* 2011).

195 Although normality of the data sets was not required since we did not perform any parametric
196 test, we limited skewed variances that could respond heterogeneously to statistical analyses
197 by logarithm or square-root transformation after visual examination of the frequency
198 distribution.

199 Finally, binary presence and absence data sets were obtained with a threshold at third quartile
200 after removing zero values, chosen following a comparison with thresholds at first quartile
201 and median (results not shown).

202 In the presentation of results for the following analyses, we comment on only the 15% largest
203 values to focus on prominent features, resulting in specific thresholds for Pearson coefficients,
204 overlap ratio and Chi² test residuals.

205 **Step 1: Detecting consistent associations at regional scale**

206 Two complementary analyses were used to detect consistent associations between ecological
207 parameters at regional scale (Egoh *et al.* 2009).

208 First, we used Pearson's coefficients to test positive and negative associations between pairs
209 of ecological parameters at the scale of the entire study area.

210 Second, spatially consistent associations between pairs of ecological parameters considered as
211 binary presence / absence were detected using an overlap index (Gos & Lavorel 2012). For
212 pixels with "present" ecological parameters, we calculated the fraction O of pixels in the
213 smaller data set that overlapped with the second one. O can vary from 0 (no overlap) to 1 (all
214 cells of the smallest data set overlapping with the second one).

215 **Step 2: Identifying clusters at sub-regional scale**

216 In order to explore sub-regional ES associations (Anderson *et al.* 2009), we used Kohonen's
217 algorithms to build a Self-Organizing Map (SOM) delineating five clusters of pixels with
218 specific ecological profiles, each supplying a consistent bundle of ES. The number of clusters
219 represented the best compromise between analysis complexity and interpretability. We
220 analysed their geographic distributions, altitude and land cover patterns.

221 **Step 3: Exploring links with land cover at landscape scale**

222 Links between ecological parameters and landscape were investigated by: i) the overlaps
223 between individual ecological parameters and dominant land cover types, and ii) the relation
224 between ES diversity and landscape heterogeneity.

225 High value clusters for individual ecological parameters and land cover types were detected
226 with ArcGIS Hot Spot Analysis tool parameterized to calculate Getis-Ord G_i^* statistics using
227 the “Distance Band or Threshold Distance” cut-off to a window of $3 \text{ km} \times 3 \text{ km}$. Significant
228 P -values were returned when observed spatial clustering was greater than expected for a
229 random distribution, avoiding the selection of isolated pixels of high values or outliers. Each
230 variable was then transformed into a binary data set, attributing a value of 1 for clusters with
231 z -scores significant at 10% minimum and 0 otherwise. Pairwise overlap analysis detected
232 spatial matches between clusters of high value for ecological parameters and for land cover
233 types.

234 Local landscape heterogeneity and ES diversity were assessed by assigning to the central
235 pixel of a moving $3 \text{ km} \times 3 \text{ km}$ window the number of unique land cover types (ArcGIS Focal
236 Statistics tool with the “Variety” option) and the number of distinct ES (equivalent to a
237 gamma index). In the absence of socially relevant thresholds, the distributions of these two
238 variables were split between high and low values according to the median, leading to four
239 possible combinations of low or high landscape heterogeneity and gamma index. Chi^2 tests
240 were used to detect major divergences between actual distributions of altitude and land cover
241 type in the different combinations, compared with their frequencies over the whole French
242 Alps taken as null model (Chi^2 tests significant at 5%, deviation of residuals greater than 10).
243 Pairwise overlaps between pixels from the four categories and distributions of specific ES
244 were also tested.

245

246 **Results**

247 **Associations at regional scale**

248 Results from Pearson coefficients (Appendix S2.A) and pairwise overlap analysis (Appendix
249 S2.B) were highly consistent, showing some strong positive associations among ecological
250 parameters and with specific land cover types (Appendix S2.D). Based on these we identified
251 three bundles (Figure 2). Bundle A encompassed multiple positive associations among three
252 ES overlapping with agricultural areas: crop production, plant diversity and maintenance of
253 water quality, the latter being also associated with hydro-energy production. Bundle A was
254 negatively correlated to cultural ES (plant diversity vs. recreation and tourism, and crop
255 production vs. recreation). Bundle B encompassed multiple positive associations among three
256 ES overlapping with forests: wood production, carbon storage and regulation of water
257 quantities. Wood production and carbon storage were also correlated with vertebrate diversity,
258 while carbon storage was additionally correlated with erosion mitigation. Bundle B also
259 overlapped with protection against rockfalls and recreation. The negative correlation between
260 carbon storage and plant diversity resulted in a negative association between bundles A and B.
261 Bundle C encompassed multiple positive associations among biological control, protected
262 vertebrate diversity and vertebrate diversity, the latter also presenting a positive correlation to
263 bundle B (with wood and carbon storage). Bundle C also incorporated erosion mitigation
264 through its overlap with biological control. Lastly, protected plant diversity, which positively
265 overlapped with bundle A through plant diversity, correlated negatively with both bundles B
266 (through wood production and carbon storage) and C (through vertebrate diversity and
267 biological control).

268 Regarding land cover, although some groups of ecological parameters were tightly associated
269 with specific land cover types (bundles A and B with agricultural areas and forests
270 respectively), others from the same bundles overlapped with distinct types: in bundle A hydro-

271 energy production and plant diversity overlapped with grasslands and open spaces, and
272 artificial areas respectively; in bundle B protection against rockfalls and recreation overlapped
273 with open spaces, with recreation also overlapping with grasslands. Conversely individual
274 ecosystem parameters could overlap with multiple land cover types as for biological control
275 (bundle C) with agricultural areas, wetlands and semi-natural open areas (also overlapping
276 with pollination).

277 **Clusters at sub-regional scale**

278 Five clusters of ES were identified by the self-organizing mapping algorithm (Fig. 3; see
279 Appendix S2.C for altitudinal and land cover distributions).

280 Cluster 1 (dark grey pixels) contributed strongly to crop production, biological control,
281 protected vertebrate species richness and maintenance of water quality. Mainly located at low
282 altitudes in piedmonts and in the main valleys, it covered the highest proportions of urban and
283 agricultural lands, associated to gentle climate and topography.

284 Clusters 2, 3 and 4 presented richer bundles of ES and encompassed landscapes of
285 intermediate altitude with more than 50% forests.

286 Cluster 2 (medium grey pixels) concentrated in the southern Alps, contained few grasslands
287 but a high proportion of semi-natural and open areas. It supplied mostly cultural and
288 regulating services, with strong levels of fauna-related services (leisure hunting, protected
289 vertebrate species, biological control of pests and pollination) reflecting the suitability of such
290 (semi-)natural ecosystems as habitats and resources for wildlife. Biotic contribution to erosion
291 mitigation was also high due to high environmental exposure.

292 Cluster 3 (light grey pixels) contained the highest proportion of grasslands and pastures,
293 which along with forests supplied high levels of provisioning services (forage production,
294 wood production and hydro-energy potential). Cultural services (recreation, tourism, leisure

295 hunting and vertebrate protected species) and forest-related regulating ES (water quantity
296 regulation and carbon storage) were also well supplied. Although less prominent than in
297 cluster 2, biotic contribution to erosion mitigation, biological control of pests and pollination
298 were also characteristic regulation services.

299 Cluster 4 (black pixels), restricted to a small area of the central Alps, combined forests with
300 open areas with scant vegetation cover. The particularly high level of protection against
301 rockfalls by forests was explained by its location at the interface between high altitude, steep
302 cluster 5 areas uphill of cluster 3 areas containing valued and managed spaces.

303 Cluster 5 (white pixels) supplied a restricted set of ES, mainly hydro-energy potential,
304 recreation potential and protected plant species. Its high altitude location in the eastern part of
305 the French Alps, covered mainly by open spaces with little or no vegetation, suggested that
306 overall harsh climatic conditions, not favourable to vegetation development, led to a low
307 biotic contribution to ecological processes and limited ES supply.

308 **Landscape combinations of land cover heterogeneity and ES diversity**

309 The four combinations of landscape heterogeneity and ES gamma index (Fig. 4) showed that
310 high landscape heterogeneity did not necessarily convey high ES richness (see Appendices for
311 Chi² tests residuals: S2.E for land cover distributions, S2.F for altitude distributions, and S2.G
312 for overlap with ES).

313 Low values for landscape heterogeneity and gamma index (combination LL, black pixels)
314 covered 22% of the French Alps, either in agricultural areas at low altitude (0–500m) or in
315 open spaces at high altitude (>2000m). Conversely, homogenous landscapes with a high
316 gamma index of ES (combination LH, light grey pixels pixels, 18% of the region) were over-
317 represented in forests at intermediate altitudes (1000–1500m), regardless of forest type
318 (broad-leaved, coniferous and mixed forests) (data not shown).

319 Artificial areas and semi-natural areas were over-represented and forests under-represented in
320 heterogeneous landscapes supplying few ES (combination HL, dark grey pixels, 19% of the
321 region). Conversely, grasslands and pastures and semi-natural areas were over-represented but
322 open spaces under-represented in heterogeneous landscapes supplying multiple ecosystem
323 services (combination HH, white pixels, 41% of the region). Among heterogeneous
324 landscapes open spaces and artificial areas were over-represented and forests under-
325 represented in areas of low (HL) compared to high ES supply (HH).

326 Lastly, the two combinations with diverse ES (LH and HH) differed in the strength of their
327 overlaps with ecological parameters. While homogenous forest landscapes supplying multiple
328 ecosystem services (LH) presented the highest overlaps with parameters from bundle B
329 (carbon storage, wood production, recreation and regulation of water quantities),
330 heterogeneous landscapes supplying multiple ecosystem services (HH) had strong
331 associations with ecological parameters from all bundles, except for crop production,
332 protected plant species and plant diversity from bundle A.

333 **Discussion**

334 Our multi-step analysis showed how the supply multiple ecosystem services can be explored
335 by detecting consistent associations between ecological parameters at nested scales, from
336 regional bundles to sub-regional clusters and the investigation of their links to local landscape
337 heterogeneity.

338 Due to constraints in data availability and modelling capacities, our approach to multiple
339 ecosystem service supply combined proxies representing mostly potential but also actual
340 supply of ecological parameters (see Appendix S1.1). Consequently, the full range of
341 ecological parameters in a bundle might not be actually supplied. A major drawback of
342 combining potential and actual data is the need to maintain high attention to the nature of the
343 proxy, as consistency would have simplified a straightforward policy-oriented interpretation
344 of results. However, we point out that one interest of such mixed bundles is to highlight that
345 the bundle actually supplied strongly depends on land allocation and management choices.
346 For instance, consistent associations at regional scale between actual crop production and
347 potential plant diversity emphasise that actual biodiversity depends on intensity in agricultural
348 practises, i.e. is a social choice. Increased data availability is a pre-condition for progressing
349 towards homogenous treatment of potential or actual supply, depending on the research or
350 management question addressed.

351 In the following, we highlight how our results could be adopted by managers and policy
352 makers in the French Alps (Fig. 1).

353 **Policy-relevant correlations between ecological parameters at regional scale**

354 Three main factors drove associations between ecological parameters. First, positive
355 correlations between forest-related ES confirmed the multifunctional role of forests, widely
356 promoted in policy (European Commission 2013). Second, strong relationships between
357 biological control and protected vertebrate species were explained by a set of 19 common

358 service-providing species. Third, positive correlations between diversity of vertebrate or plant
359 species and several ES (e.g. wood production or crop production, respectively) relate to
360 specific land covers (e.g. forests or agricultural lands) that simultaneously supply habitats for
361 species and ES. Such associations should be carefully interpreted because these are only
362 potentially suitable habitats. Anderson *et al.* 2009 argued that “this spatial coincidence
363 [between crop production and biodiversity] is likely to be to the detriment of biodiversity”, as
364 confirmed by widespread conflicts between production and biodiversity conservation
365 (Maskell *et al.* 2013 for agriculture; Verkerk, Zanchi & Lindner 2014 for forestry).
366 Furthermore, policy promoting cultural services like nature tourism in the French Alps may
367 not warrant biodiversity protection either, as, consistent with England (Anderson *et al.* 2009;
368 Maskell *et al.* 2013), cultural services were negatively correlated to plant diversity. With these
369 regional-scale correlation analyses, we recommend to consider all bundle parameters, and in
370 particular biodiversity, even in policies targeting restricted objectives. In the French Alps,
371 such knowledge could reinforce policy orientations of the Alpine Convention (SPCA 1991) or
372 the northern Alps planning directive. Nevertheless, despite their interest, correlation analyses
373 cannot warrant causal relationships, requiring careful expert interpretation.

374 **Spatial associations of ecological parameters and bundles for planning**

375 Incorporating a spatial dimension to ES assessments is a major asset to detect regional
376 specificities and support land planning (Crossman *et al.* 2013).

377 First, some of the bundles detected by ES overlaps are already incorporated into planning.
378 Alpine forestry guides (e.g. Gauquelin & Courbaud 2006) and forestry regional strategic plans
379 recommend carbon storage, protection against rockfalls and mitigation of water flows as joint
380 objectives. Likewise, the overlap between crop production and regulation of water quality is
381 well-known (e.g. Laterra, Orúe & Booman 2012; Qiu & Turner 2013) and is integrated by
382 regional planning for sustainable farming in France and in Britain for example. While this

383 trade-off raises less concerns for the Alps than in more intensive agricultural regions, the
384 sensitivity of mountain ecosystems to human perturbations (EEA 2010) and their role as water
385 towers for surrounding regions (Grêt-Regamey, Brunner & Kienast 2012) are two critical
386 reasons for attention. Second, our analyses revealed overlaps which to our knowledge are less
387 considered in planning. For instance, the overlap between fodder production and regulation of
388 water quantity is seldom targeted by specific measures in the French Alps, despite the known
389 benefit of maintaining grasslands for regulation of water flows. Thus, as for biodiversity, non-
390 provisioning services must be considered explicitly in natural resources planning for long-
391 term sustainability (Maskell *et al.* 2013), as their supply is interlinked with those from the
392 same bundle.

393 Self-Organizing Mapping complemented overlap analyses by characterizing five sub-regional
394 ecological clusters. These clusters were visually linked to commonly described eco-regions of
395 the French Alps. In addition to these biophysical patterns, historical land uses should also be
396 considered to better understand these clusters (Tappeiner, Borsdorf & Tasser 2008). For
397 example, the southern Alps have undergone a significant decline in their rural population
398 since World War II, leading to agricultural area abandonment and explaining the shift from
399 crop and pasture production to forest-based ES (Cluster 2).

400 Such description and mapping of ES clusters at sub-regional scale has strong potential for
401 increased appropriation of ecological relationships by stakeholders involved in planning,
402 conditional to in-depth analysis for each sub-region before actual decision making. Also,
403 administrative boundaries can be useful mapping units coherent with social management and
404 decisional units to be added in the clustering process (Raudsepp-Hearne, Peterson & Bennett
405 2010). We suggest applying sequentially unconstrained and administratively-constrained
406 approaches to first account for internal ecological diversity that is not congruent with

407 administrative boundaries, and then incorporate the operational scale for land planning (e.g.
408 municipalities).

409 **Considering landscape-scale linkages between land cover and ecological parameters for**
410 **management**

411 High values of specific ecological parameters were linked to either a specific land cover (e.g.
412 carbon storage to forests), or to multiple land covers (e.g. biological control of pests to
413 wetlands, agricultural areas and semi-natural open areas). Therefore, the supply of multiple
414 services would require “an area large enough to encompass the spatial heterogeneity in
415 service supply” (Qiu & Turner 2013). However, high value clusters attributed to a dominant
416 land cover may contain a diversity of land covers, as for the overlap found between artificial
417 areas and plant diversity, which reflected favourable wetland and agricultural fragments
418 within areas dominated by artificial land cover.

419 Overlaps between land covers and ES provide the basis for region-specific look-up matrices
420 proposed to support landscape analysis and management (Burkhard, Kroll & Müller 2009).

421 Consistent with an expert-based assessment in a German peri-urban area (Burkhard, Kroll &
422 Müller 2009), we found a high combined capacity of forests for erosion regulation, carbon
423 storage and wood production. However, our results diverged for agricultural areas which,
424 probably due to less intensive management in the Alps, had high rather than low water quality
425 regulation.

426 Overlap analysis could support locally-tailored management schemes. Current
427 recommendations in the Alps already incorporate some of the relationships we found. For
428 instance, the overlap of both fodder production and recreation potential with grasslands and
429 pastures justified the subsidies by municipalities to livestock grazing and mowing to maintain
430 open landscapes with extensive agriculture that provide naturalness and recreational
431 attractiveness (see Schirpke, Tasser & Tappeiner 2013 for Austria). Other associations not yet

432 included in management strategies would gain in being made explicit to local decision-
433 makers. For instance, we confirmed the relevance of productive forests and grasslands for
434 hydro-energy production but, to our knowledge, vegetation cover is not yet incorporated into
435 watershed management in the French Alps, partly due to a lack of available robust evidence
436 for impacts.

437 Lastly, the understanding of bundles of ES needs to be supported by overlap analyses with
438 land cover in addition to overlaps among ecosystem properties, as land cover is the first entry
439 to planning and management.

440 **Relationships between supply of multiple ES and landscape heterogeneity**

441 Overall, we did not find a unidirectional relationship between landscape compositional
442 heterogeneity and ES richness for the French Alps, which highlights three issues for
443 management.

444 First, we explain the low ES richness of homogeneous landscapes (LL) by two mechanisms:
445 i) specialization of ES due to management in lowland agricultural areas (Laterra, Orúe &
446 Booman 2012), and ii) biotic limitation and specialization of ES in high altitude open
447 ecosystems.

448 Second, forest landscapes, although spatially homogenous, supplied a high diversity of ES
449 (LH), though necessarily more restricted than that of highly multifunctional heterogeneous
450 landscapes (HH). We suggest that this multifunctionality reflects both ecological adaptation to
451 current environmental conditions and historical management combining diverse objectives
452 (Courbaud *et al.* 2010).

453 Third, mosaic landscapes were either linked to low or high multifunctionality. These
454 alternative patterns may be explained by the contrast between artificial areas and open spaces,
455 over-represented in the former case (HL) and unfavourable to the supply of multiple ES, and

456 forests and grasslands, over-represented in the latter case (HH) and favourable to
457 multifunctionality.

458 Our results demonstrated that homogeneous landscapes can be multifunctional under specific
459 conditions. Such findings could feed debates on landscape design (Maskell *et al.* 2013).
460 However we considered land cover categories as homogeneous across the French Alps,
461 ignoring significant variations due to management and biophysical gradients (e.g. variations
462 in tree species and age-structure in forests). Agri-environment schemes explicitly managing
463 landscape heterogeneity are required to increase (or even create) benefits for farmland
464 biodiversity (Mitchell, Bennett & Gonzalez 2014). In line with this argument, we call for a
465 broader inclusion of landscape patterns for agricultural, forestry, touristic and urban planning.

466 **Conclusion**

467 Our study explored pattern-based multifunctionality reflecting the repeated coincidence
468 between ecological parameters and landscape features. Its main strength is to promote the
469 management of ES and biodiversity as bundles rather than as individual targets. Bundles arose
470 from the joint effects of two factors. First, biophysical characteristics defined the constraints
471 (e.g. temperature or slope limitations restricting bundles at high altitudes) and opportunities
472 (e.g. favourable abiotic conditions for wild species and for ecological functioning in the
473 southern Alps) for potential joint supply. Second, bundles have been shaped through human
474 history by land allocation and management choices. The resulting bundles and their
475 relationships to landscape features may be generalizable to biophysically and socially
476 comparable regions.

477 Our analysis supports the explicit consideration of bundles in management, and in particular
478 the integration of biodiversity and regulating services even in policies targeting other
479 objectives. Current management already considers such bundles, such as the joint supply by

480 alpine forests of carbon storage, protection against rockfalls and mitigation of water flows.
481 Others such as the association between forage production and regulation of water quantities in
482 extensive grasslands would deserve consideration. Additionally multifunctionality can
483 depending on the abiotic context arise either from deliberate management in homogeneous
484 landscapes or from spatial heterogeneity. Such solutions will require ecosystem-based
485 management at landscape scale, and may be generalizable.

486 We stress the interest of complementing our results by identifying functional mechanisms
487 underlying associations, which would foster a process-based approach of multifunctionality
488 (Mastrangelo *et al.* 2014). However increased availability of models (e.g. phenomenological
489 or trait-based models) and data at fine resolution over regional geographical extents (species
490 distributions – abiotic properties) precondition such progress.

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498 Catolica del Sacro Cuore’ for technical support and collaboration on erosion data.

499

500 **Data accessibility**

501 GIS information on land use, ES distributions (aggregated indicator of ES richness) and
502 distributions of the clusters from the self-organizing map are available from the Dryad Digital
503 Repository: <http://dx.doi.org/10.5061/dryad.3qk15> (Crouzat *et al.* 2015).

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553 [raster-3/clc-2006-100m/g100_06.zip](http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3/clc-2006-100m/g100_06.zip) (accessed 21/06/2013)
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662 **Supporting Information**

663 Additional Supporting Information may be found in the online version of this article:

- 664 - **Supporting Information S1 – Complementary elements on ecological parameters**
- 665 ○ Appendix S1.A. Ecological parameters complementary description
- 666 ○ Table S1.1. Formalized description of ecological parameters modelled and
- 667 analysed
- 668 ○ Appendix S1.B. Forage production: methodological information
- 669 ○ Appendix S1.C. Leisure hunting: methodological information
- 670 ○ Appendix S1.D. Carbon storage: methodological information
- 671 - **Supporting Information S2 – Statistical results**
- 672 ○ Table S2.A. Pearson correlation coefficients between ecological parameters
- 673 ○ Table S2.B. Pairwise overlap rates between ecological parameters
- 674 ○ Table S2.C. Altitude and land cover proportions by clusters (SOM)
- 675 ○ Table S2.D. Overlap rates between high value clusters
- 676 ○ Table S2.E. Chi² test residuals – Land cover distributions by Combination
- 677 ○ Table S2.F. Chi² test residuals – Altitude distributions by Combination
- 678 ○ Table S2.G. Overlap rates between Combinations and ecological parameters
- 679
- 680

681 **Tables**

682 Table 1: Ecosystem service and biodiversity parameters considered in the assessment of ecological relationships over the French Alps. Abbreviated names between brackets are those used for all
 683 analyses. Type specifics: P = provisioning service, C = cultural service, R = regulating service, B = biodiversity parameter

Type	Parameter	Description (unit)	Sources
P	Agricultural production (crop)	Yields for annual crops, vineyards and orchards (kg ha ⁻¹ yr ⁻¹)	Agreste 2009
P	Forage production (fodd)	Yields of pastures, meadows and mountain grasslands (kg dry matter ha ⁻¹ yr ⁻¹)	Agreste 2009; Appendix S1.B
P	Wood production (wood)	Potential woody biomass supply for stemwood and logging residues (Gg dry matter km ⁻² yr ⁻¹)	Verkerk <i>et al.</i> 2011; Brus <i>et al.</i> 2012; Elbersen <i>et al.</i> 2012
P	Hydro-energy potential (hydro)	Theoretical potential hydroelectric power delivered by river basin (classes)	Agence de l'eau RMC 2008
C	Recreation potential (recre)	Recreation potential for daily recreation (index)	Paracchini <i>et al.</i> 2014
C	Tourism (tour)	Territorial capital of rural tourism involving overnight stays (index)	Paracchini & Capitani 2011; Maes <i>et al.</i> 2012 ; Paracchini <i>et al.</i> 2014
C	Leisure hunting (hunt)	Density of shot wild ungulates (number of animals km ⁻² yr ⁻¹)	Convention with « Réseau Ongulés Sauvages ONCFS / FNC / FDC » ; Appendix S1.C
C	Protected plant species (protp)	Species richness for 45 protected plant species with Red List status critical, endangered and vulnerable (number of species km ⁻²)	Thuiller <i>et al.</i> 2014
C	Protected vertebrate species (protv)	Species richness for 107 protected vertebrate species with Red List status critical, endangered and vulnerable (number of species km ⁻²)	Maiorano <i>et al.</i> 2013
R	Erosion mitigation (eros)	Biotic contribution to erosion risk mitigation (classes)	Bosco <i>et al.</i> 2008; Bosco <i>et al.</i> 2009
R	Protection against rockfalls (rock)	Ability of forests to decrease rockfall hazard and protect sensitive human areas (index)	Berger <i>et al.</i> 2013
R	Chemical water quality regulation (wql)	Nitrogen retention capacity by river basin (tN km ⁻¹ year ⁻¹)	Grizzetti & Bouraoui 2006
R	Physical water quantity regulation (wqt)	Relative water retention enabling flood regulation (index)	Stürck, Poortinga & Verburg 2014
R	Biological control of pests (cbiol)	Species richness for 110 vertebrate species providing natural pest control (number of species km ⁻²)	Civantos <i>et al.</i> 2012; Maiorano <i>et al.</i> 2013
R	Pollination (poll)	Relative landscape suitability for pollinators (index)	Zulian, Maes & Paracchini 2013
R	Carbon storage (csto)	Sum of carbon stocks from above-ground and below-ground biomass, dead organic matter and soils (tC km ⁻²)	Martin <i>et al.</i> 2011; Meersmans <i>et al.</i> 2012a, 2012b; Supporting Information S1.D

B	Plant diversity (plant)	Species richness for 2748 plant species using their potential ecological niche distributions (number of species km ²)	Thuiller <i>et al.</i> 2014
B	Vertebrate diversity (vert)	Species richness for 380 vertebrate species using their potential ecological niche distributions (number of species km ²)	Maiorano <i>et al.</i> 2013

685 **Figures**

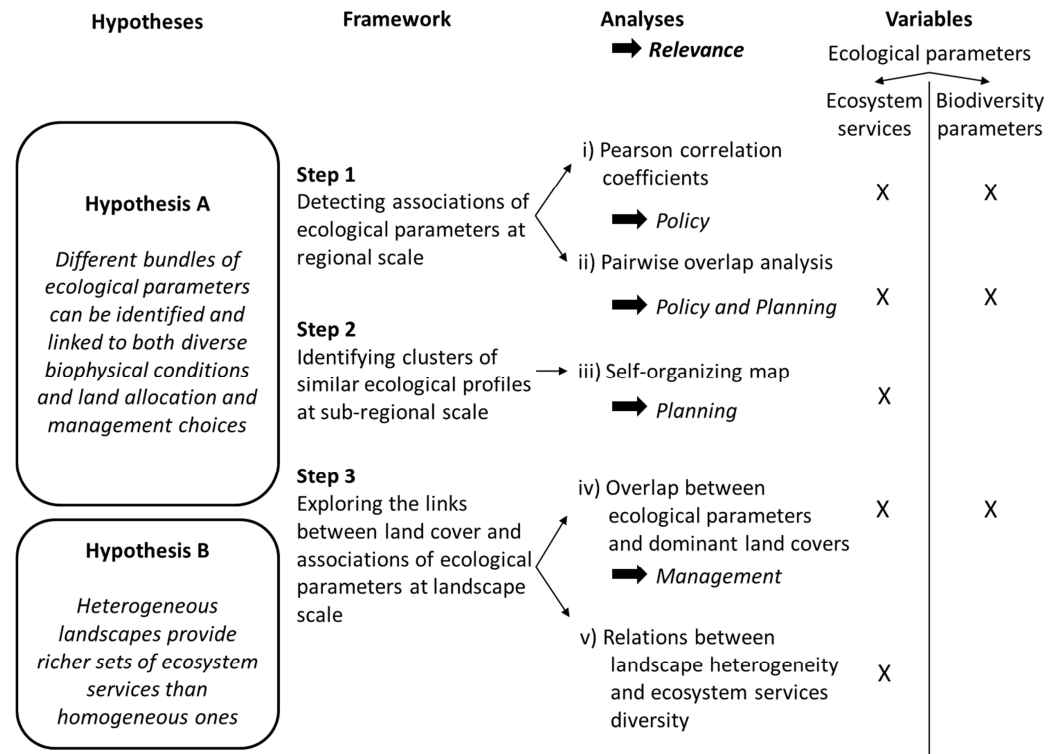
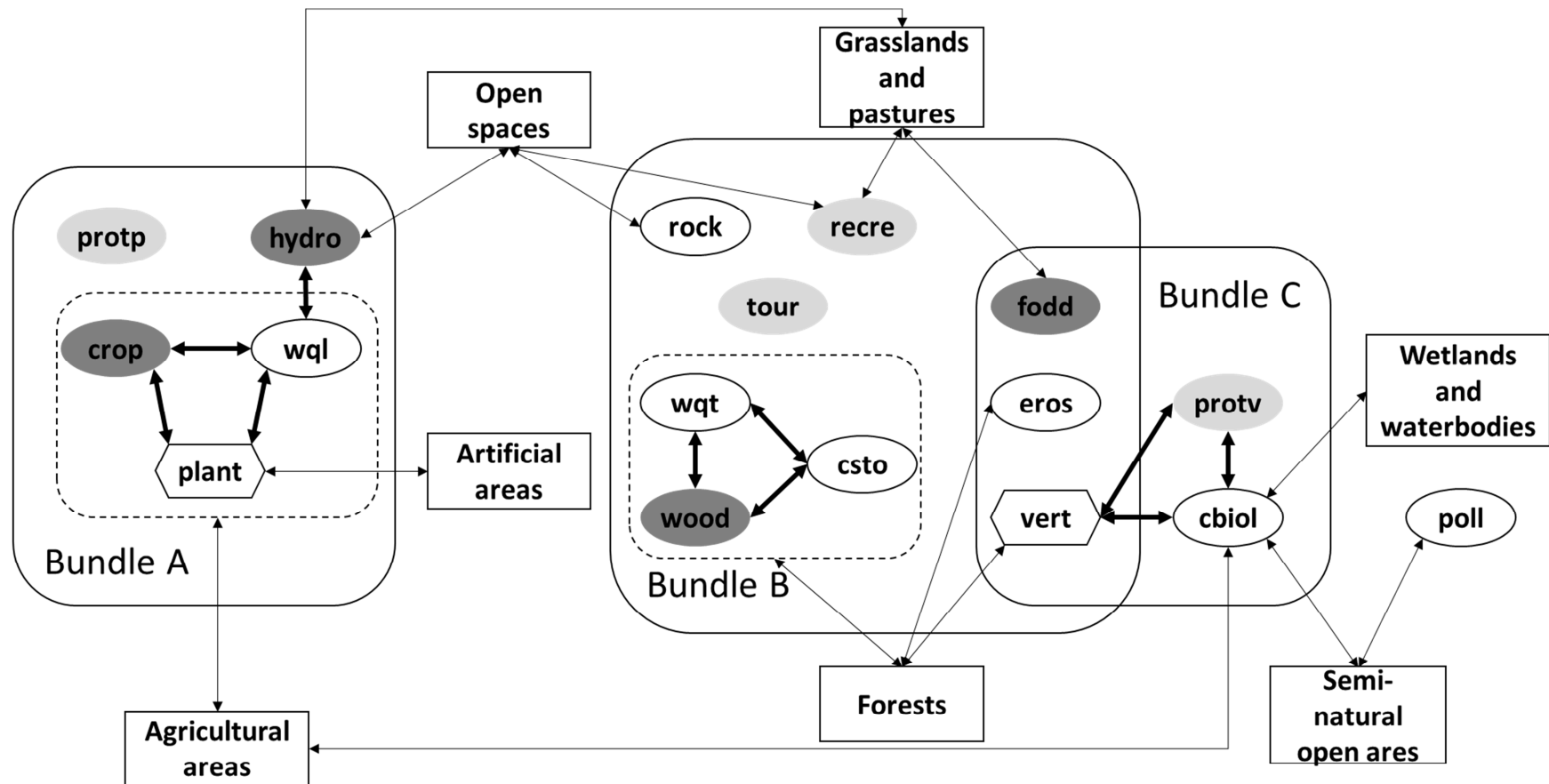


Figure 1: Analytical framework and hypotheses tested.

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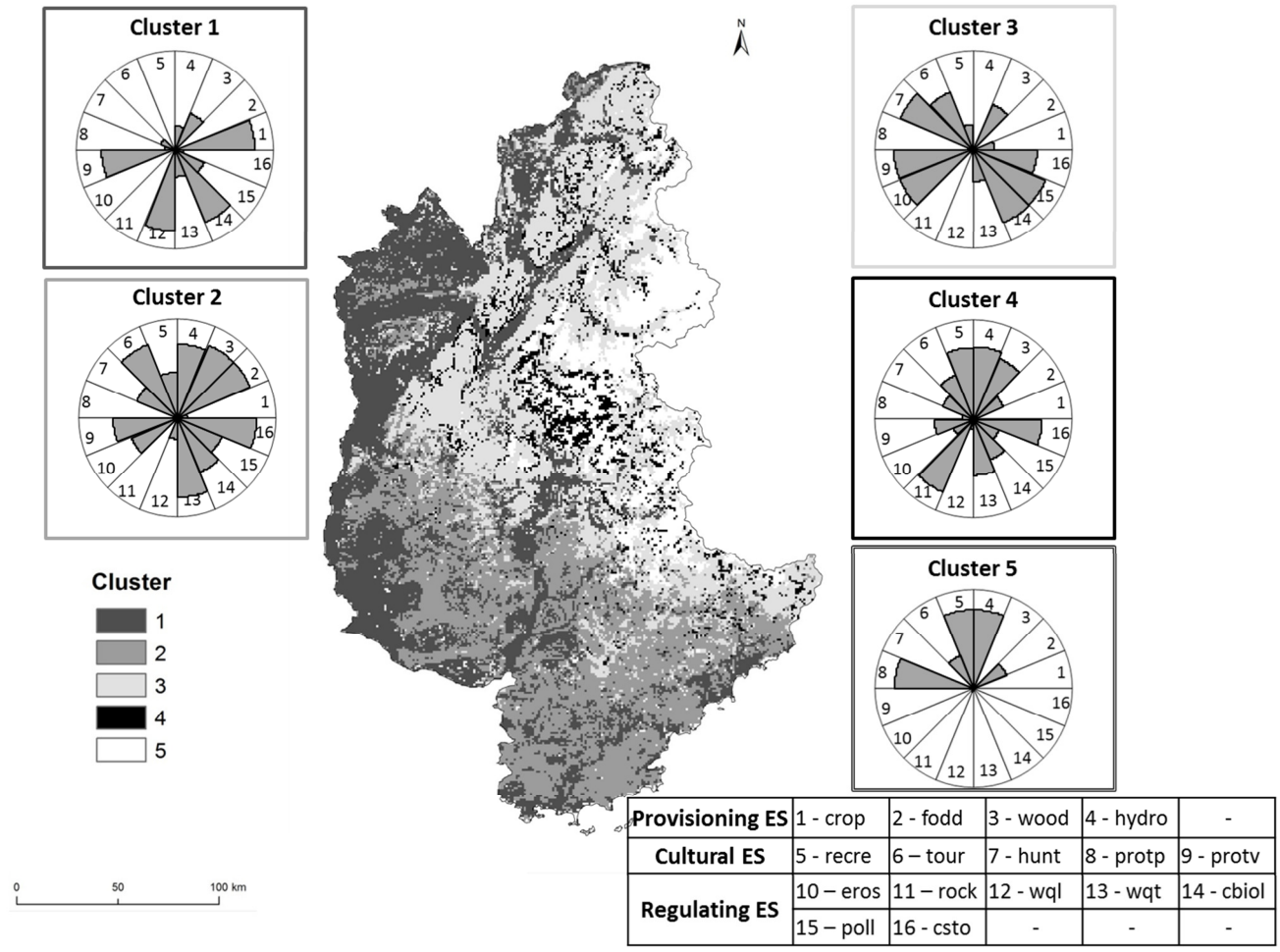
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Figure 2: Bundles of ecological parameters (ecosystem services (ES) and biodiversity parameters) and overlaps with dominant land covers. Bundles were identified by Pearson coefficients and pairwise overlaps (solid lines). Bold arrows: consistent associations between parameters for both analyses. Associations with land cover types were identified through overlaps between ecological parameters and land cover high value clusters (plain arrows to individual parameters or to multiple parameters encompassed in dotted lines). Biodiversity parameters are presented as hexagons and ES as ellipses (dark grey: provisioning services, light grey: cultural services; white: regulating services). See Table 1 for abbreviations.

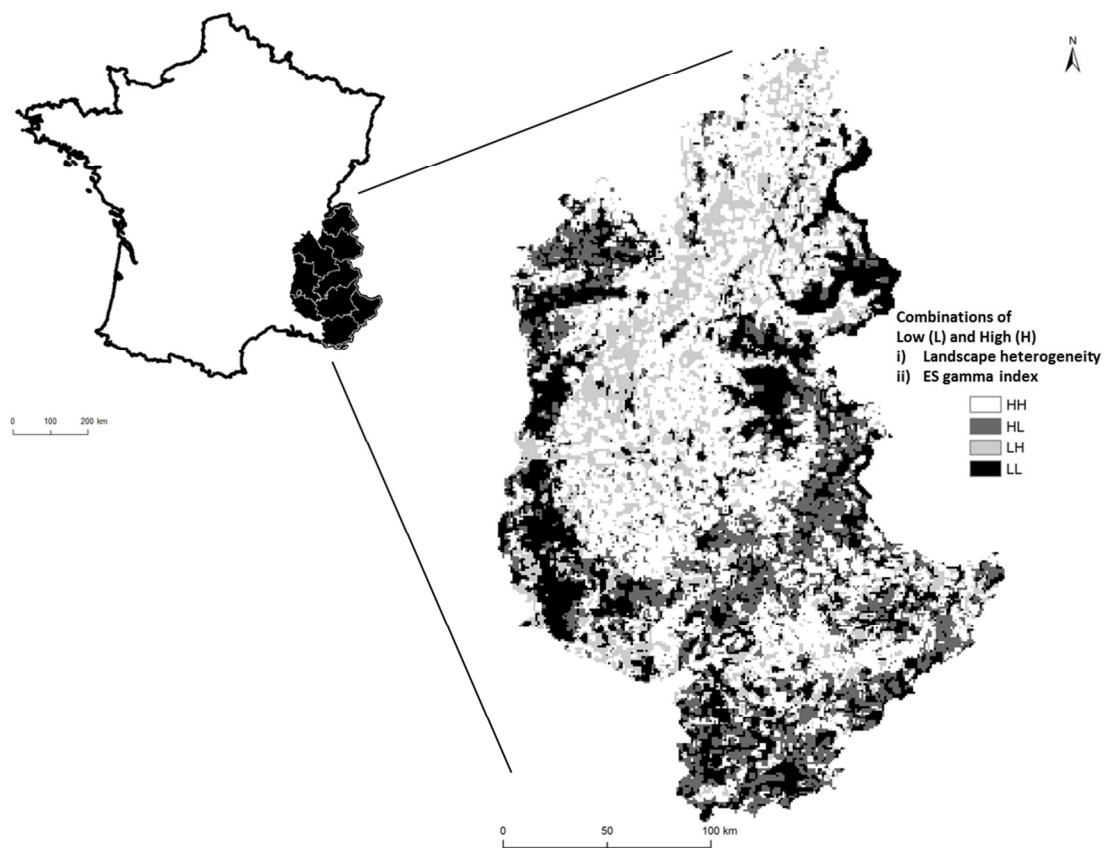


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Figure 3: Self-organizing map with five clusters and related ecological profiles (values standardized to 0–1). See Table 1 for abbreviations.

696



697

698 Figure 4: French Alps – Combined landscape heterogeneity and ecosystem services (ES) gamma index. LL: low
 699 landscape heterogeneity and low gamma index; LH: low landscape heterogeneity and high gamma index; HL: high
 700 landscape heterogeneity and low gamma index and HH: high landscape heterogeneity and high gamma index.