IDEA AND PERSPECTIVE

N-dimensional hypervolumes to study stability of complex ecosystems

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Abstract

Although our knowledge on the stabilising role of biodiversity and on how it is affected by perturbations has greatly improved, we still lack a comprehensive view on ecosystem stability that is transversal to different habitats and perturbations. Hence, we propose a framework that takes advantage of the multiplicity of components of an ecosystem and their contribution to stability. Ecosystem components can range from species or functional groups, to different functional traits, or even the cover of different habitats in a landscape mosaic. We make use of *n*-dimensional hypervolumes to define ecosystem states and assess how much they shift after environmental changes have occurred. We demonstrate the value of this framework with a study case on the effects of environmental change on Alpine ecosystems. Our results highlight the importance of a multidimensional approach when studying ecosystem stability and show that our framework is flexible enough to be applied to different types of ecosystem components, which can have important implications for the study of ecosystem stability and transient dynamics.

Keywords

Climate change, ecosystem stability, land-use changes, *n*-dimensional hypervolumes, perturbations.

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INTRODUCTION

Across the globe, ever-increasing changes to ecosystems such as regional intensification or land-use abandonment, and climate change, threaten taxonomic and functional composition and associated ecosystem functions and services (Díaz *et al.* 2006; Weiner *et al.* 2014; Kortsch *et al.* 2015; Oliver *et al.* 2015). These changes may compromise the ability of ecosystems to recover from future perturbations and lead to departures from stability, which may ultimately result in shifts to other ecosystem states (see, for instance, the review by Standish *et al.* 2014).

Therefore, studying stability is important to understand the response of ecosystems to afore mentioned land-use and climate changes. Stability is a multifaceted concept that can be studied in different ways (e.g. Ives 1995 mathematically explored equilibria, while Mazancourt *et al.* 2013 studied the temporal variability of particular ecosystem components). However, most empirical studies on ecosystem stability have been focused on the role of biodiversity for the stabilisation of a particular ecosystem function – biodiversity-ecosystem functioning (BEF) studies (e.g. Tilman & Downing 1994; Jousset *et al.* 2011; Pillar *et al.* 2013). The majority of these studies have aimed at understanding how biodiversity maintains and promotes productivity (e.g. Cadotte *et al.* 2012; Roscher *et al.* 2012; but see Hautier *et al.* 2015) and have shown that the processes through which this occurs can differ between communities (Morin *et al.* 2014). Fewer studies investigated the stability of biodiversity itself to perturbations – perturbation-biodiversity studies. These have shown that relationships between taxonomic and functional diversity can change across environmental and disturbance gradients (Flynn *et al.* 2009; Biswas & Mallik 2011), affecting the relationship between ecosystem function and biodiversity (shown for steppe communities by Zhou *et al.* 2006). However, studies rarely investigated the impact of disturbances on the stability of ecosystem function and of biodiversity together (but see Steudel *et al.* 2012). This is an important drawback, since both the stability of ecosystem functions and of ecosystem structure and composition can be important aspects in terms of management planning and policy making for complex ecosystems, especially if several types of habitats exist and ecotone dynamics can change (MacDonald *et al.* 2015).

Considering how different components of an ecosystem – e.g. species abundances, their functional and phylogenetic composition, and resulting ecosystem functions and services (cf. Table 1 for a non-exhaustive list of components relevant for different facets of ecosystem stability) – contribute to its stabilisation can be important in complex ecosystems, where summarising stability into a single metric might be a challenge and likely inaccurate. For instance, diverse habitat mosaics can be composed of communities that are very different in terms of productivity levels and their seasonality, but all equally stable in terms of species richness. In such cases, ecosystem stability is not easily summarised by a single metric, such as productivity, and considering multiple taxonomic and

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Table 1 Examples of components that can be considered for assessing ecosystem stability using the hypervolumes framework. In this non-exhaustive list, types of ecosystem components are sorted by increasing level of organisation, although some can be considered across different organisational scales (e.g. diversity metrics). We distinguished between ecosystem functioning components and ecosystem services components following Lavorel & Grigulis (2012).

Ecosystem components	
Increasing level of organisation	• Organisms (usually raw/relative abundances, cover) e.g. species, guilds, functional groups, MOTUS (molecular operational taxonomical units).
	• Community trait values (generally averaged and weighted by species abundance, but variances in trait values can also be used)
	• Diversity metrics e.g. taxonomic richness and evenness, functional richness, evenness, divergence and dispersion, mean phylogenetic distance.
	• Properties of ecological networks e.g. species diversity, connectance, modularity
	• Habitat/vegetation cover
	• Ecosystem functioning (often productivity, but other functions like nutrient cycling can also be considered) e.g. biomass, nitrogen, carbon and water availability
	• Ecosystem services e.g. quantity and quality of fodder, nutrient cycling, carbon storage, water quality

functional community components is likely to provide better information about overall ecosystem stability.

Defining the state of a complex ecosystem can be challenging, since ecosystems and their multiple components often have temporal fluctuations. In a two-dimensional case, these oscillations are usually well represented in phase portraits, where the two response variables are plotted against each other at several points in time (Fig. 1). If the system reaches equilibrium, its trajectory will converge to an equilibrium point, or a limit cycle in an oscillatory equilibrium (Fig. 1b). In complex systems involving more than two response variables (Fig. 1c), the trajectory becomes a path in *n*-dimensional space. In this case, the ecosystem state can be described as an *n*-dimensional cloud of points or an *n*-dimensional hypervolume (Fig. 1d). An ecosystem state is then determined by both the intrinsic dynamics of its components and environmental conditions. If changes in these conditions occur and the ecosystem is disturbed, ecosystem components and their trajectories may be affected, leading to another *n*-dimensional hypervolume (Fig. 1d). Comparing the two hypervolumes will provide an assessment of the magnitude of changes the ecosystem suffered, i.e. its shift from the initial state. Although in this study we were not interested in detecting shifts between alternative stable states, *sensu* Scheffer *et al.* (2001), the ball-and-cup analogy of resilience (Holling 1996; Folke *et al.* 2004) provides an intuitive visual representation of how *n*-dimensional hypervolumes relate to ecosystem stability. If we consider that *n*-dimensional hypervolumes represent the states of a system under different environmental

conditions, comparing hypervolumes before and after perturbations will reflect how far the system has moved from its initial basin of attraction (i.e. state; Figs. 1e, f, g). Our focus is not on how fast a community returns to its pre-perturbation state (engineering resilience, or the basin's slope), nor to assess whether the community has undergone a permanent state shift. Although these can be investigated, here, we focus on the departures from an ecosystem state (stable or transient), i.e. the magnitude of changes that the ecosystem suffered.

We, thus, propose using hypervolumes built from several components of an ecosystem as a means to reflect their integrated variability. The choice of the type of components will depend on what the analysis of stability falls unto. We believe that ecosystem stability should be investigated across different components; the approach we propose here is sufficiently flexible to be applied to different sets of data and can be used for this integrative approach (Table 1). For example, if the research focus is on the stability of biodiversity at the community scale, time series of species abundances or community-weighted means (CWMs) or variances (CWV) of functional traits (i.e. trait values of all species in the community weighted by species abundances) can be used. At a larger scale, the stability of biodiversity can also be assessed using taxonomic, functional and phylogenetic diversity metrics that can constitute the hypervolumes. At the landscape scale, in mosaic ecosystems, it may be interesting to analyse stability in terms of proportions of different habitat patches, building hypervolumes from coverage values of each habitat type.

We present this novel approach using simulated plant communities of different habitats in the European Alps. In Alpine mountain ecosystems, sharp gradients drive both abiotic and biotic constraints that result in the presence of distinct plant communities within relatively small spatial extents. These systems are especially vulnerable to climate and land-use changes (LUC; Serreze *et al.* 2000; Tappeiner & Bayfield 2004; Dullinger *et al.* 2012; Thuiller *et al.* 2014), since they harbour species that are frequently at their niche limits and are likely to respond faster to environmental change (Wookey *et al.* 2009; Rigling *et al.* 2013). For example, land-use abandonment and climate warming can cause shifts in grassland composition and structure, leading to woody encroachment (Tasser & Tappeiner 2002; Asner *et al.* 2004) and changes in forest-grassland ecotones (Boulangeat *et al.* 2014a; Carlson *et al.* 2014). Hence, these ecosystems provide a rich study case for our proposed framework. Our results show that the framework successfully distinguishes what types of perturbations most affect Alpine communities and can provide indication of how different community components respond to the same perturbation. More importantly, this framework is a successful first step into integrating the multiplicity of ecosystem components for the analysis of ecosystem stability in a global change context.

A GENERAL FRAMEWORK FOR COMPARING COMMUNITY STATES

Our framework to study ecosystem stability in face of environmental changes using *n*-dimensional hypervolumes is presented in two sections. In the present section, we explain the workflow and its four steps in general terms (Fig. 2). In
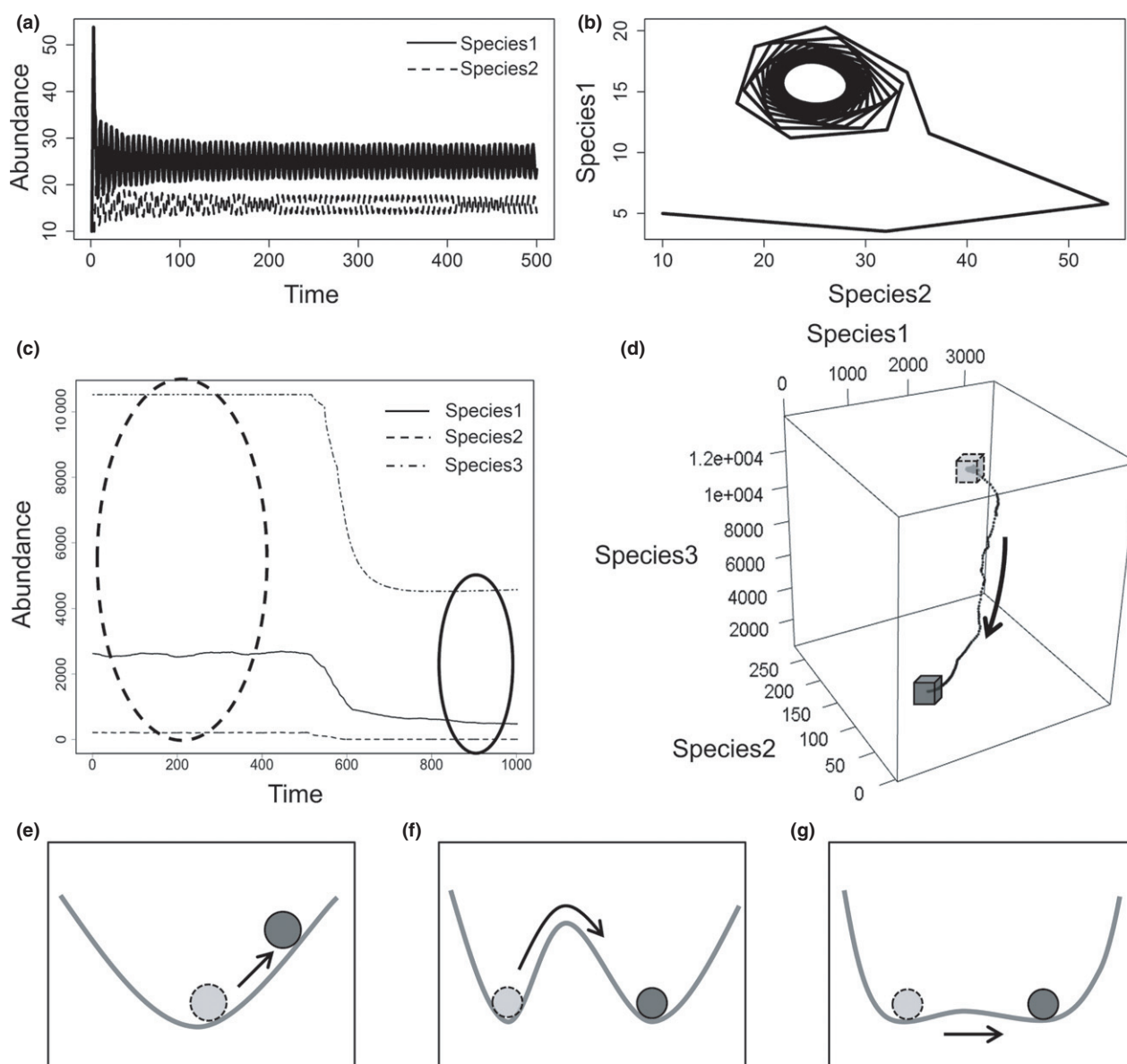
Figure 1 The utility of phase portraits for studying stability. A system of (a) two species can be represented by (b) a classical two-dimensional phase portrait. The system's state at equilibrium is represented by a circling behaviour in (b) that corresponds to oscillations of species abundances in (a). This concept can be extended to higher dimensions, where the (c) dynamics of a three species community are represented by (d) a three-dimensional phase portrait. In multidimensional space, states at equilibrium become clouds of points in (d), which can be represented by *n*-dimensional hypervolumes (schematic cubes). Comparisons between hypervolumes can be related to the ball-and-cup analogy of resilience, as they indicate departures from the initial state that can happen (e) within the same basin of attraction, (f) when the system shifts to an alternative stable state, or (g) when the equilibrium is displaced (see Beisner *et al*. 2003; Horan *et al*. 2011).

the second section, we present its application to a case study, aiming to assess the departures of distinct plant communities from their initial states in a national park, in the French Alps.

Step 1. Choice of components

To detect changes in ecosystem states, we propose building *n*-dimensional hypervolumes using time series of *n*-ecosystem components at equilibrium (Fig. 2, Step 1). A wide range of different components can be used (Table 1). Ultimately, the choice of components depends on what properties and

changes are under focus. For instance, if the user wishes to focus on changes in community structure and evenness patterns, relative species abundances should be considered, while changes in overall species abundances should be followed using raw abundances if the rareness of species is important for the research question. On the other hand, if the focus is on a community's functional characteristics and structure, then functional traits should constitute the hypervolumes. Also, depending on the chosen components, stability can be assessed at different spatial scales. For simplicity, we henceforth speak about community stability, but the same approach can be applied at the habitat and landscape scales.
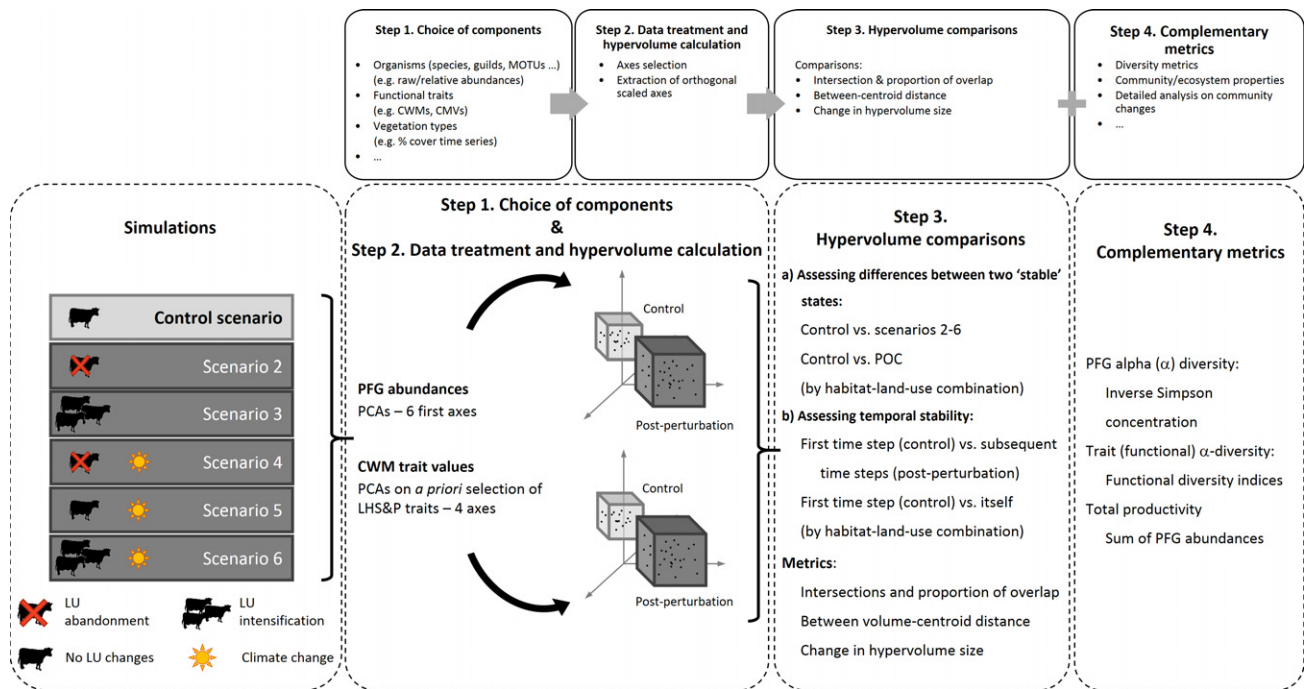
Figure 2 Framework scheme. Several types of time series data can be used (Step 1). In our study case, we used simulated plant functional groups' (PFG) abundances and community-weighted mean (CWM) trait values per habitat-land-use combination, under a given scenario of land-use and/or climate changes. Variables used for hypervolume calculations should be scaled and uncorrelated (Step 2), which was ensured by selecting axes extracted from principal components analyses (PCAs) on scaled time series of PFG abundances and of CWM trait values. Pre- and post-perturbation hypervolumes are then calculated using, in this example, the PCAs factor scores referring to control (scenario 1) and post-perturbation data (remaining scenarios), and then compared (Step 3). Comparisons between hypervolumes can be complemented using other metrics (Step 4) for a further analysis of community changes. In Step 3, 'POC' stands for 'POC' hypervolumes (see methods section 'Step 3. Comparing hypervolumes to analyse community changes').

Finally, hypervolumes can be used to follow community changes in time, by building separate hypervolumes for different time slices and comparing between them, or against a reference period. Alternatively, 'space-for-time' comparisons can also be used if hypervolumes are built from replicates of communities under different disturbance treatments.

Step 2. Data treatment and hypervolume calculation

Components that will constitute the axes for hypervolume calculation must follow certain criteria (Fig. 2, Step 2). To start with, the number of dimensions will influence hypervolume metrics and should be fixed to ensure comparability between hypervolumes (Blonder *et al.* 2014). Components entering the analysis should be in comparable units (e.g. centred and scaled) and uncorrelated (Blonder *et al.* 2014). When the different components one wants to include are correlated, we suggest the use of multivariate analyses, such as principal components analyses (PCAs), or Hill and Smith analyses (Hill & Smith 1976) if a mix of continuous, categorical and ordinal variables are used (e.g. Heiser *et al.* 2014). Alternatively, principal coordinates analyses (PCoAs) based on distance matrices and designed to represent differences between objects as faithfully as possible (i.e. distances based on traits values), are also a suitable option (Maire *et al.* 2015). These approaches will reduce dimensionality and extract a number of centred and scaled orthogonal axes

from the data. Hypervolumes are then built using the factor scores on the chosen principal components (PCs), or the pre-selected uncorrelated (and eventually scaled) variables. Since the interest is to assess differences between pre- and post-perturbation states of a given community (comparing pre- and post-perturbation hypervolumes), the PCA is calculated on the pre- and post-perturbation datasets together; separate hypervolumes should then be calculated from the factor scores corresponding to each dataset. The final number of variables, or PCs, to be used should be decided based on knowledge of key components for community stability, the percentage of explained variance, or expert knowledge. When using a PCoA, Maire *et al.* (2015) proposed to assess the quality of the reduced space using the mean squared deviation between the initial distances between objects (e.g. trait values) and the standardised distances in the new space. In any case, the number of variables/PCs should not exceed 5–8, to avoid having highly disjunct hypervolumes (hypervolumes with 'holes'; Blonder *et al.* 2014).

The calculation of hypervolumes follows a multidimensional kernel density estimation procedure. Briefly, this consists in the estimation of overlapped hyperbox kernels from which a uniform point density is extracted using random sampling, importance-sampling and range-testing techniques (see Blonder *et al.* 2014 for detailed description). The values of kernel bandwidths can be chosen by the user and should avoid

having disjoint observations (which cause disjunct hypervolumes; Blonder *et al.* 2014). Although there is no minimum number of data points needed to compute the hypervolumes, analyses with few observations (roughly < 10 times the number of dimensions) are more influenced by the choice of bandwidth (Blonder *et al.* 2014). In the scope of our approach, we suggest a standardised method to choose the bandwidth value in Appendix S1, guaranteeing comparability between different hypervolumes even with low sample size.

Step 3. Comparing hypervolumes to analyse community changes

Sufficiently large changes in environmental conditions are expected to produce shifts in community structure and composition that will cause the hypervolume to shift. We propose three metrics to assess differences in pre- and post-perturbation states (Fig. 2, Step 3) that focus on: (1) the overall similarity/dissimilarity between two states, (2) changes in mean values of the chosen components and (3) changes in their variance.

First, the proportion of overlap between pre- and post-perturbation hypervolumes (Fig. 1d) will reflect overall differences between the two corresponding states. Overlap is calculated as the ratio between the intersection volume and the total volume occupied by the two hypervolumes, being expected to decrease as a community changes. For instance, if a plant community has suffered significant changes in structure and composition and became another vegetation type, hypervolumes will be farther away and may not intersect (overlap = 0). Whether or not this indicates a permanent state-shift (i.e. irreversible even if environmental conditions are returned to pre-shift values) will depend on the community in question and the type of disturbance. Conversely, if hypervolumes intersect, their overlap will be indicative of similarities between them.

Second, the distance between the centroids of the pre- and post-perturbation hypervolumes will reflect how much mean values of the ecosystem components have departed from their pre-perturbation levels (changes in mean values).

Third, changes in hypervolume size may indicate changes in the amplitude of variation of the selected components (changes in variance).

It is also important to consider that in certain cases, the number of observations used to calculate the hypervolumes may differ. Blonder *et al.* (2014) did not discuss this issue and seemed to compare hypervolumes calculated using data with different sizes (see their example of morphological comparisons of species of Darwin's finches); however, we suggest that in these cases, the user can perform randomised permutation testing with data subsets (see e.g. Brandl & Bellwood 2014) to avoid influencing comparisons between hypervolumes.

Step 4. Complementary metrics for more detailed analyses

Hypervolume comparisons *per se* do not provide information about what type of changes the community went through. Hence, we suggest analysing complementary metrics that reflect changes in community composition or structure (Fig. 2, Step 4). The choice of these metrics depends on the focus of the analysis and on the ecosystem components being analysed.

For instance, when studying the stability of taxonomic and functional composition, we recommend using indices that reflect changes in taxonomic, functional or phylogenetic diversity (or their combination), both in average terms and in terms of dispersion (see Pavoine & Bonsall 2011 for a detailed review).

ILLUSTRATION: A MOSAIC ALPINE LANDSCAPE UNDER LAND-USE AND CLIMATE CHANGES

Our general framework has the ability of deciphering the consequences of environmental changes for ecosystems over large spatial scales and heterogeneous landscapes, while analysing multiple ecosystem components at the same time. This is illustrated by the following analysis of a mosaic alpine landscape within a national park subject to abrupt land-use and climate changes.

Case study and simulated vegetation dynamics

The Ecrins National Park (ENP) is situated in southeast France in the French Alps, covering a surface area of 178 400 ha. It is composed of a mosaic of mountainous to alpine ecosystems, harbouring a rich flora (~ 2000 species) and present land-use practices are accurately mapped (extensive grazing, 50%, crop fields and mown grasslands, 15%, and forest management, 10%). The ENP presents an interesting case where highly diverse Alpine landscapes face current threats of changing land-use practices and climate warming, which are likely to have synergistic effects.

To simulate the vegetation dynamics and associated community shifts resulting from climate and LUCs, we used FATE-HD, a recently developed dynamic landscape vegetation model that has been previously parameterised for the ENP (Boulangeat *et al.* 2014b). The model simulated the spatiotemporal dynamics of 24 plant functional groups (PFGs, see Table S1; Boulangeat *et al.* 2012) at 100 m resolution. Competition for light between PFGs, their population dynamics, dispersal and responses to land-use regimes and climate are all explicitly modelled. Land-use regimes were modelled spatially and included grazed areas with three levels of intensity (low, medium and high) and mown areas. Yearly outputs used here were the abundance of each PFG in each pixel. A more detailed description of the study area and of FATE-HD can be found in Appendix S2; we refer the reader to Boulangeat *et al.* (2014b) for model details and parameterisation, and to Boulangeat *et al.* (2014a) for details on chosen climate and LUC scenarios.

Scenario building

FATE-HD is an equilibrium model, having the capacity of internal regulation and feedback mechanisms that contribute to a directional response of equilibrium system behaviour. Therefore, it successfully simulated the equilibrium vegetation dynamics of the ENP subject to present land-use (mowing and grazing; Boulangeat *et al.* 2014b). Based on those validated simulations, we analysed six different scenarios (after Boulangeat *et al.* 2014a): no change at all (control scenario),

abandonment of all grazing and mowing activities (scenario 2), intensification of grazing (to high levels) in all grazed areas and creation of new grazing and mowing areas (scenario 3) and the previous three scenarios combined with climate change (scenarios 4–6; Fig. 2).

An initialisation phase was run for 1650 years to reach present equilibrium vegetation dynamics (see Appendix S2 for details). Scenarios were then applied to the equilibrium state. LUCs were applied 4 years after the equilibrium was reached and changes were kept until the end of the simulation; climate change (CC) was applied continuously from the 15th to the 90th year after equilibrium was reached and remained constant afterwards until the end of the simulation. Scenario simulations were run for a total of 500 years after the initialisation phase to allow the establishment of new equilibria. Both the initialisation phase and scenario simulations were replicated three times.

Given the high heterogeneity of the ENP and to avoid mixing together ecosystems with contrasted vegetation dynamics, we decided to analyse community stability through the lens of habitat type (see Appendix S2 for the list of habitat types and their map in Fig. S1a) and current land uses (grazing intensities low, medium and high, mowing and non-disturbed habitats, as well as potentially grazed, mown and non-disturbed habitats under intensification scenarios; see Fig. S1b for land-use maps), taking advantage of the very detailed habitat and land-use characterisation of the ENP (Esterni *et al.* 2006). For example, all woodland mosaics under present grazing pressure were considered together (the pixel-based abundances of PFGs being summed across the same habitat type). This resulted in temporal information on the 24 PFG abundances in 56 pairs of habitat and land-use types.

We applied our framework to explore the differences between pre-perturbation and post-perturbation community states in two ways: (1) an analysis focusing on differences between pre- and post-perturbation states and (2) an example focused on analysing temporal stability. Where appropriate, we distinguish the methodology and results referring to these two approaches.

Step 1. Choice of components

As we were interested in the stability of taxonomic and functional diversity at the community level, we chose to use the time series of PFG abundances (24 components) and the time series of CWM trait values (4 components), which we analysed independently from each other. We calculated yearly raw and relative PFG abundances for each habitat and land-use combination by summing them across the ENP.

To estimate changes in the overall trait combination of each habitat type for a given land use, we calculated CWM trait values based on the simulated abundances of each PFG and their respective trait values (Table S1). We selected three traits reflecting the leaf-height-seed (LHS) plant ecology strategy by Westoby (1998) – mean specific leaf area (SLA), log-height, log-seed mass – plus one reflecting PFG responses to grazing – palatability. Palatability was treated as a continuous trait to allow a better representation of the variability in its CWM values (hence, we followed the assumption that palatability classes are evenly spaced; Jouglet 1999).

Step 2. Data treatment and hypervolume calculation

To ensure orthogonality and a feasible number of dimensions for hypervolume calculations, we used PCAs on the abundances (raw or relative) of the 24 PFGs and on the CWM trait values. Data scaling was done prior to the PCA, using root mean squares on both the control and scenario of change datasets together. We then selected the first six orthogonal PCs to be used as dimensions for the 'PFG hypervolumes', which still retained a cumulative explained variance > 95% (obtained using raw PFG abundances; Fig. S2). The same number of axes was used to build hypervolumes from relative PFG abundances. As for 'trait hypervolumes', we used the totality of the four PCs, since only four traits were selected, the PCA only ensuring orthogonality. Hypervolumes were then built using the factor scores on the selected axes. Although we treated all traits as continuous variables, in other situations, a mix of continuous, categorical and ordinal traits may be wanted. In these cases, the PCA can be substituted by a generalisation of the Hill and Smith analysis available in the 'ade4' *R* package, *dudi.mix* (Dray & Dufour 2007).

Comparing two states
To assess differences between pre-perturbation and post-perturbation states, we compared PFG and trait hypervolumes of the control scenario (no LUC, no CC) to the five scenarios of LUC and/or CC (post-perturbation hypervolumes), for each habitat-land-use combination and each of the three repetitions. Control hypervolumes were calculated from the 500 years of the control scenario (no climate and no LUCs, equivalent to a pre-perturbation state), while the last 100 years of the five scenarios of LUC/CC were used to calculate post-perturbation hypervolumes, since vegetation had stabilised by then.

Assessing temporal stability
In addition, we analysed the potential of our framework to investigate temporal stability using a demonstrative example. We selected two habitats (grasslands and thickets and scrublands) subjected to current land-use practices (three intensities of grazing, mowing and no-disturbance) and CC (scenario 5). We focused on community responses during and shortly after climate changes, analysing the first 150 years of the scenario simulation. Time series of raw and relative PFG abundances were broken into time steps of 15 years length, from which hypervolumes were built. The calculation of hypervolumes followed the description above, with control datasets spanning the 15 years prior to the first climate change (control hypervolume) and subsequent time steps of 15 years considered as post-perturbation data (post-perturbation hypervolumes).

Step 3. Comparing hypervolumes

As a proof-of-concept (POC) of our method, we first tested our framework on the control scenario where nothing should be detected in theory. We did this by (1) comparing control hypervolumes to 'POC' hypervolumes calculated from an additional 100 years ran from the end of the initialisation phase (for both PFG abundances and CWM traits) and (2) comparing the first time step hypervolume to itself (i.e.

control hypervolume, built from the first 15 years of the scenario simulation). These comparisons provided a 'no change' baseline that was used as reference for statistical analyses and to interpret results.

Comparing two states

Hypervolume comparisons (proportion of overlap, centroid distances and changes in size) were made for pairs of control and post-perturbation hypervolumes (control vs. scenario hypervolumes; control vs. POC hypervolumes) for each habitat-land-use combination and each repetition, resulting in 1008 comparisons (five scenarios against the control and POC against the control × 56 habitat-land-use combinations × 3 repetitions). Changes in control vs. post-perturbation hypervolume sizes (Δsize) were calculated as the difference between post-perturbation and control hypervolume sizes, after scaling them relatively to the largest hypervolume obtained across communities (enabling a comparison between PFG and trait hypervolumes).

Repetitions were analysed together as samples of a same treatment. Effects of CC, LUC and habitat-land-use combinations (explanatory variables) on overlap, centroid distances and Δsize (response variables) were assessed using analyses of variance (ANOVAS). In all model analyses, control vs. POC hypervolume comparisons were used as 'no change' observations that corresponded to no climate and no LUCs. Linear model assumptions (normality and homoscedasticity of residuals) were ensured by doing a square-root transformation on overlap values from raw PFG abundance and from trait hypervolumes, and a variant of the logit transformation on overlap values from relative PFG abundances (see Appendix S3 for details). Centroid distances and Δsize values did not require any transformation; however, extreme outliers were removed from the analyses of Δsize values of relative PFG abundances and trait hypervolumes (two and three outliers respectively); best models were selected on the basis of AICc scores, starting with full models (one response variable in function of all explanatory variables and all their possible interactions) that were gradually simplified (final models are listed in Table S2 and in Appendix S3). Model outputs were analysed in terms of the importance of main effects and interaction effects, while differences between factor levels were analysed graphically (fitted values were back-transformed where appropriate), due to the high number of level combinations.

Assessing temporal stability

To assess changes in hypervolumes through time, the first time step [control] hypervolume was compared against each hypervolume from subsequent time steps. This was done for 270 pairs of hypervolumes (first time step against 9 subsequent time steps × 1 scenario × 10 habitat-land-use combinations × 3 repetitions). We focused on the temporal evolution of overlap and analysed its response to CC under different habitat-land-use combinations using generalised additive models (GAMs), with a Gaussian smoother fitted for each habitat-land-use combination. Overlap values of relative PFG abundances were analysed after a square-root transformation, which improved the residual distribution of the models.

Step 4. Complementary metrics for more detailed analyses

For a deeper analysis on how pre- and post-perturbation states differed, we calculated yearly complementary metrics for each habitat-land-use combination and each scenario. Yearly PFG α-diversity was calculated as the inverse Simpson concentration to reflect changes in taxonomic richness and evenness (Leinster & Cobbold 2012). Two functional diversity indices, functional dispersion (FDis; Laliberté & Legendre 2010) and functional evenness (FEve; Villéger *et al.* 2008) were used to assess changes in average functional distances in the community and their variance among PFGs respectively (Pavoine & Bonsall 2011). Analogously to hypervolume comparisons, these indices indicated changes in the mean and variance of functional α-diversity. Finally, we also calculated total productivity, in the form of total PFG abundance, since it has been used to study ecosystem responses to perturbations (e.g. Kerkhoff & Enquist 2007; Polley *et al.* 2013; Keersmaecker *et al.* 2014).

The responses of diversity indices and productivity to CC, LUC and habitat-land-use combinations were also analysed statistically (detailed in Appendix S4). Since the analysis of temporal stability was merely demonstrative, complementary metrics were not used in this situation.

Hypervolumes were calculated using the recently made available *R* package 'hypervolume' (Blonder *et al.* 2014). Selection of optimal bandwidth sizes for each set of components is detailed in Appendix S1 (along with a sensitivity analysis of bandwidth effects on overlap). All hypervolumes were built using a quantile threshold of 0% (Blonder *et al.* 2014). Functional diversity indices were calculated within the *R* package 'FD' (Laliberté & Legendre 2010). Source code for calculating and comparing hypervolumes, together with nine example datasets are available in Appendix S5.

RESULTS

Comparing two states

We assessed differences between pre- and post-perturbation states by comparing hypervolumes built from the control scenario with hypervolumes built from each scenario of change (but see examples of full system trajectories in Fig. 3). Concerning PFG hypervolumes, here, we present results obtained using raw abundances, instead of relative abundances, because we were interested in accounting for changes in the abundances of all PFGs, rather than focusing on structural and dominance changes. In general, comparisons between hypervolumes built from relative abundances resulted in more frequent intersections and larger overlaps, smaller distances between hypervolumes and smaller size changes (full results are available in Appendix S3).

Testing the framework: confronting POC and control hypervolumes

When comparing 'POC' and control hypervolumes, 100% of all pairs of hypervolumes intersected and the proportion of overlap between them was much larger than that obtained between control and post-perturbation hypervolumes (Fig. 4). Also, centroid distances (Fig. 5a, b) were always small, despite
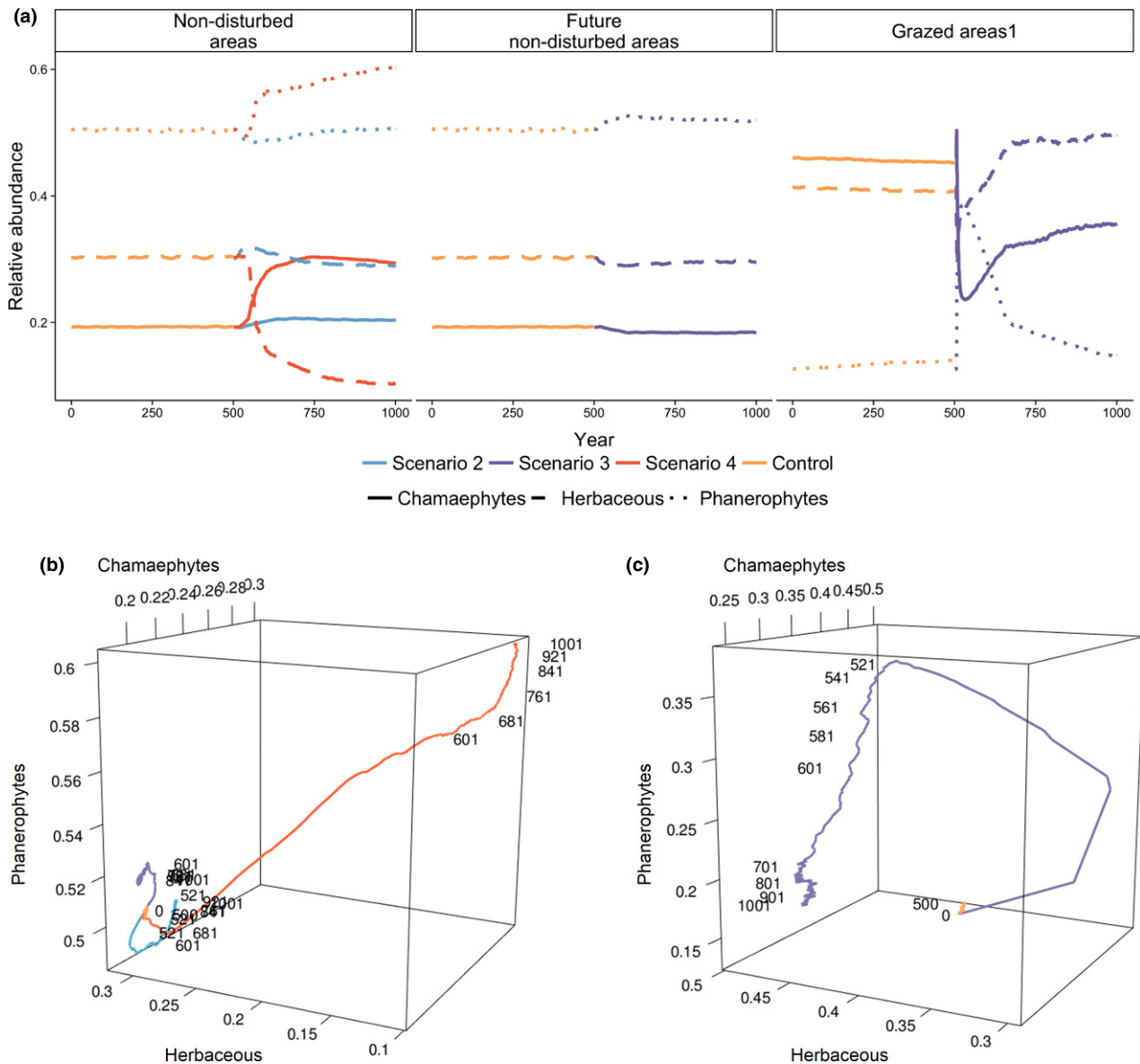
Figure 3 Full system trajectories under different scenarios and land-use practices. The full trajectories of thickets and scrubland vegetation are shown for three scenarios of climate and/or land-use changes (LUCs), under three types of land-use practices. The first 500 years correspond to the control scenario (in orange), followed by another 500 years of climate and/or LUCs: land-use abandonment without and with climate change in blue and red (scenarios 2 and 4 respectively) and land-use intensification in purple (scenario 3). Since we are graphically constrained to three dimensions, we plotted the trajectories using relative abundances of chamaephyte (full lines), herbaceous (dashed lines) and phanerophyte (dotted lines) plant functional groups (by adding up separate group's abundances per life form type). The three-dimensional plot in (b) corresponds to trajectories in non-disturbed areas – first two panels in (a) – whereas in (c) it corresponds to trajectories in intensified grazed areas – last panel in (a).

changes in hypervolume size in disturbed areas (Δsize; Fig. 5c, d). These results confirmed that our approach is not prone to detecting wrong community shifts.

Hypervolume intersections and overlap
Only 3% of all PFG hypervolume comparisons and 13% of all trait hypervolume comparisons resulted in intersections and overlap was generally small, especially between PFG hypervolumes (Fig. 4a). Overlap was significantly affected by CC, LUC and habitat-land-use combinations, as well as their two- and three-way interactions (all effects being significant for *P*-value < 0.01), but the order of their importance changed

depending on the type of components used (Fig. S3; Table S2). Generally, overlaps between pre- and post-perturbation hypervolumes indicated that all communities were unstable under CC (note the absent or small overlaps both for PFG abundance and trait hypervolumes, Fig. 4). In addition, land-use abandonment strongly affected disturbed communities (in terms of PFG abundances and CWM trait values; Fig. 4a, b) and land-use intensification strongly affected non-disturbed communities (only in terms of PFG abundances; Fig. 4a, c). It is interesting to note that PFG hypervolumes generally intersected and overlapped less than trait hypervolumes (Fig. 4). A more detailed analysis of the importance of CC, LUC, and habitat-land-use
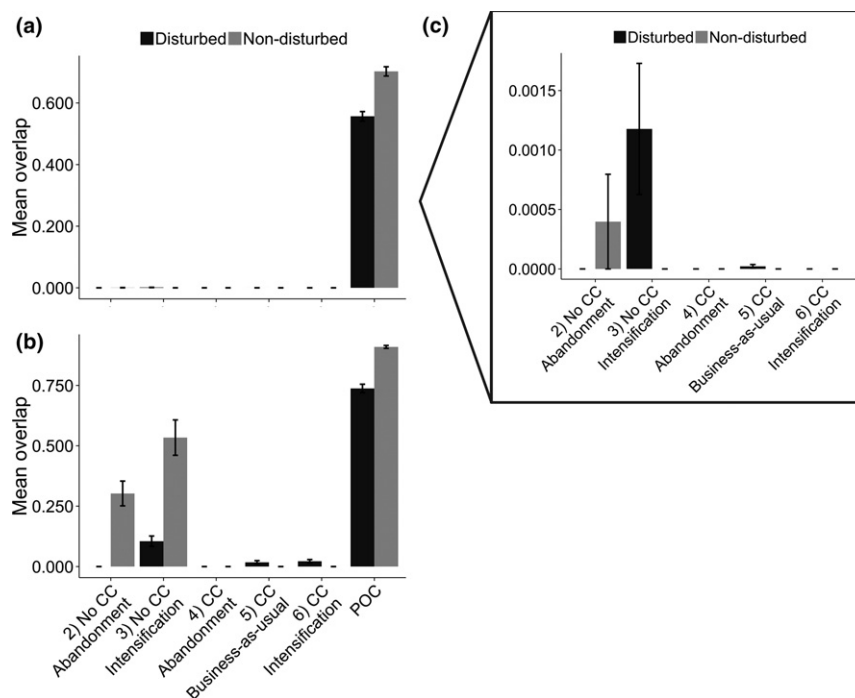
Figure 4 Overlap in disturbed and non-disturbed areas. Proportion overlap between control and post-perturbation hypervolumes of (a, c) PFG raw abundances – (a) and (c) only differ in the *y*-axis scale – and (b) CWM trait values. The proportion of overlap (overlap) was calculated as the ratio between the intersection volume and the total volume occupied by the two hypervolumes (standard errors shown as error bars). Observed mean overlaps are shown by scenario, across all habitat types and grouped by disturbed areas (areas under present grazing or mowing regimes and areas that will become grazed on mown under scenarios of land-use intensification) and non-disturbed areas (all areas that are not currently grazed or mown and those that will remain so, under land-use intensification scenarios). Standard errors are shown as error bars. Comparisons between 'POC' and control scenario hypervolumes are shown in (a) and (b), but not in (c), so that overlap values obtained in other scenario comparisons can be seen.

combinations for hypervolume overlaps for the different components is presented as Supporting Information (see Fig. S3, Table S2 and Appendix S6).

Finally, hypervolume overlaps were mostly independent from hypervolume size, with an exception for POC comparisons for which the two were negatively correlated (Fig. S4). This indicates that, all else remaining equal (under no perturbations), larger sizes did not drive larger overlaps.

Distances between hypervolumes and changes in size
In all situations, models explaining the response of centroid distances and changes in size (Δsize) included all three main factors (CC, LUC and habitat-land-use combinations) and possible interactions between them; all model terms were significant, but again their relative importance changed depending on the type of components used and the response variable (Table S2). While mean PFG abundances were most affected by CC, LUC and their interaction, the variance in PFG abundances was most affected by habitat-land-use combinations and their interaction with LUC, followed by CC and remaining terms. On the other hand, mean trait values were most affected by LUC, CC and their interaction, while trait variances were most affected by CC and its interactions with LUC and with habitat-land-use combinations (Table S2).

Plotting the observed mean centroid distances has shown that, considering the same LUC, CC almost always increased

the distance between hypervolume centroids, driving changes in mean PFG abundances and CWM traits (Figs. 5a, b). However, observed Δsize values show a different pattern. Changes in variance of PFG abundances seemed to be mostly associated with habitats being disturbed or not (disturbed habitats showing decreases in variance in post-perturbation hypervolumes; Fig. 5c), while changes in variance of trait values are associated with the presence of CC (CC driving increases of variance; Fig. 5d). Finally, it is also interesting to note that trait hypervolumes had generally much smaller sizes (data not shown) and Δsize values than PFG hypervolumes. We provide further results of the effects of CC, LUC and habitat-land-use combinations on centroid distances and Δsize as Supporting Information (see Figs. S5 and S6, Table S2 and Appendix S6).

Exploring temporal stability

We exemplify the use of our framework to explore the temporal stability of two different communities that showed opposite results in terms of overlap, when only subjected to CC (scenario 5, considering PFG hypervolumes): grasslands and thickets and scrublands. For this analysis, only the first 150 years of the scenario simulation were considered, as we were interested in following community responses during and shortly after CC. Again, results presented here were obtained using raw PFG abundances (see Appendix S3 for results using relative PFG abundances).
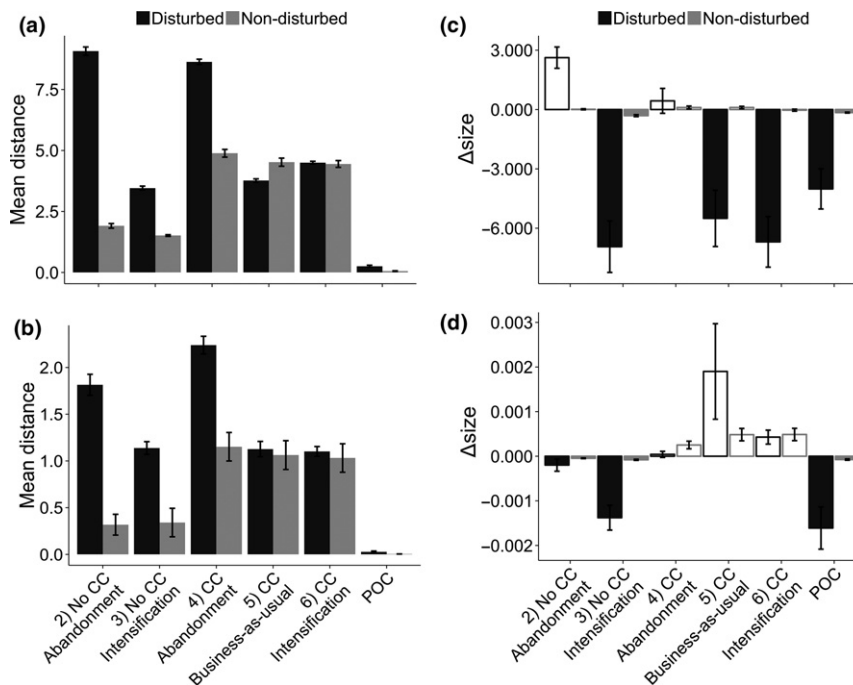
Figure 5 Mean distances and changes in size, in disturbed and non-disturbed areas. Mean centroid distances between control and post-perturbation hypervolumes and differences in their sizes (post-perturbation minus pre-perturbation; Δsize) are shown for (a, c) PFG raw abundances and (b, d) CWM trait values. Negative Δsize values indicate that the post-perturbation hypervolume was smaller than the pre-perturbation hypervolume, and vice-versa for positive Δsize values. Both metrics are shown by scenario, across all habitat types and grouped by disturbed areas (areas under present grazing or mowing regimes and areas that will become grazed on mown under scenarios of land-use intensification) and non-disturbed areas (all areas that are not currently grazed or mown and those that will remain so, under land-use intensification scenarios). Standard errors are shown as error bars. Comparisons between 'POC' and control scenario hypervolumes are also shown.

Testing the framework: comparing first time step hypervolume with itself

Confronting the first time step hypervolume to itself provided an estimate of the variability associated with the calculation of hypervolumes and their overlap, as well as a baseline values for the temporal analysis of changes in hypervolumes. Overlap was always positive and generally similar between habitat-land-use combinations (Fig. 6). It was also always larger than the overlap measured between the first time step and subsequent time steps (Fig. 6).

Hypervolume overlap in time

Overlap decreased in time as communities changed, reaching 0 before the CC period ended; yet, the rate at which it decreased depended on the habitat-land-use combination (Fig. 6). Mown grasslands were less stable, showing larger and faster decreases of overlap, while grasslands grazed at low intensity ('grazed areas1') were more stable, showing slower decreases of overlap (Fig. 6). Thickets and scrublands were generally less stable, with overlap values reaching 0 before they did so in grassland habitats. Mown thickets and scrublands had smaller overlaps even before CC started.

Complementary metrics

Models of PFG α-diversity showed that this metric was not significantly affected by any of the model terms included (Table S3). However, a graphical analysis of mean PFG α-diversity across the last 100 years of the simulations showed that when compared with control levels, the abandonment of disturbed areas increased PFG diversity, while CC and land-use intensification generally decreased it (Fig. S7).

Metrics of functional α-diversity responded significantly to all effects, with the exception of FEve, which was not differently affected by CC when land-use was intensified (see 'set 2' models and Appendix S4; Table S3). Yet, the importance of CC, LUC and habitat-land-use combinations depended on the metric used (Table S3). For instance, like hypervolume metrics, FEve was most affected by LUC, CC and their combination; yet, FDis was more affected by the interaction between CC and LUC, followed by habitat-land-use combinations, while CC alone had a comparatively weaker effect. As with PFG α-diversity, FEve generally increased after land-use abandonment and decreased after CC and land-use intensification (when compared to control levels; Fig. S8b). FDis had similar responses to FEve, but differences between disturbed and non-disturbed areas in terms of mean FDis were usually smaller (Fig. S8c).

Finally, productivity was also significantly affected by all model terms included, with habitat-land-use combinations having the strongest effect on its variation (sets 1 and 2; Table S3). Mean productivity in non-disturbed areas was much higher than in disturbed areas, even after abandonment. As with metrics of taxonomic and functional diversity, mean productivity increased after land-use abandonment and decreased after CC and land-use intensification (Fig. S10).
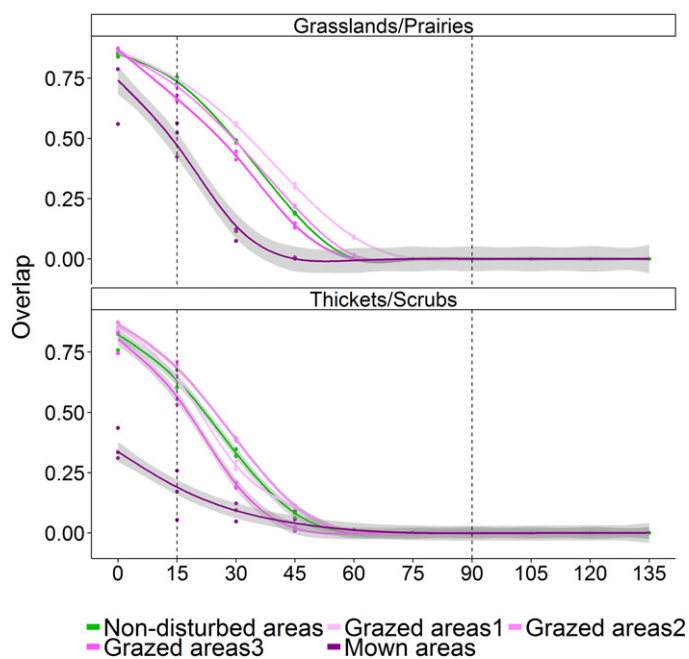
Figure 6 Temporal stability measured by hypervolume overlap. Temporal stability was analysed by modelling the temporal response of the proportion of overlap (overlap) under different habitat-land-use combinations, using generalised additive models (GAMs) with a Gaussian smoother fitted for each habitat-land-use combination. Each coloured point corresponds to the comparison between a hypervolume at a given time slice and the first hypervolume, with colours referring to land-use (the 1 year of each 15 year time slice is indicated in the x-axis). Dashed vertical lines indicate the start and end of simulated climate changes.

DISCUSSION

Environmental changes impact biodiversity at different levels and may lead to changes in community and ecosystem structure and functioning. Instead of studying ecosystem stability through the lens of single diversity or ecosystem functioning metrics, we propose that the contribution of different taxonomic, functional or landscape entities should be considered. Our framework makes use of n-dimensional hypervolumes to assess changes in ecosystem states that are driven by the responses of different ecosystem components to environmental changes. It provides a flexible way to quantitatively assess ecosystem changes and the relative impact of different disturbances on ecosystem stability. Most importantly, it allows analysing ecosystem responses at different levels of biodiversity and/or ecosystem functioning, enabling an integrative analysis of stability. Moreover, our framework can be combined with other metrics for a detailed analysis of the type of changes the system suffered.

Assessing the magnitude of change

Comparing hypervolumes in terms of their intersection and overlap, the distance between their centroids and their changes in size, provides a measure of the magnitude of changes an ecosystem has suffered. If different types of components are used, these hypervolume metrics are also informative about their relative stability. In our example, we have

shown that both taxonomic and functional diversity are destabilised by climate and LUCs; yet, functional traits changed less than PFG abundances, suggesting higher functional stability. Also, hypervolume metrics allow analysing changes in ecosystem states both in terms of mean values of the chosen components (centroid distances) and in terms of changes in their variance. For instance, climate and LUCs affected mean PFG abundances and mean trait values similarly, but differed in their effect on PFG and trait variances. Moreover, since hypervolumes do not summarise different components into a single metric, but instead describe them as a multidimensional cloud, changes in volume may not only indicate changes in oscillatory patterns of the considered components, but also changes in synergies and trade-offs between them.

Furthermore, since the approach can be applied across different types of perturbations, their relative effects on ecosystem stability can be directly compared. This can be achieved by modelling the response of hypervolume metrics to the combinations of perturbations under focus, as we have done here. In our simulated plant communities, the interaction between climate and LUCs had a larger impact on hypervolume overlap and centroid distances than the effect of habitat and land-use regime types, indicating that the synergy between these two global change threats has an overall large effect that may be generalised across the different Alpine ecosystems.

Additionally, because our framework can be applied to different types of habitats, it allows comparing their responses to similar perturbations; although we did not present the full extent of the results from our case study application, we were able to detect cases where particular habitats did not follow the general pattern of responses to the simulated perturbations (see Appendix S6).

Assessing the type of change

Using n-dimensional hypervolumes is not only useful to detect overall changes in ecosystems but can also be informative about what facets of an ecosystem were most affected by perturbations. For instance, in our case study, hypervolume comparisons indicated that PFG abundances were more affected by land-use and climate changes than trait values. In case we had been interested in investigating how perturbations impacted the communities under focus, this information would have directed our attention towards changes in taxonomic structure and composition, and in population dynamics, perhaps saving a broader exploratory analysis.

Complementing the analysis of the global variation of the ecosystem with diversity metrics, productivity measurements, or even a more detailed analysis on changes that occurred to particular ecosystem components (not shown here, but see, for example, Lenoir et al. 2010) adds a finer understanding of changes that occurred in the system. Complementary metrics must be carefully chosen with regard to the focal research question. How to do this has been discussed elsewhere (see Pavoine & Bonsall 2011) and we recommend that users select metrics that add complementary information to hypervolume metrics, reflecting changes in both community structure and composition.

However, using these metrics independently may provide a false notion of stability. For instance, if we had followed

classical ways of analysing stability and focused only on productivity, we would have concluded that land-use abandonment and climate change do not cause major changes to Alpine communities; similarly, had we only investigated perturbation effects on taxonomic and functional diversity, we would have not detected large changes in mean trait values of undisturbed rocky and scree vegetation in result of land-use abandonment in adjacent areas (see Appendix S6).

Following changes in time

The approach we propose here also enables tracking transient dynamics when communities have lagged responses to perturbations. To do so, the user should have several observations *per* time period and we remind them to fix bandwidths across time periods for hypervolume calculations. As we have demonstrated, this can be done across various communities and perturbations to analyse which communities are more sensitive and which perturbations cause the fastest changes. In our case study, both grasslands and thickets and scrublands suffered large changes in PFG composition and/or structure in result of climate change, regardless of land-use management type, due to the expected species turnover caused by climate warming (Asner *et al.* 2004; Gottfried *et al.* 2012). Alternatively, it is possible to do 'space-for-time' comparisons, where communities are subjected to treatments of different perturbation intensities; in this case, hypervolumes built from different replica can be compared within community types and across perturbation treatments, or across community types for a given perturbation treatment, to allow investigating the effect of perturbations and how different communities respond.

In either case, we believe that the overall measure of ecosystem state that this framework provides may allow applying the concepts of ecosystem resilience while accounting for the multivariate and stochastic nature of complex ecosystems. Since hypervolumes measure and define different states of an ecosystem and enable their comparison, they may be used to estimate ecosystem resilience, i.e. measuring rates of return to equilibria – engineering resilience – or the magnitude of perturbation a community can withstand before shifting states – ecological resilience (*sensu* Holling 1996; Gunderson 2000). Although we have not directly applied our framework to quantify ecosystem resilience *per se*, we provide a short discussion on these aspects in Appendix S6. In future work, it would be interesting to investigate whether communities are able to return to their pre-perturbation states (or hypervolumes) if environmental changes are reversed and assess whether irreversible state-shifts are associated with particular thresholds of hypervolume metrics, such as the distance between centroids. This can have important implications for the provisioning of ecosystem services if we consider that large changes in a community state will also imply large changes in the ecosystem services it provides (Folke *et al.* 2004; Nagendra *et al.* 2013). Also, investigating under which conditions communities revert to their original states would enable finding a criterion to define a 'new' hypervolume after a disturbance (new stable state). Although hypervolumes can be said to be 'different' if they do not intersect (overlap = 0), very small overlaps can already be indicative of large changes in a community. Although this is

not an issue in our simulation data because sufficient time was allowed for communities to reach new equilibria after perturbations, it can be if real data are used. In this case, we suggest that users report to changes in overlap to assess the magnitude of the effect and describe transient dynamics.

Advantages of using hypervolumes to assess community stability

Accounting for the multiplicity of components within an ecosystem, may reveal changes that cannot be detected if only one dimension is accounted for (e.g. productivity, diversity). The reason for this is that measures of diversity and productivity are community properties, which indicate ecosystem stability from a particular perspective. Diversity metrics will often be weighted differently according to species/PFG abundances. The choice of abundance currency has been shown to affect predictive models of biodiversity (Certain *et al.* 2014) and it is likely that it can impact results obtained when following stability of diversity in time. In addition, productivity will usually represent variations of the most productive species (Doak *et al.* 1998; Polley *et al.* 2007), which may not allow detecting finer changes in less productive species that may be important for other ecosystem functions. One strong advantage of our proposed method is that all community components chosen can have equal contributions to the analysis of stability of biodiversity. This allows detecting changes in the variability of community components without the need to weight components differently, or to summarise them into a one-dimensional measure, while still providing an overall measure of community stability. Furthermore, in complex situations where habitat mosaics exist and ecotone dynamics are observed, or when different types of communities are considered, relationships between community stability and metrics such as productivity and diversity indices are likely to change between communities, as well as across different disturbance regimes, hampering integrated analyses of community stability. When analysing ecosystem stability by directly integrating ecosystem components, this ceases to be an issue: changes occurring in different communities become comparable and analysing community stability at the landscape scale or across different organisational levels becomes possible.

Also, the approach we propose is flexible enough to be applied to different types of components, from real or simulated data. The choice of components depends on the focus of the analysis, but several components can be used separately to provide comparative analyses of stability, as we demonstrated here by comparing PFG abundances and CWM trait values. With the increasing popularity of environmental DNA approaches (Taberlet *et al.* 2012) and the continuously growing remote sensing datasets, temporal data on community and ecosystem composition, at taxonomical, functional, phylogenetic and landscape levels are more and more available. As these different datasets open new avenues for the study of ecosystem stability, integrative tools like the one presented here will be needed to assess stability across different types of communities, ecosystems and environmental and disturbance gradients in a consistent and robust way. They also become increasingly important to assess ecosystem stability under future environmental conditions. With evidence pointing to increases in frequency and intensity of extreme

climatic events, such as drought (Allen *et al.* 2010; IPCC 2012), it is crucial that models incorporate these events for future biodiversity predictions. We have shown that our framework can be coupled with a dynamic landscape vegetation model to study community stability under realistic scenarios of future land-use and climate changes. It can certainly be applied to other ecological models – like forest gap models (Lischke *et al.* 2006), dynamic global vegetation models, DGVMs (Krinner *et al.* 2005), or dynamic network models (see e.g. Steenbeek *et al.* 2016) – to study community stability under diverse scenarios (e.g. climate warming, extreme events, management).

In conclusion, integrating the variability of multiple ecosystem components can provide indication on general ecosystem stability. It is also informative about what types of perturbations cause the largest changes in ecosystems and which ecosystem facets are most affected by a given perturbation, which is useful for assessing community and ecosystem stability under forecasts of global change. Although here applied to Alpine ecosystems, our approach can be extended to any type of ecosystem and different ecosystem components, having the potential to be used for different purposes and at different landscape scales. Finally, this framework is a first step into the study of stability from a multidimensional perspective in complex ecosystems composed of habitat mosaics.

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