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

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Summary

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

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

Keywords

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

Introduction

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

ES assessments increasingly use the concept of so-called "landscape multifunctionality", understood as "the capacity of a landscape to simultaneously support multiple benefits to society from its interacting ecosystems", relying on the "joint supply of multiple ES at the landscape level" (Mastrangelo *et al.* 2014). Landscape heterogeneity closely links to supply of multiple ecosystem services (Brandt 2003) and appears 'easy to access' for scientists and 'easy to grasp' for stakeholders (Laterra, Orúe & Booman 2012). Yet, the extent and generality of spatial or functional associations between landscape heterogeneity and multiple ecosystem services are still debated (Anderson *et al*. 2009; Mastrangelo *et al.* 2014). In this context, a better understanding of associations among ES and of their relationship to spatial patterns of underlying biophysical variables is needed for more effective land allocation and management (Briner *et al.* 2013).

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

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

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

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

Materials and methods

Study region

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

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

Modelling and mapping ecological parameters

Selection of ecological parameters: ES and biodiversity

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

Modelling ecological parameters

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

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

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

ALTI® IGN.

Statistical analyses

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

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

Data transformation

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

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

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

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

Step 1: Detecting consistent associations at regional scale

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

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

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

Step 2: Identifying clusters at sub-regional scale

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

Step 3: Exploring links with land cover at landscape scale

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

High value clusters for individual ecological parameters and land cover types were detected with ArcGIS Hot Spot Analysis tool parameterized to calculate Getis-Ord Gi* statistics using the "Distance Band or Threshold Distance" cut-off to a window of 3 km × 3 km. Significant *P*-values were returned when observed spatial clustering was greater than expected for a random distribution, avoiding the selection of isolated pixels of high values or outliers. Each variable was then transformed into a binary data set, attributing a value of 1 for clusters with z-scores significant at 10% minimum and 0 otherwise. Pairwise overlap analysis detected spatial matches between clusters of high value for ecological parameters and for land cover types.

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

Results

Associations at regional scale

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

Regarding land cover, although some groups of ecological parameters were tightly associated with specific land cover types (bundles A and B with agricultural areas and forests respectively), others from the same bundles overlapped with distinct types: in bundle A hydro-energy production and plant diversity overlapped with grasslands and open spaces, and artificial areas respectively; in bundle B protection against rockfalls and recreation overlapped with open spaces, with recreation also overlapping with grasslands. Conversely individual ecosystem parameters could overlap with multiple land cover types as for biological control (bundle C) with agricultural areas, wetlands and semi-natural open areas (also overlapping with pollination).

Clusters at sub-regional scale

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

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

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

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

Cluster 3 (light grey pixels) contained the highest proportion of grasslands and pastures, which along with forests supplied high levels of provisioning services (forage production, wood production and hydro-energy potential). Cultural services (recreation, tourism, leisure hunting and vertebrate protected species) and forest-related regulating ES (water quantity regulation and carbon storage) were also well supplied. Although less prominent than in cluster 2, biotic contribution to erosion mitigation, biological control of pests and pollination were also characteristic regulation services.

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

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

Landscape combinations of land cover heterogeneity and ES diversity

The four combinations of landscape heterogeneity and ES gamma index (Fig. 4) showed that high landscape heterogeneity did not necessarily convey high ES richness (see Appendices for Chi^2 tests residuals: S2.E for land cover distributions, S2.F for altitude distributions, and S2.G for overlap with ES).

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

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

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

Discussion

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

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

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

Policy-relevant correlations between ecological parameters at regional scale

Three main factors drove associations between ecological parameters. First, positive correlations between forest-related ES confirmed the multifunctional role of forests, widely promoted in policy (European Commission 2013). Second, strong relationships between biological control and protected vertebrate species were explained by a set of 19 common service-providing species. Third, positive correlations between diversity of vertebrate or plant species and several ES (e.g. wood production or crop production, respectively) relate to specific land covers (e.g. forests or agricultural lands) that simultaneously supply habitats for species and ES. Such associations should be carefully interpreted because these are only potentially suitable habitats. Anderson *et al.* 2009 argued that "this spatial coincidence [between crop production and biodiversity] is likely to be to the detriment of biodiversity", as confirmed by widespread conflicts between production and biodiversity conservation (Maskell *et al.* 2013 for agriculture; Verkerk, Zanchi & Lindner 2014 for forestry). Furthermore, policy promoting cultural services like nature tourism in the French Alps may not warrant biodiversity protection either, as, consistent with England (Anderson *et al.* 2009; Maskell *et al.* 2013), cultural services were negatively correlated to plant diversity. With these regional-scale correlation analyses, we recommend to consider all bundle parameters, and in particular biodiversity, even in policies targeting restricted objectives. In the French Alps, such knowledge could reinforce policy orientations of the Alpine Convention (SPCA 1991) or the northern Alps planning directive. Nevertheless, despite their interest, correlation analyses cannot warrant causal relationships, requiring careful expert interpretation.

Spatial associations of ecological parameters and bundles for planning

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

First, some of the bundles detected by ES overlaps are already incorporated into planning. Alpine forestry guides (e.g. Gauquelin & Courbaud 2006) and forestry regional strategic plans recommend carbon storage, protection against rockfalls and mitigation of water flows as joint objectives. Likewise, the overlap between crop production and regulation of water quality is well-known (e.g. Laterra, Orúe & Booman 2012; Qiu & Turner 2013) and is integrated by regional planning for sustainable farming in France and in Britain for example. While this trade-off raises less concerns for the Alps than in more intensive agricultural regions, the sensitivity of mountain ecosystems to human perturbations (EEA 2010) and their role as water towers for surrounding regions (Grêt-Regamey, Brunner & Kienast 2012) are two critical reasons for attention. Second, our analyses revealed overlaps which to our knowledge are less considered in planning. For instance, the overlap between fodder production and regulation of water quantity is seldom targeted by specific measures in the French Alps, despite the known benefit of maintaining grasslands for regulation of water flows. Thus, as for biodiversity, non-provisioning services must be considered explicitly in natural resources planning for long-term sustainability (Maskell *et al.* 2013), as their supply is interlinked with those from the same bundle.

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

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

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

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

Overlaps between land covers and ES provide the basis for region-specific look-up matrices proposed to support landscape analysis and management (Burkhard, Kroll & Müller 2009). Consistent with an expert-based assessment in a German peri-urban area (Burkhard, Kroll & Müller 2009), we found a high combined capacity of forests for erosion regulation, carbon storage and wood production. However, our results diverged for agricultural areas which, probably due to less intensive management in the Alps, had high rather than low water quality regulation.

Overlap analysis could support locally-tailored management schemes. Current recommendations in the Alps already incorporate some of the relationships we found. For instance, the overlap of both fodder production and recreation potential with grasslands and pastures justified the subsidies by municipalities to livestock grazing and mowing to maintain open landscapes with extensive agriculture that provide naturalness and recreational attractiveness (see Schirpke, Tasser & Tappeiner 2013 for Austria). Other associations not yet included in management strategies would gain in being made explicit to local decision-makers. For instance, we confirmed the relevance of productive forests and grasslands for hydro-energy production but, to our knowledge, vegetation cover is not yet incorporated into watershed management in the French Alps, partly due to a lack of available robust evidence for impacts.

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

Relationships between supply of multiple ES and landscape heterogeneity

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

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

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

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

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

Conclusion

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

Our analysis supports the explicit consideration of bundles in management, and in particular the integration of biodiversity and regulating services even in policies targeting other objectives. Current management already considers such bundles, such as the joint supply by alpine forests of carbon storage, protection against rockfalls and mitigation of water flows. Others such as the association between forage production and regulation of water quantities in extensive grasslands would deserve consideration. Additionally multifunctionality can depending on the abiotic context arise either from deliberate management in homogeneous landscapes or from spatial heterogeneity. Such solutions will require ecosystem-based management at landscape scale, and may be generalizable.

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

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Data accessibility

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

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Supporting Information

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

- **Supporting Information S1 – Complementary elements on ecological parameters**
    - Appendix S1.A. Ecological parameters complementary description
    - Table S1.1. Formalized description of ecological parameters modelled and analysed
    - Appendix S1.B. Forage production: methodological information
    - Appendix S1.C. Leisure hunting: methodological information
    - Appendix S1.D. Carbon storage: methodological information
- **Supporting Information S2 – Statistical results**
    - Table S2.A. Pearson correlation coefficients between ecological parameters
    - Table S2.B. Pairwise overlap rates between ecological parameters
    - Table S2.C. Altitude and land cover proportions by clusters (SOM)
    - Table S2.D. Overlap rates between high value clusters
    - Table S2.E. Chi² test residuals – Land cover distributions by Combination
    - Table S2.F. Chi² test residuals – Altitude distributions by Combination
    - Table S2.G. Overlap rates between Combinations and ecological parameters

Tables

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 analyses. Type specifies: 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 *et al*. 2011; Brus *et al*. 2012; Elbersen *et al*. 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 *et al.* 2014
C	Tourism (**tour**)	Territorial capital of rural tourism involving overnight stays (index)	Paracchini & Capitani 2011; Maes *et al.* 2012 ; Paracchini *et al.* 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 *et al.* 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 *et al.* 2013
R	Erosion mitigation (**eros**)	Biotic contribution to erosion risk mitigation (classes)	Bosco *et al.* 2008; Bosco *et al.* 2009
R	Protection against rockfalls (**rock**)	Ability of forests to decrease rockfall hazard and protect sensitive human areas (index)	Berger *et al.* 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 *et al.* 2012; Maiorano *et al.* 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 *et al.* 2011; Meersmans *et al.* 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 *et al.* 2014
B	Vertebrate diversity (**vert**)	Species richness for 380 vertebrate species using their potential ecological niche distributions (number of species km^{-2})	Maiorano *et al.* 2013

Figures

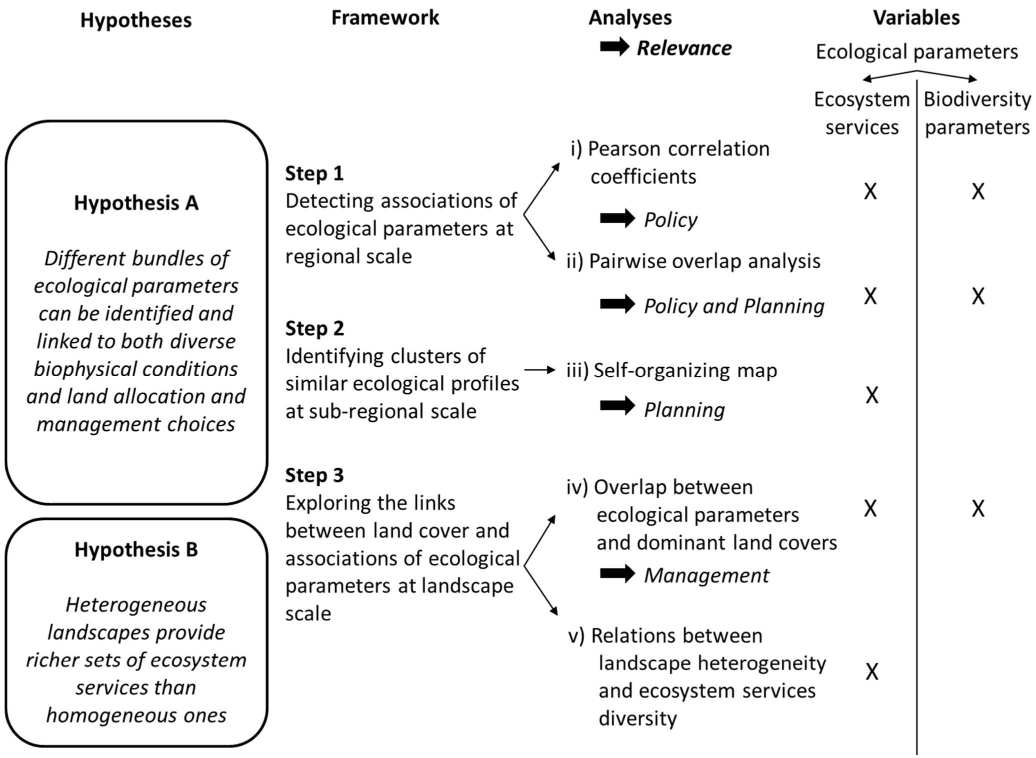


Figure 1: Analytical framework and hypotheses tested.

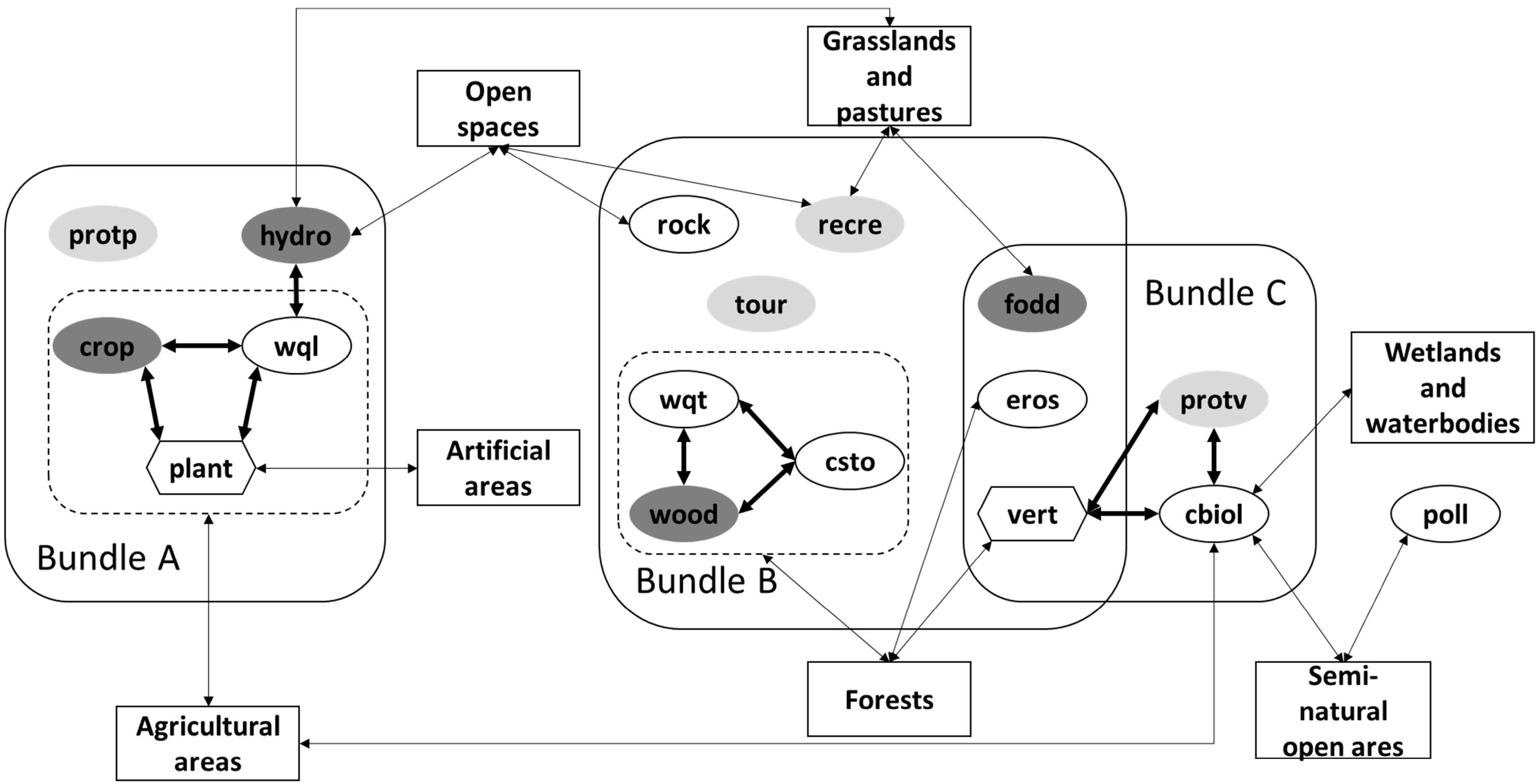
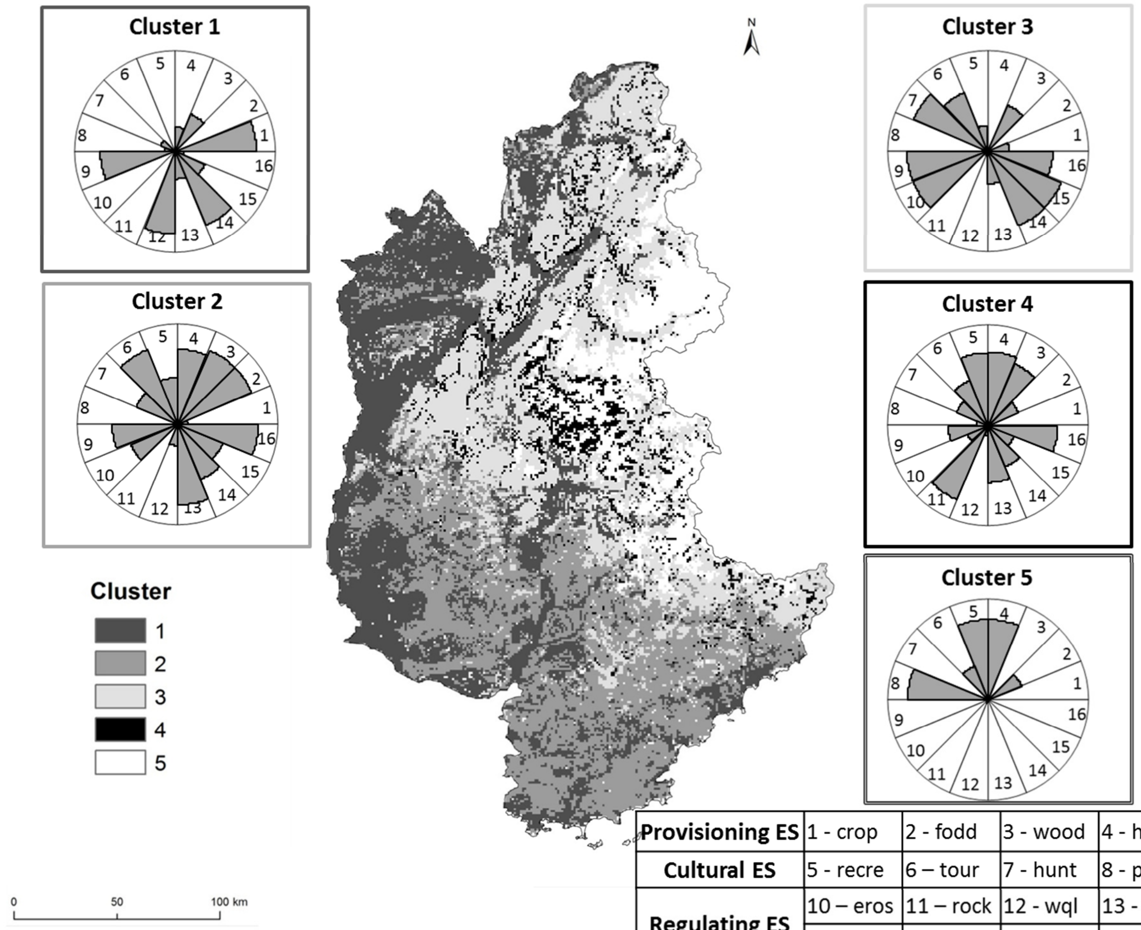


Figure 2: Bundles of ecological parameters (ecosystem services (ES) and biodiversity parameters) and overlaps with dominant land covers. Bundles were identified by Pearson coefficients and pairwise overlaps (solid lines). Bold arrows: consistent associations between parameters for both analyses. Associations 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.



Provisioning ES	1 - crop	2 - fodd	3 - wood	4 - hydro	-
Cultural ES	5 - recre	6 – tour	7 - hunt	8 - protp	9 - protv
Regulating ES	10 – eros	11 – rock	12 - wql	13 - wqt	14 - cbiol
	15 – poll	16 - csto	-	-	-

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

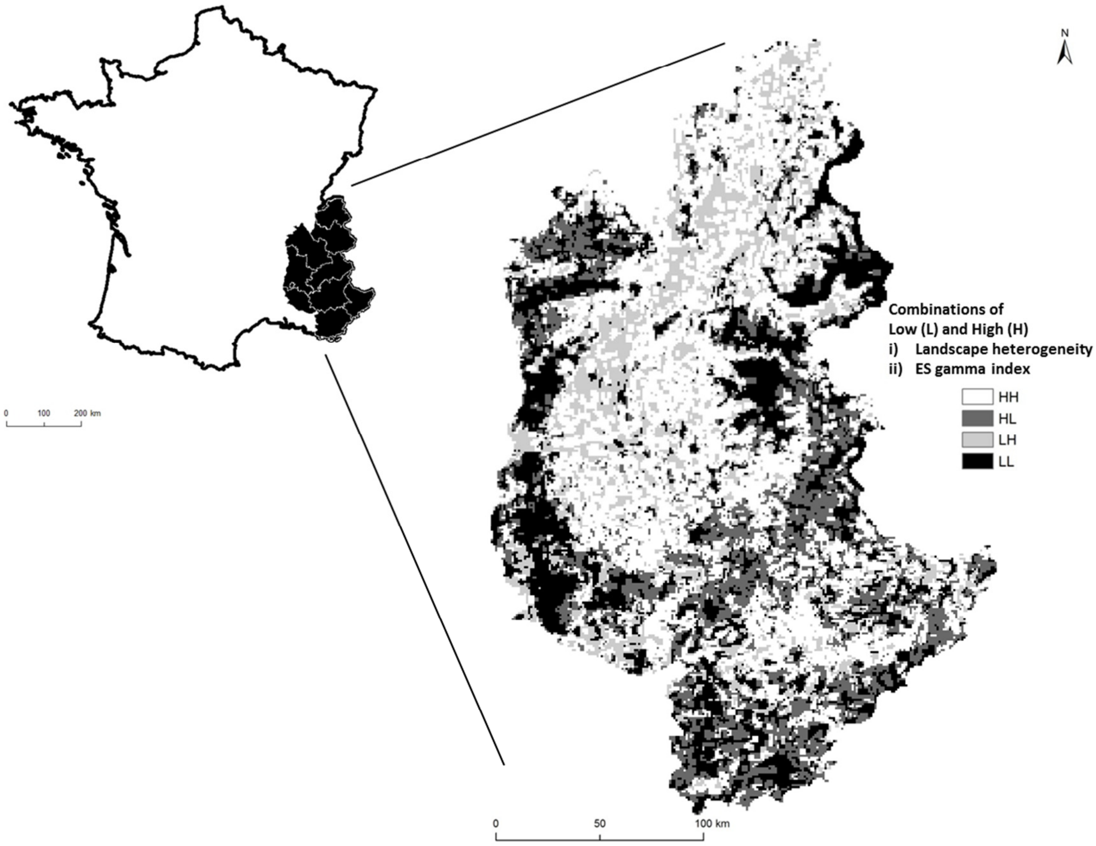


Figure 4: French Alps – Combined landscape heterogeneity and ecosystem services (ES) gamma index. LL: low landscape heterogeneity and low gamma index; LH: low landscape heterogeneity and high gamma index; HL: high landscape heterogeneity and low gamma index and HH: high landscape heterogeneity and high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