BIODIVERSITY RESEARCH

Combining point-process and landscape vegetation models to predict large herbivore distributions in space and time—A case study of *Rupicapra rupicapra*

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Abstract

Aim: When modelling the distribution of animals under current and future conditions, both their response to environmental constraints and their resources' response to these environmental constraints need to be taken into account. Here, we develop a framework to predict the distribution of large herbivores under global change, while accounting for changes in their main resources. We applied it to *Rupicapra rupicapra*, the chamois of the European Alps.

Location: The Bauges Regional Park (French Alps).

Methods: We built sixteen plant functional groups (PFGs) that account for the chamois' diet (estimated from sequenced environmental DNA found in the faeces), climatic requirements, dispersal limitations, successional stage and interaction for light. These PFGs were then simulated using a dynamic vegetation model, under current and future climatic conditions up to 2100. Finally, we modelled the spatial distribution of the chamois under both current and future conditions using a point-process model applied to either climate-only variables or climate and simulated vegetation structure variables.

Results: Both the climate-only and the climate and vegetation models successfully predicted the current distribution of the chamois species. However, when applied into the future, the predictions differed widely. While the climate-only models predicted an 80% decrease in total species occupancy, including vegetation structure and plant resources for chamois in the model provided more optimistic predictions because they account for the transient dynamics of the vegetation (−20% in species occupancy).

Main conclusions: Applying our framework to the chamois shows that the inclusion of ecological mechanisms (i.e., plant resources) produces more realistic predictions under current conditions and should prove useful for anticipating future impacts. We have shown that discounting the pure effects of vegetation on chamois might lead to over-pessimistic predictions under climate change. Our approach paves the way for improved synergies between different fields to produce biodiversity scenarios.

KEYWORDS
biodiversity modelling, biodiversity scenarios, dynamic modelling of vegetation, plant–herbivore interaction, protected area, species distribution model

1 | INTRODUCTION

Land use, climate change and other related anthropogenic disturbances are impacting species distributions across spatial scales at an unprecedented rate (Barnosky et al., 2011; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). As a consequence, predicting the response of biodiversity to global change has become an active field of research with high potential for conservation (Guisan et al., 2013). The development of models able to predict the future of biodiversity is now an important field of research (Mouquet et al., 2015). Apart from dynamic vegetation models, most biodiversity models of terrestrial ecosystems still ignore basic mechanisms, such as biotic interactions and links between biodiversity compartments (e.g., plants–herbivores) (Thuiller et al., 2013; Van der Putten, Macel, & Visser, 2010). The last two decades have indeed witnessed the rapid development of species distribution models that relate occurrence or abundance data to environmental variables (Elith & Leathwick, 2009). However, nearly all the available techniques make the assumption that species are distributed in isolation of each other (Guisan & Thuiller, 2005). This assumption goes against niche theory which postulates that observed distributions depict species' realized niches, which are the outcome of environmental filtering and biotic interactions (Soberón, 2007). However, biodiversity is not merely the sum of species, but results from interacting species that form multi-trophic assemblages. Models which ignore these basic mechanisms are prone to providing erroneous predictions of how global changes will impact biodiversity (Davis, Jenkinson, Lawton, Shorrocks, & Wood, 1998).

This issue is particularly important when it comes to understanding and predicting the distribution of herbivores which depends on both the suitability of the physical environment (e.g., climate, habitat structure) and the availability of their main plant resources (Mysterud & Ostbye, 1999). As climate or land use change is likely to influence the distribution and abundance of these resources, those changes have to be accounted for when analysing the potential impacts of climate change on herbivore distribution and intensity. One potential way of dealing with their trophic dependence on plants is to specifically introduce information on food resources (e.g., plant distributions) into the distribution models. While this is a sound approach, it runs into several hurdles. Firstly, the different resources the herbivores rely on, and their respective distributions need to be assessed. Secondly, in a global change context, the resources are also expected to shift their range in response to both climate and land use changes. Thirdly, adding all the potential resources for a given herbivore into the distribution models, on top of other climatic and land use variables might lead to overparameterized models producing unreliable predictions. A preferable method is to build a hierarchical framework in which the plant resources of a given herbivore are identified and then modelled as a function of climate. The potential distribution of plant resources is then projected over space under current and future conditions. Finally, the distribution of the herbivore is modelled as a function of both climate and the availability of the resources.

In this paper, we implemented a novel framework in which the distribution of the emblematic mountain herbivore of the European Alps, *Rupicapra rupicapra* (chamois), is modelled in a regional park in France, using climatic, resource and land cover variables, by integrating multiple sources of information and combining point-process model with spatially explicit vegetation simulations. In order to do this, we first used a unique database on the compositional diet of the chamois obtained for the study site by sequencing the environmental DNA found in multiple faeces of the species (Bison et al., 2015). Secondly, we built sixteen plant functional groups (PFGs) that account for the chamois' diet, as well as climatic requirements, dispersal limitations, successional stage, competitive ability and competitive tolerance (Boulangeat et al., 2012). Thirdly, we simulated the distribution of these PFGs using FATE-HD (Boulangeat, Georges, & Thuiller, 2014), a spatially and temporally explicit vegetation model, under current and future climatic conditions. Fourthly, by means of intensive field monitoring, we modelled the distribution of the intensity of the chamois according to topo-climatic variables and the simulated plant functional groups using a point-process model (PPM). PPM has recently been introduced as a suitable approach for modelling the number of presences, or individuals per unit area (intensity hereafter) (Renner et al., 2015).

This framework allowed us to successfully model the current and future distribution of the chamois in the Bauges Natural Regional Park at fine spatial (100 m) and temporal (ten-years interval) resolution according to climatic change and its resources' response to climate change. Our framework is readily applicable to all sorts of animal species that rely on vegetation structure and resources and should pave the way for more integrated biodiversity models that take into account multiple interactions.

2 | METHODS

2.1 | Study site and species information

The study was carried out in the Bauges Natural Regional Park (BNRP), a typical subalpine massif of 90,000 ha located in the northern French Alps (45.69°N, 6.14°E), with an elevation ranging from 250 m to 2,217 m (Figure 1). More than 70% of the BNRP is covered by forests up to 1,500 m, dominated by beech (*Fagus sylvatica*) and silver fir (*Abies alba*). The remaining areas are covered by open pasture, scree and cliffs. In subalpine pastures (at 1,630 m), snow covers the ground from November to April and frost lasts 123 (±19) days per year. These climatic conditions have favoured high plant diversity with more than 1,500 plant species. The study site also encompasses a National Game and Wildlife Reserve (NGWR; 5,205 ha), occupying the highest part of the massif where chamois populations have been monitored since 1985.

The alpine chamois is an emblematic, widespread (occupied area: >2 million hectares) and abundant (>100,000 individuals) species of the French Alps (Corti, 2011). The chamois is considered as a highly valued game species. Chamois are gregarious species with a clan-like organization, and the adult females keep to the same home ranges from year to year (Loison, Darmon, Cassar, Jullien, & Maillard, 2008). Natural
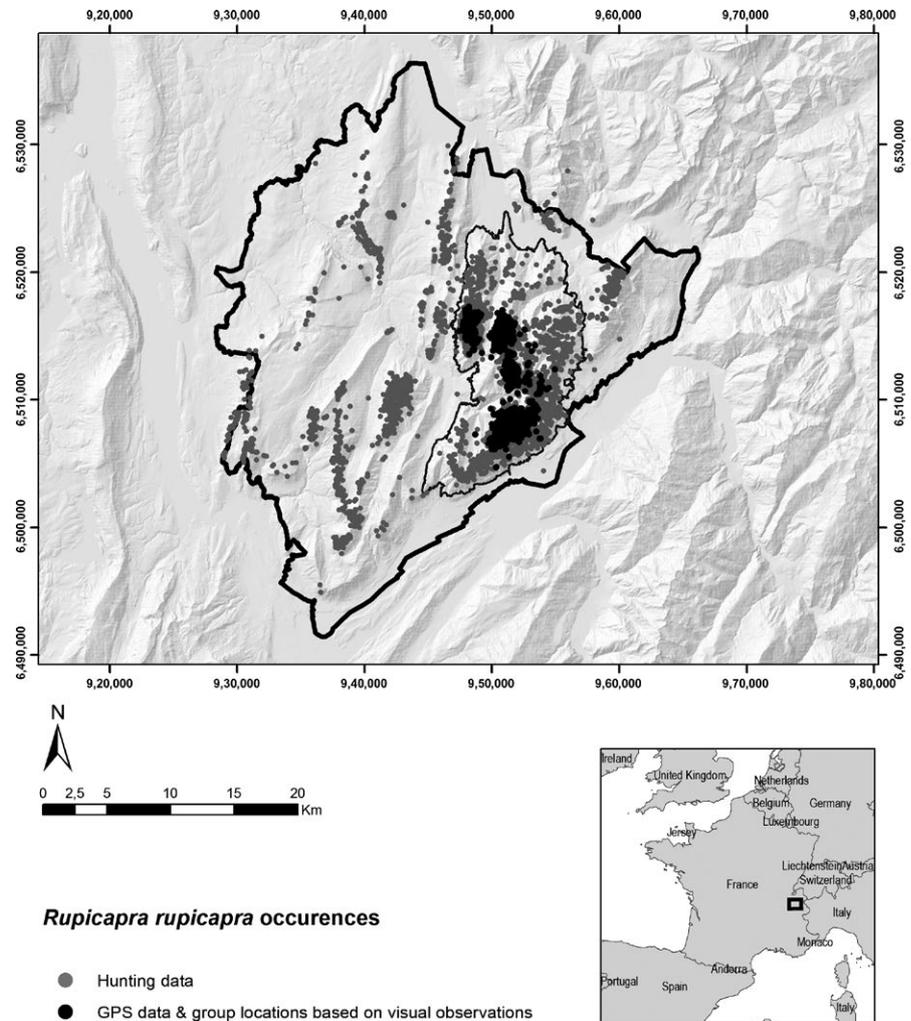
FIGURE 1 Study area and distribution of the chamois presences

predation is restricted to free-roaming dogs, golden eagles (*Aquila chrysaetos*) and red foxes (*Vulpes vulpes*), which may occasionally prey on newborn or sick animals, and to the sporadic presence of wolves.

2.2 | Modelling framework

Our framework is composed of five successive steps (Figure 2). Step 1 relates to the estimation of the compositional diet of the chamois. Step 2 concerns the selection of the plant species to be modelled to represent both the overall vegetation structure of the regional park and the compositional diet of the chamois. Step 3 relates to the building of plant functional groups that both link to chamois diet, but also to vegetation dynamics and structure. Step 4 concerns the spatially and temporally explicit simulation of the plant functional groups in the study area under current and future climatic conditions. Step 5 focuses on the habitat suitability modelling of the chamois under current and future climate and vegetation changes.

2.3 | Step 1—Compositional diet of the chamois

We collected 659 fresh faeces of chamois within the NGWR from April to November 2007 and 2008, either in the field or directly from trapped and hunted chamois. The dietary composition of the faeces was determined using DNA metabarcoding techniques (Bison et al., 2015; Rayé et al., 2011). We identified 326 plant taxa in the faeces sampled. We removed plant species which were present at levels under 2.5% of DNA sequences in the faeces, considering that under this threshold, the taxa detected represent a marginal resource for the chamois or may result from barcoding errors (Bison et al., 2015). This 2.5% threshold was taken as it marked a rupture in the frequency distribution of the sequences (Pompanon et al., 2012). The remaining 96 plant taxa were dominated by evergreen shrub, deciduous shrub, forb and leguminous species.

2.4 | Step 2—Selection of the dominant plant species to simulate vegetation structure

In order to represent the overall vegetation structure of the park, we first selected a restricted set of dominant species among those present in the region (over 1,500 species located within 17,351 vegetation plots available from the Alpine Botanical Conservatory, CBNA, Figure S1). To select the dominant species in high productivity plots, we followed Boulangeat et al. (2012) by selecting species whose presence counts in vegetation plots were within the 95% quantiles among all
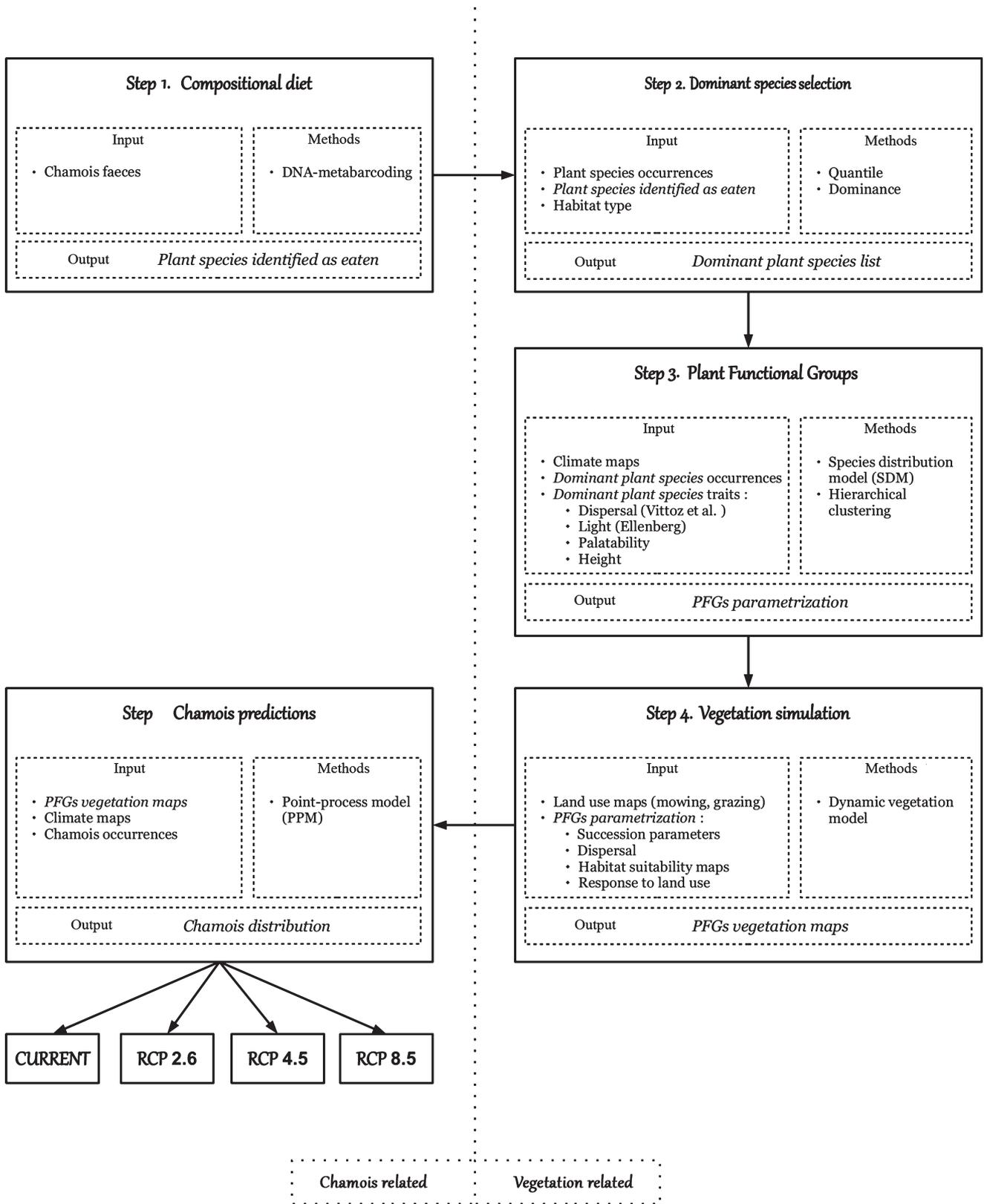
Step 1. Compositional diet

Input	Methods
• Chamois faeces	• DNA-metabarcoding

Output   *Plant species identified as eaten*

Step 2. Dominant species selection

Input	Methods
• Plant species occurrences • *Plant species identified as eaten* • Habitat type	• Quantile • Dominance

Output   *Dominant plant species list*

Step 3. Plant Functional Groups

Input	Methods

• Climate maps
• *Dominant plant species* occurrences
• *Dominant plant species* traits :
   • Dispersal (Vittoz et al.)
   • Light (Ellenberg)
   • Palatability
   • Height
	• Species distribution model (SDM)
	• Hierarchical clustering

Output   *PFGs parametrization*

Step   Chamois predictions

Input	Methods
• *PFGs vegetation maps* • Climate maps • Chamois occurrences	• Point-process model (PPM)

Output   *Chamois distribution*

Step 4. Vegetation simulation

Input	Methods

• Land use maps (mowing, grazing)
• *PFGs parametrization* :
   • Succession parameters
   • Dispersal
   • Habitat suitability maps
   • Response to land use
	• Dynamic vegetation model

Output   *PFGs vegetation maps*

CURRENT	RCP 2.6	RCP 4.5	RCP 8.5

Chamois related   Vegetation related

FIGURE 2 Schematic description of the modelling approach. Each of the steps is described with regard to the input variables, the methods and the outputs that then feed into the next step

species, those with a high average abundance (above the 95% quantile) and species that are characteristic of each habitat of the park and thus occur in at least 25% of the vegetation plots within those habitats. The

habitat classification and mapping were extracted from the CBNA data at a 1:5,000 resolution and used the Corine biotopes typology. Finally, we added all the plant species that make up the compositional diet

of the chamois (Step 1). A total of 136 dominant species were finally retained to build the different plant functional groups.

2.5 | Step 3—Building the plant functional groups to represent the vegetation structure and resource availability for the chamois

We built plant functional groups (PFGs) that represent both the vegetation structure and diversity of the park, and the compositional diet of the chamois, and which are consistent with the parameters and processes of the vegetation model. We thus adapted the framework proposed by Boulangeat et al. (2012), in which PFGs are defined on the basis of their tolerance of abiotic conditions, their dispersal abilities, resistance to disturbance (grazing and mowing), response to competition for light (whether they germinate and grow under specific light conditions), competitive effects (estimated by the height of the species) and their demographic characteristics (life-form, longevity, age of maturity). The aforementioned characteristics were collected for the 136 selected species based on expert knowledge and an in-house trait database (Appendix S1). Information was also added to specify if the plant species is part of the compositional diet of the chamois (see Appendix S1). We then used a hierarchical clustering approach to build the PFGs (see Appendix S1). This framework gave us sixteen plant functional groups (Table 1) made up of two chamaephyte groups (C1–2), eight herbaceous groups (H1–8) and six phanerophyte groups (P1–6), each

occupying up to six height strata and passing through four age classes (1–4) with different responses to disturbances (grazing and mowing).

2.6 | Step 4—Simulation of the vegetation structure and dynamics

We used FATE-HD, a spatially and temporally explicit landscape vegetation model which explicitly simulates the selected PFGs' population dynamics and dispersal, interactions for light resources and the responses to climate and different land use regimes (Boulangeat, Georges, & Thuiller, 2014). The abundance of a given stratum in a pixel determines the amount of light that reaches the lower strata. Interactions for light resources are simulated by accounting for the amount of light reaching each PFG cohort in a stand and the PFG's light preferences. Responses to climate are simulated using habitat suitability (HS) maps (constructed a priori based on observed occurrences of plant species using the R package BIOMOD2; Thuiller, Lafourcade, Engler, & Araujo, 2009) for each PFG, and climate change was simulated by changing HS maps at predefined intervals. Land use disturbances are modelled in a spatially explicit manner, by assigning mowing, grazing or no disturbance to each pixel. Model output consists of yearly strata and PFG abundances per pixel.

Demographic parameters and seed dispersal distance classes were assigned to all representative species from each PFG from the

TABLE 1 List of plant functional groups (PFGs) used for simulating the spatial structure of the vegetation in the Bauges Regional Park. These groups have been defined according to the species' dispersal abilities, canopy height, shade tolerance, bioclimatic niche, palatability and importance in the chamois' diet. C1 and C2 represent chamaephytes, P1 to P6 represent phanerophytes, and H1–H8 are herbaceous plants. The interpretation of PFGs was carried out a posteriori based on expert knowledge of determinant species and the PFG's average attributes. Diet preference refers to the importance of the plant functional group for the chamois (from 1 to 5, low to high level of importance)

PFG	Interpretation	Diet preference
C1	Shrubs found in meso-xerophiles forests and forest edges.	4
C2	Subalpine meso-hygrophiles heath and undergrowth chamaephytes, which tolerate acidic soils.	5
H1	Mountainous to lowland species.	4
H2	Mountainous to subalpine species that tolerate acidic soils and cold climates.	3
H3	Mountainous to subalpine species found on neutral soils.	4
H4	Mountainous to lowland species which tolerate wet climates and nutrient-rich soils.	2
H5	Mountainous to subalpine thermophile species found on neutral to acidic soils.	2
H6	Plant species found in mountainous undergrowth (beech fir).	2
H7	Mountainous to lowland species, found in grasslands and forest edges, and which tolerate wet climates and nutrient-rich soils.	4
H8	Mountainous undergrowth hygrophilous species.	1
P1	Mountainous to lowland thermophile trees found on neutral soils.	4
P2	Small trees from lowland to subalpine elevation, found in wet and cold climates and which tolerate acidic soils.	4
P3	Late succession trees found in wet climates.	2
P4	Late succession trees found in wet climates.	1
P5	Subalpine deciduous tree.	4
P6	Tall forest edge tree.	1

literature and expert assessment, and the median class was given to the group. PFG responses to mowing and grazing, depending on their age and their palatability class, were calculated as in Boulangeat, Georges, Dentant et al. (2014).

FATE-HD was run over a regular grid containing 88,337 pixels representing the regional park at a resolution of 100 m (yearly time step). Our simulations aimed to reconstruct the current vegetation distribution. The landscape was first initialized with annual seeding (addition of seeds from each PFG at all locations across the map) for 300 years. A stabilization phase requiring 500 additional years was then necessary to restore a realistic demography (limited fecundity), and current disturbance regimes were applied during the last 200 years of this phase, to compare model outputs to current observations.

We then simulated future vegetation distribution by changing HS maps every 10 years for 90 years after reaching equilibrium, to predict the vegetation structure and chamois' resource distributions until 2100. Future climate was characterized by three different IPCC5 scenarios following the Representative Concentration Pathways: RCP2.6 ("mild" scenario), RCP4.5 ("intermediate" scenario) and RCP8.5 ("severe" scenario). Data were downloaded from the Cordex portal (http://www.euro-cordex.net). We calculated mean predicted values of the four selected bioclimatic variables for the years 2010–2100 under these three scenarios. Climatic layers were extracted from Thuiller et al. (2014).

Validating FATE-HD is tricky as it predicts potential vegetation and the modelled plant functional groups are abstract entities and do not match the land cover data extracted from satellite imaging. Following Boulangeat et al. (2012), we assessed the capacity of FATE-HD to simulate the current forest cover in the park. Forest cover is indeed relatively easy to retrieve from our simulated PFGs (relative abundance of forest tree PFGs in a pixel) and is also easy to extract from the habitat mapping (forested and non-forested areas). In order to contrast a continuous variable (simulated forest cover) with a categorical variable (forested and non-forested), we used True Skill Statistics (TSS), a metric commonly used in species distribution modelling to relate the modelled species' probability of occurrence to observed presence–absence data (Allouche, Tsoar, & Kadmon, 2006). TSS takes into account both omission and commission errors, and success as a result of random guessing, and ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random.

2.7 | Step 5—Distribution modelling of the chamois under current and future conditions

Finally, we built a species distribution model that integrates both climatic information, the structure of the vegetation, and the distribution of the chamois' resources. We used different sources of data to map the spatial locations of chamois (Figure 1). At both the BNRP and NGWR scales, hunters recorded spatial locations of chamois killed since 2004 (n = 3,830). Such data were completed within the NGWR by data recorded from yearly censuses, long-term

re-sightings of marked animals and the GPS locations of chamois fitted with GPS collars (see Appendix S2). From the 51,982 GPS locations, we randomly selected 10,000 points to reduce the problem of pseudo-replication of the same animal. The final number of presences was thus 13,830.

As the available data consisted of presence-only data, we used a point-process model (PPM), which is specifically designed to predict the intensity of surveyed points over a spatial grid. PPM does not require background data (or pseudo-absences) but only quadrature points to approximate model likelihood (quadrature points are not considered as absences by the model) (Renner et al., 2015). PPM output is the number of presences per unit area (i.e., intensity, see Appendix S3 for the R code). Intensity depends on presence-only data and on the spatial measurement units, which we set to 10,000 m², for consistency with all climatic layers and the FATE-HD outputs. Intensity was modelled as a log-linear function of the predictors. To further test whether including vegetation information helps to predict the spatial distribution of the chamois, we first built a PPM with climate-only variables and then a second model including both climatic and vegetation structure (e.g., PFG abundances simulated using FATE-HD). Before running the models, we first checked for multicollinearity between variables. We found important correlations between abundances of PFGs that naturally coexist within the same habitat (see Appendix S4). The final set of variables was built by choosing from the correlated groups of PFGs, the PFGs which featured most prominently in the chamois' diet. We finally kept C2, H1, H4, H6, H7 and P2. For the topo-climatic variables, we only retained annual temperature and slope (hereafter referred to as the climate-only model). As the presence of the chamois could be influenced by the interaction between slope and vegetation, we considered potential interactions between climatic and PFG variables. This gave us five variables (linear terms and interactions) for the climate-only PPM and 29 variables for the climate and vegetation PPM. We ran a stepwise forward procedure based on the Akaike information criterion (AIC) to select the most important variables.

We evaluated the predictive performance of the two models based on two different criteria: the Boyce index that only requires presences and measures the extent to which model predictions differ from the random distribution of the observed presences across the predictions (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). It varies between −1 and +1. Positive values indicate predictions consistent with the distribution of presences in the evaluation dataset, values close to zero mean that predictions are not different from random, and negative values indicate counter predictions (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006). We also calculated Spearman's rank correlation coefficients between the intensity (i.e., model output) and the density of presence-only data. This latter criterion measured the accuracy of the model to predict intensity (as the number of presence records per area). We aggregated both maps up to a 500-m resolution (factor five), for a less precise, but more stable analysis.

Once fitted, the two PPMs were also used to project the future potential species intensity using the same climatic scenarios as used for
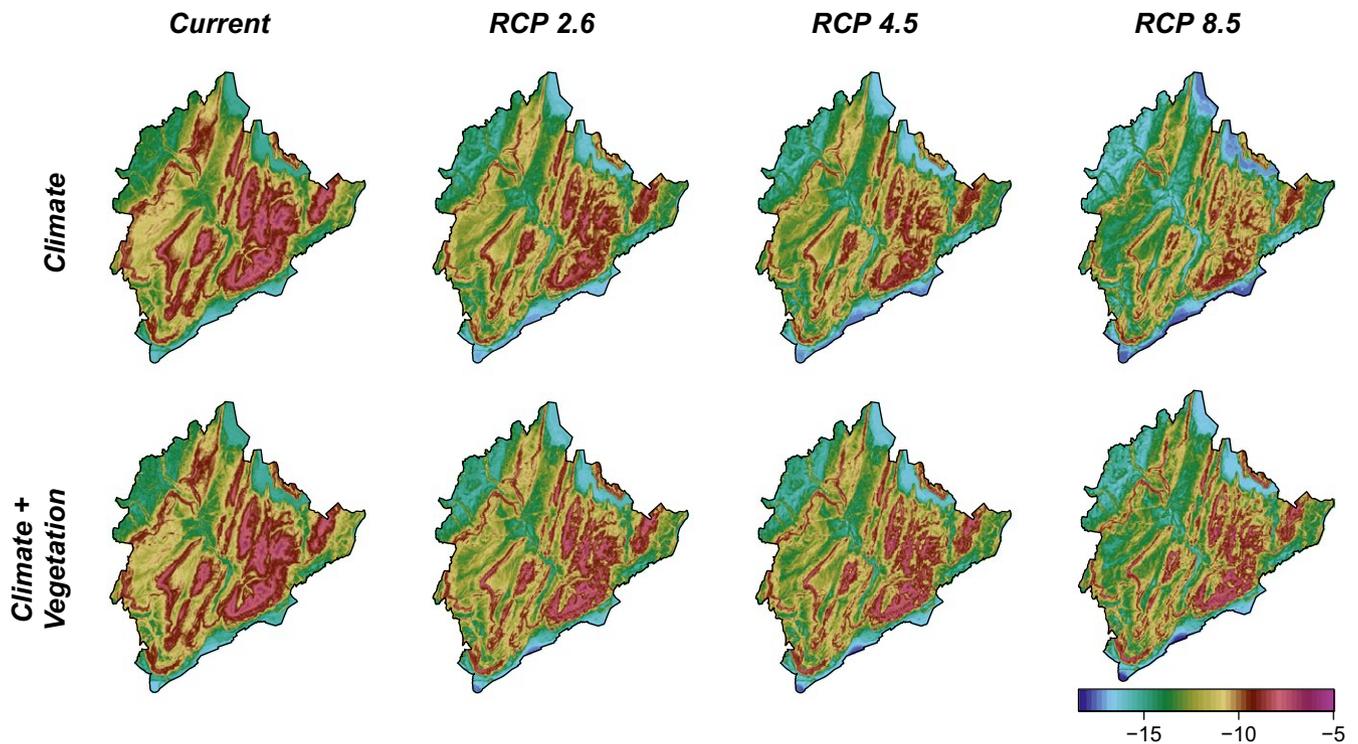
FIGURE 3 The chamois' predicted current and future intensity (as log of intensity) under current and future conditions by 2100. The top row presents the results of the climate-only models and the bottom row presents the results for the climate and vegetation model. The colour scale represents the log of the intensity of the chamois per unit of area (100 × 100 m), from blue to purple (low to max intensity)

the vegetation (see Step 4). We then analysed how species occupancy (i.e., the size of the predicted attractive areas) is expected to change in the future in response to changes in climate and vegetation structure and resources.

We calculated the Pearson correlation between the projections from the two models (climate-only and climate, vegetation structure and resource) for each of the time slices (10-year interval) to measure the disagreement between the two models over time.

3 | RESULTS

3.1 | Simulation of vegetation structure and the chamois' resources

Under current climate conditions, our spatially and temporally explicit vegetation model reproduced the overall vegetation structure of the park very well with True Skill Statistics close to 0.5 (TSS = 0.46). Interestingly, most functional groups were predicted to expand, or at least to remain in a stable state in response to climate change (Figure S2). This was the case for instance of P5 (subalpine deciduous trees) that was predicted to increase its cover over time and the PFGs which are key components of the chamois' diet such as H1, H4 and H6 (herbaceous species). Plant functional groups from subalpine habitats, which are important in the chamois' diet, were predicted to slightly increase mean abundance over the park. These results showed that under climate change, most of the plant functional groups that are important in the chamois' diet are predicted to expand in the future

and mostly at high altitudes (se C2, H1 and H7 in Figure S3 above 1,500 m a.s.l.).

3.2 | Point-process modelling of the current spatial distribution of the chamois

While the stepwise procedure retained 4 and 13 variables for the climate-only and climate and vegetation models, respectively, the two models produced similar predictions of chamois intensity (Spearman's rank correlation between models 0.98, Figure 3). The climate-only and climate and vegetation models had a similar Boyce index (0.96 and 0.94, respectively) and were equivalent in predicting overall intensity (0.59 and 0.60, respectively). The two models also predicted a similar total sum of intensity throughout the entire regional park (1.383 and 1.382, respectively), while the climatic-only model predicted a slightly larger attractive zone than the climate and vegetation model across the park (species occupancy 0.13% and 0.11%, respectively).

3.3 | Contrasting the current and future potential distribution of the chamois

While predictions from the climate-only and climate and vegetation models were almost identical under current conditions, they strongly diverge under future conditions. Pearson's correlation coefficient between projections from the two models did indeed decrease over time going from 0.9 to 0.4 for instance in the RCP 8.5 scenario (Figure S4). In other words, the inclusion of vegetation structure and the
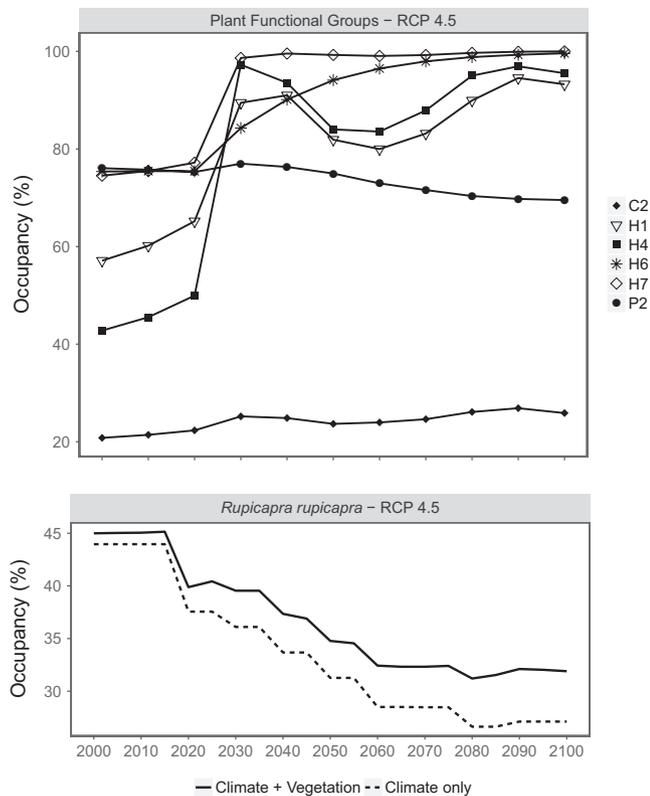
FIGURE 4 Change in the predicted species occupancy of the chamois (*Rupicapra rupicapra*) over time and for the two point-process models (i.e., *climate + vegetation* and *climate-only*) as a function of the RCP 4.5 climate scenarios. The top figure represents the change in occupancy of the plant functional groups (PFGs) selected by the point-process model (*climate + vegetation*). *C2* refers to subalpine meso-hygrophiles heath and undergrowth chamaephytes, *H1* to mountainous to lowland species, *H4* to mountainous to lowland species which tolerate wet climates and nutrient-rich soils, *H6* to species found in mountainous undergrowth, *H7* to mountainous to lowland species, found in grasslands and forest edges and which tolerate wet climates and nutrient-rich soils, and *P2* to small trees from lowland to subalpine elevation, found in wet and cold climates and which tolerate acidic soils. The effect of the transient dynamics of the vegetation is visible at year 2020–2040 where the increase in occupancy of key PFGs counteracts the negative effects of climate change on the occupancy of the chamois

compositional diet of the chamois drastically changed the predictions over space and time. The climate-only model predicted the chamois species as being concentrated in high elevation massifs, regardless of the regional concentration pathway (Figure 3), while the climate and vegetation model predicted a less drastic upward shift in the potential suitable space for the species. More interestingly, some new habitats on the central plateau in the park were predicted to be suitable for the chamois in the future.

When looking at the overall species occupancy of the species over time, both the climate-only and climate and vegetation models predicted a reduction (Figure 4). However, while the climate-only model predicted a drastic reduction in occupancy (41% decrease in occupancy on average depending on the RCP scenario, that is, a decrease

from 45% of the park covered to 28%–35%), the climate and vegetation model only predicted a 30% reduction in occupancy on average, with occupancy decreasing from ca. 45% to 21%–31% depending on the RCP scenario (Figure 4, Figures S5 and S6). The inclusion of vegetation structure and resources in the chamois model buffers the negative impacts of climate change over time (Figure 4). For example, the transient dynamics of vegetation (increase in occupancy of most important PFGs for chamois) from 2020 to 2040 moderates the decrease in chamois occupancy in response to climate change. Similarly, the increase in occupancy of C2, H1 and P2, the most important PFGs for the chamois' diet (Table 1) in years 2080–2100 again buffered the negative impacts of climate change only for the overall occupancy of the herbivore.

4 | DISCUSSION

In this paper, we have presented a novel framework that makes it possible to predict the intensity of a wild herbivore based on climate, vegetation structure and its known resources. We have shown that discounting the pure effects of vegetation on the intensity of the species might lead to overpessimistic predictions. We have also shown effects of the transient dynamics of the vegetation on the herbivore species' response to climate change which can buffer the pure effects of climate change on herbivore intensity.

4.1 | Integrating ecological realism into species distribution models

There have been several attempts to integrate more realism into species distribution models. Leathwick and Austin (2001), for example, modelled the abundance of non-*Nothofagus* species in old-growth forests in New Zealand according to environmental drivers and the abundance of *Nothofagus* species. They showed the importance of *Nothofagus* for predicting the abundance of other species through asymmetric competition. For animals, the few attempts made so far have mostly focused on integrating habitat descriptors into species distribution models initially built with climate-only models (Triviño, Thuiller, Cabeza, Hickler, & Araújo, 2011; Wintle, Bekessy, Venier, Pearce, & Chisholm, 2005). While vegetation descriptors have helped to improve the predictive accuracy of the models, they do not explicitly integrate known competitive or trophic relationships (but see Hughes, Thuiller, Midgley, & Collins, 2008). Here, we took advantage of environmental DNA metabarcoding to introduce the composition of the chamois' diet into the model. As animal species are also influenced by habitat configuration (open vs. closed habitats, fragmentation), we used FATE-HD to simulate the dynamics of not only the vegetation structure, but also the main plant groups consumed by the chamois. This type of duality diagram has the advantage of not simulating too many plant species or groups at the same time. Some plants which are an important part of the chamois' diet could have been lost in our very broad PFGs; however, the retained PFGs were assumed to be representative of the

chamois' diet, as they took into account most of the edible plant species. The fact that the final point-process model for the chamois included PFGs which are important for the chamois supports this decision. Another advantage of using a spatially and temporally explicit vegetation model is that the vegetation is modelled using an annual time step and at very high resolution. This makes it possible to simulate transient dynamics in vegetation succession that might create temporally unsuitable or suitable conditions for the chamois over the years (Figure 4). As such, the distribution of the chamois was modelled dynamically with a phenomenological model (ten-year time interval) as we assumed here that chamois dispersal was not an issue in the park due to the lack of natural connections with surrounding massifs (Loison, Jullien, & Menaut, 1999). This allowed us to demonstrate a transient dynamic with a reduction in chamois occupancy and total intensity due to an unfavourable climate, but also transient unsuitable plant conditions between now and 2020, which then recovered after 2020.

4.2 | Plant resources and vegetation structure as a buffer against climate change

An important result of our study is that plant resources and vegetation structure act as a buffer to the predicted detrimental effects of climate change on chamois distribution. Interestingly, while both models (climate-only and climate and vegetation) predicted more or less the same intensity under current conditions, the climate and vegetation model predicted lower species occupancy. In other words, the vegetation structure and plant resources act as a constraint in the model, as some areas are climatically suitable, but do not have the suitable vegetation structure or resources. Overall, the close correlation between the two predictions under current conditions reflects that the vegetation is close to equilibrium with climate and that adding a vegetation layer to a climate-only model does not significantly improve the quality of the model (see also Thuiller, Araújo, & Lavorel, 2004). However, when it comes to future conditions, the vegetation structure departs from equilibrium as new vegetation dynamics with transient responses are predicted in response to climate change (see Figure 4, PFGs' occupancy through time). These transient vegetation dynamics strongly influence the occupancy and intensity of the chamois and lead to drastic differences between models which ignore vegetation structure and plant resource distribution and the more ecologically realistic models. Ungulate distribution shift due to climate change is slowed down by the slower shift of vegetation, and areas which are climatically unattractive could still be populated by ungulates because of their suitable vegetation and plant resources. This results in a shift in potential suitable habitat, for the most pessimistic RCP for example, in which species occupancy increases, and new suitable areas appear at year 2100 (Figure 4). Models ignoring these ecological relationships will not be able to predict this type of delayed response in the chamois and instead will suggest that in our case, the chamois will come to the brink of extinction in the park in the next 70 years. Instead, taking into account vegetation and plant resources sheds light on management strategies that could potentially be implemented to safeguard

the chamois in the Bauges Regional Park, and probably throughout the European Alps. Protecting the diversity of habitats and the few most commonly consumed plant groups could counteract the pure effect of climate change.

4.3 | Future perspectives

There are several areas for improvement in our framework. The most obvious one concerns the feedback loop between the modelled herbivores and the vegetation, given that wild ungulates can have a significant impact on vegetation composition and structure (Augustine & McNaughton, 1998). As the vegetation dynamics are simulated independently of the chamois, the intensity of the chamois has no influence on the vegetation dynamics. This assumption is unlikely to be true for the chamois and probably for most ungulates in Europe, for which density dependence is commonly reported (Bonenfant et al., 2009), although there are currently almost no studies estimating the impacts of wild mountain ungulates on alpine grasslands (Erschbamer, Virtanen, & Nagy, 2003). In our case, and given that we modelled presence-only data and not population abundance here, we suggest that this feedback effect is unlikely to change or radically modify the vegetation dynamics of broadly defined plant functional groups. Explicitly modelling the feedback loop between herbivores and plant structure would require building a spatially explicit meta-population model and using the dynamic vegetation model to define the habitat quality and structure for the herbivores. Feedback between the herbivores and the vegetation could be implemented via the grazing disturbance models in FATE-HD. However, a critical step for coupling the two approaches is to clearly identify the connecting drivers and processes. For instance, linking the meta-population and the vegetation succession models is far from obvious and raises several questions. How does habitat quality influence recruitment, survival, growth and the dispersal patterns of herbivores? What is the shape of the relationship between habitat quality and demographic parameters (is the best approximation function logistic, asymptotic or Gaussian)? These and other necessary decisions require a better understanding of the effects of habitat quality on demography, for which there is still a lack of empirical data on wild mountain herbivores (but see in other environments, e.g., Pettorelli et al., 2005 on roe deer; Nussey et al., 2007 on red deer).

The second area for improvement concerns modelling simultaneously interacting herbivores, whether wild–wild, wild–domestic large herbivores or large–small (e.g. insect) herbivores, to better mirror actual herbivore communities in mountain ecosystems. While traditional species distribution models (SDMs) ignored biotic interactions, recent advances now mean they can match ecological theory much more closely by considering how species interact to form communities (Pollock et al., 2014; Warton et al., 2015). These joint species distribution models (JSDMs) predict species distributions based on environmental and spatial variables (as in typical SDMs), but also consider the effect of all other co-occurring species. Extending point-process models to joint point-process models that simultaneously consider two or three herbivores species in the same area coupled

with simulated vegetation dynamics will open up new avenues in the conservation and management of these species in an era of climate and land use change. The ever-increasing use of environmental DNA metabarcoding to reconstruct the diet of the species should allow for the explicit modelling between a herbivore and its plant resources while accounting for the direct and indirect effect of climate.

DATA AVAILABILITY

Data for chamois are accessible through the ONCFS (contact: Mathieu Garel; mathieu.garel@oncfs.gouv.fr). All other data are available upon request.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.