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Taxonomic and functional approaches of trophic interactions between large herbivores and plant communities in a mountain ecosystem

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Bison Marjorie

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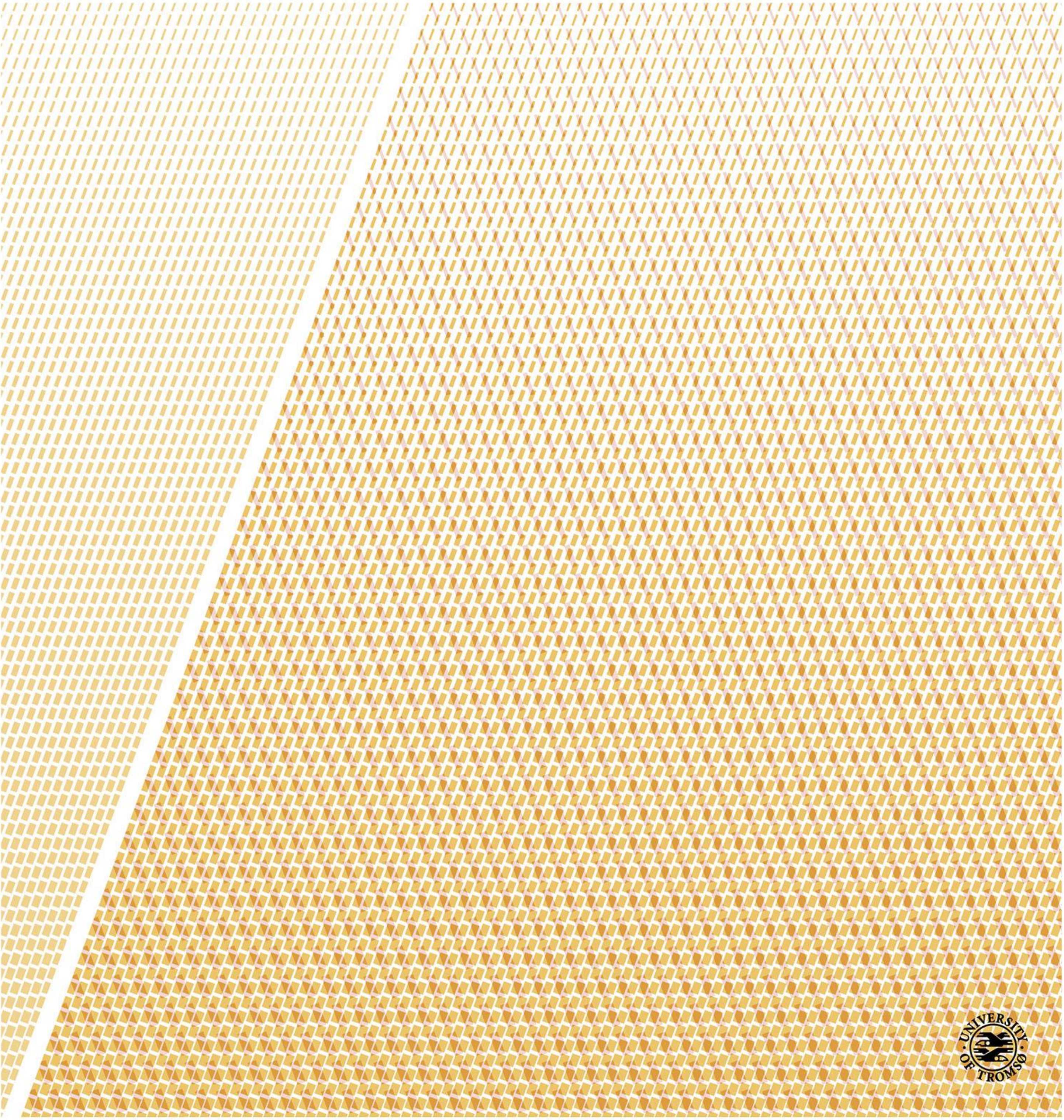

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"The more I learn, the more I realize how much I don't know" - Albert Einstein

Here we are. The writing of this part announces the approaching end of the compilation of the thesis manuscript.
This three-year work would not have been realized without the help of many people, and highlights once again the collective nature of research.

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I am sorry for the people I forgot. It was not on purpose. Thank you as well.

“If we didn’t have the failure, what fun would climbing be” - Daniel Woods, professional climber.
Doing a PhD is pretty much like climbing. The belayer is you supervisor, and you need to be sure that he/she could carry you if you fall, but also that he/she could guide and advise you during the ascent. Trust needs to be established between both of you. You have to think about the position of your hands and feet. If, additionally, you need to oversee you belayer, just don’t go.
Quickdraws are your background, and you should know how and when to use it at the right time. Sometimes during the ascent, you will meet other climbers, arriving on routes next to you. These people are highly important, as they are able to completely change your point of view and give you cues to overcome a difficult move, or a small slippery hold that you don’t know how to use. This is exactly the same in research, you need to be open to new ideas and be able to change your way of thinking.
Climbing and PhD are both a matter of balance: while the first one needs well-positioned hands and feet, the second one needs a well-shared time between your personal life and your work. Climbing and PhD are also both a matter of determination and temerity. For each, barriers and failures need to be kept in perspective to be able to go on or to discover your own limits. Easier said than done.
At the end of the route, you reach the belay stance, but sometimes not. In both cases, you should enjoy the view. It is now time to move on to another piece of the puzzle.

ABSTRACT

Given the key role of large herbivores on species and functional plant diversity, we aimed at better understanding the relationship between herbivory and plant communities mainly at a fine-scale, in order to reconcile objectives of population management and plant conservation. For this purpose, we used both taxonomic and functional approaches, and studied interactions at the inter- and intra-specific levels. We combined information coming from three databases: (1) diet data from DNA-metabarcoding applied on chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*) and mouflon (*Ovis gmelini musimon*) faeces from the Bauges Massif, (2) characteristics of plant communities (plant composition, biomass, phenology), (3) plant functional traits. Analyses of intra-specific variability of the three large herbivores allowed us to upscale the niche variation hypothesis (NVH) of Van Valen from the intra- to the inter-specific level, i.e. we observed a positive relationship between the species niche breadth and among-individual variation. Then, based on two chamois subpopulations living in pastures, one living in sympatry with the mouflon and the other living in allopatry, we revealed the absence of negative effects of the introduced mouflon population on native chamois population diet, both for the taxonomic and functional dietary niche. Analyses of diet selection criteria allowed us to highlight differences in choice criteria between chamois and mouflon in some seasons, which helped to partially explain the partial taxonomic and functional niche partitioning of the two species. Furthermore, the proposed scenario of the evolution of diet selection over the year for both species were consistent with ungulate-specific morpho-physiological features. Finally, contrary to the literature where no studies could discriminate the direct and indirect effects of functional traits on diet selection because of correlations, we used path analyses, which allowed us to show that in most cases, biomechanical traits had a direct effect on diet choices, whereas chemical traits had indirect effects. Furthermore, from a methodological point of view, we advised to use nitrogen fecal indices only to study the evolution of species-specific and location-specific population long-term diet quality, but not to compare diet quality between species, nor to study slight fluctuations at the intra-seasonal level. The complementarity of the approaches allowed us to better account for the structuration of herbivore communities, which should help to better assess the actual state and the evolution of relationships among individuals, species and their environment.

Key-words: ungulates, intra- and inter-specific interactions, taxonomic and functional approaches, DNA metabarcoding, NIRS, Bauges Massif, diet selection

RÉSUMÉ

Etant donné le rôle clé des grands herbivores sur la diversité végétale spécifique et fonctionnelle, notre objectif était de mieux comprendre la relation entre l'herbivorie et les communautés végétales principalement à une échelle spatiale fine, afin de concilier des objectifs de gestions des populations et de conservation de la flore. Pour cela, nous avons abordé cette problématique en intégrant des approches taxonomique et fonctionnelle, et en étudiant les interactions aux niveaux inter- et intra-spécifiques. Nous avons combiné les informations de trois bases de données : (1) des données de régime alimentaire issus d'analyses d'ADN metabarcoding réalisées sur des faeces de chamois (*Rupicapra rupicapra*), chevreuil (*Capreolus capreolus*) et mouflon (*Ovis gmelini musimon*) du Massif des Bauges, (2) des données sur les caractéristiques des communautés végétales (composition floristique, biomasse, phénologie), (3) des données de traits fonctionnels des plantes. L'analyse de variabilité intra-spécifique des trois grands herbivores nous a permis de valider l'hypothèse de variation de niche (NVH) de Van Valen au niveau intra-spécifique mais aussi au niveau inter-spécifique, soit une relation positive entre la largeur de niche de l'espèce et sa variabilité intra-spécifique. Ensuite, grâce à deux populations de chamois d'alpage, l'une vivant en sympatrie avec le mouflon et l'autre vivant en allopatrie, nous avons pu mettre en évidence l'absence d'effets négatifs de la population introduite de mouflon sur le régime alimentaire de la population native de chamois, autant au niveau de la niche alimentaire taxonomique que fonctionnelle. L'analyse des critères de sélection alimentaire nous a finalement permis de mettre en avant des différences de critères de choix entre les deux espèces à certaines saisons, expliquant ainsi partiellement le partitionnement partiel des niches taxonomique et fonctionnelle des deux espèces. Par ailleurs, les scénarios proposés d'évolution de la sélection alimentaire au cours de l'année pour les deux espèces concordaient avec les caractéristiques morphologiques spécifiques à l'espèce d'ongulé. Finalement, contrairement à la littérature où aucune étude n'était capable de discriminer les effets directs et indirects des traits fonctionnels à cause de corrélations, nous avons pu, grâce à des analyses de pistes, démontrer que, dans la plupart des cas, les traits biomécaniques avaient un effet direct sur le choix alimentaire alors que les traits chimiques n'avaient qu'un effet indirect. Enfin, d'un point de vue méthodologique, nous conseillons l'utilisation d'indices d'azote fécaux uniquement dans l'étude de la variation à long terme de la qualité des régimes de manière spécifique à chaque espèce et chaque site, et non pas pour comparer des qualités de régime entre espèces ni pour étudier les variations fines à l'échelle intra-saisonnière. La complémentarité des approches nous a permis de mieux appréhender la structuration des communautés d'herbivores, et devrait nous aider à mieux évaluer l'état actuel et l'évolution des relations entre individus, entre espèces et avec leur environnement.

Mots-clés : ongulés, interactions intra- et inter-spécifiques, approche taxonomique et fonctionnelle, ADN metabarcoding, NIRS, massif des Bauges, sélection alimentaire

LIST OF PAPERS

Paper I. Bison M., Ibanez S., Redjadj C., Boyer F., Coissac E., Miquel C., Rioux D., Saïd S., Maillard D., Taberlet P., Yoccoz N.G., Loison A. *Upscaling the niche variation hypothesis from the intra- to the inter-specific level.* Oecologia, 2015.

Paper II. Bison M., Dupeyras P.A., Redjadj C., Miquel C., Rioux D., Taberlet P., Maillard D., Yoccoz N.G., Loison A. *Taxonomic and functional niches differentiation between two large herbivore species.* In prep. for Ecology or Journal of Ecology.

Paper III. Bison M., Ibanez S., Puijalon S., Dehédin A., Langrand E., Redjadj C., Miquel C., Rioux D., Taberlet P., Maillard D., Loison A., Yoccoz N.G. *The relative contribution of biomechanical and biochemical traits in plant selection by ungulates over the year.* In prep. for Functional Ecology.

Paper IV. Ancin Murguzur F.J., Smis A., Bison M., Struyf E., Bråthen K.A. *Over the frontiers: a single NIRS calibration for sub-arctic and temperate ecosystems.* In prep. for PeerJ.

Note. Bison M., Redjadj C., Miquel C., Rioux D., Taberlet P., Maillard D., Yoccoz N.G., Loison A. *Comparison between two methods for estimating diet quality in large herbivores: NIRS-derived fecal nitrogen vs dietary nitrogen from ingested plants.*

OTHER COMMUNICATIONS

Oral:

ECOVEG. 25-27 March 2015. *Quels traits fonctionnels comme critères de sélection alimentaire chez le chamois ?*

Ecology and Behavior. 18-21 May 2015. *Taxonomic and functional niche differentiation between two ungulate species*

Poster:

Doctoral School EDCSV, Grenoble. *Upscaling the Niche Variation Hypothesis from the intra- to the inter-specific level.* Bison M., Boyer F., Coissac E., Ibanez S., Maillard D, Miquel C., Rioux D., Saïd S., Taberlet P., Yoccoz N.G., Loison A.

Popularizing “our” science:

Meeting with hunters. *Apport de l’ADN des faeces sur la connaissance d’espèces d’ongulés.*

Research in the Bauges Massif. *Interactions fonctionnelles entre grands herbivores et communautés végétales : présentation des résultats.*

Herbivorie Info n°18. *Le choix des plantes par les ongulés.*

Popularizing the science of others researchers (internship in the Industrial, Technical and Scientific Culture Center of Grenoble):

- Des champignons sur la falaise
  http://www.echosciences-grenoble.fr/actualites/des-champignons-sur-la-falaise
- Francis Hallé, botaniste et militant
  http://www.echosciences-grenoble.fr/actualites/francis-halle-botaniste-et-militant
- Faire travailler son esprit critique avec le CorteX
  http://www.echosciences-grenoble.fr/actualites/faire-travailler-son-esprit-critique-avec-le-cortex
- A la recherche des ondes gravitationnelles avec Frédérique Marion
  http://www.echosciences-grenoble.fr/actualites/la-recherche-des-ondes-gravitationnelles-avec-frederique-marion
- Au détour d’une comète : la mission Rosetta avec Wlodek Kofman
  http://www.echosciences-grenoble.fr/actualites/au-detour-dune-comete-la-mission-rosetta-avec-wlodek-kofman
- Les détectives du changement climatique
  http://www.echosciences-grenoble.fr/actualites/les-detectives-du-changement-climatique
- Du fossile aux géoparcs
  http://www.echosciences-grenoble.fr/actualites/du-fossile-aux-geoparcs

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INTRODUCTION

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« Qui cherche à façonner le monde,
Je vois, n'y réussira pas.
Le monde, vase spirituel, ne peut être façonné.
Qui le façonne le détruira.
Qui le tient le perdra.
[...] »

Lao-tseu
Tao-tö king

Chapter I: How to get excited about ecology

1.1 Picture of the actual world

According to the Nobel price Paul Crutzen, we are currently at the heart of the Anthropocene era, which began at the dawn of the industrial revolution (end of 18th century) and left behind the Holocene era. Even if the concept is still debated by the scientific community (Lewis and Maslin 2015), the origin of the idea is clear: human activity is global and has great implications on environmental changes, from biogeochemical cycles to the evolution of life (Lewis and Maslin 2015).

Given that the "natural" world cannot be viewed without incorporating the action of humans, the relationship and the question of how to interact with Nature is essential, but varies according to culture and society. By the beginning of the previous sentence, my thoughts are already constrained by the idea of a difference of essence between Humanity and Nature. This vision of our modern science, initiated during the 17th century by Galileo, lead to the idea of independency of Nature against humans (Larrère & Larrère 1997). Even if humans are part of the Nature, we – people having grown up within the "modern western" society – still feel outside of it. We tend to think that we are able to describe it with mathematical laws and regard it as a tool for which we can define a value. Diversity in nature is therefore considered in terms of benefits brought for human populations (ecosystem services, Maris 2011). This point of view is rooted in our Western society, but does not exist everywhere. For example, for Amazonian people (Kayapos indians), humanity is not restricted to humans, but includes the air they breathe, the plants they feed on, the animals they hunt, etc (Klein 2010).

Given that action of humans causes global changes leading to biodiversity loss that might affect the dynamic and functioning of ecosystems (Halpern et al. 2008, Cardinale et al. 2012, Newbold et al. 2015, McGill 2015), the "modern society" tries to maintain an environment as stable as possible by reaching a compromise with the economic and industrial development. Hence, we realize that the "protection/management of Nature" only exists with the emergence of industrial societies (Larrère 2013). Philosophers come to the conclusion that it is not the Nature that dominates humans, neither humans that dominate the Nature, but that a new interaction arises that we do not know how to define (Larrère & Larrère 1997, Maris 2007). Hence, it appears necessary to integrate a new vision of our interaction with the environment, in order to propose solutions to ongoing ecosystem changes.

The first step is to clearly identify the causes of ecosystem changes to better understand ecosystem functioning and their response to environmental fluctuations. The term “ecosystem functioning” includes ecosystem properties, ecosystems goods and ecosystem services (Christensen et al. 1996). In the following, we will refer to ecosystem properties when referring to “ecosystem functioning”. It includes the size of compartments (e.g. pools of carbon or organic matter) and the processes involving fluxes of biomass and energy between trophic levels and the environment (Hooper et al. 2005). As stated by Naeem et al. (1999), “functioning” means “showing activity”. When an ecosystem is altered, for example in terms of species identities, community composition or diversity, but also in terms of abiotic conditions, its rate of plant production, rate of decomposition, carbon storage or nutrient cycling are some processes that can be deteriorated (Naeem et al. 1999). The stability of the ecosystem can consequently be modified.

Climate and land use are the most influential drivers of changes in biodiversity in temperate regions (Boulangeat et al. 2014). Species distribution and diversity are affected by climate change (Parmesan 2006, Lenoir et al. 2010, Gottfried et al. 2012). Land use change has also been shown to have a strong influence on vegetation structure and diversity (Foley et al. 2005) through two scenarios: the land abandonment leading to the closure of open areas (Gehrig-Fasel et al. 2007); and the intensification of agriculture leading to species extinctions (Hodgson et al. 2005). Land use is also associated with habitat fragmentation (Wallis De Vries et al. 1998) and destruction (Wright & Muller-Landau 2006), such as forest conversion to agriculture, river channelization or road settlements. Four other factors can affect the biodiversity, and they act at a shorter time-scale than climate change: pollution such as nitrogen deposition (Thuiller 2007, Zvereva et al. 2008) or chemical contaminants (Bickham et al. 2000, Ricciardi et al. 2009); biological invasions, species introductions and reintroductions (Wilcove et al. 1998, Thuiller 2007, Hahn & Orrock 2014); the increase of carbon dioxide levels in the atmosphere (Thuiller 2007); and the overexploitation leading to resource depletion (Lotze et al. 2006). All those impacts and their interactions contribute to affect the biotic and abiotic environment of a lot of species (Wilcove et al. 1998, Hahn 2014). While the major consequences of climate and land use changes on biodiversity are generally associated with a loss of species, the increase of some population census size is conversely important (Buntgen et al. 2014). Indeed, some species take full advantage of the new environmental conditions associated with the increase of temperature, land use changes, decrease of predators, limitations of hunting quotas, or introductions in environments where they are released from predators (“enemy release hypothesis”, Maron & Vilà 2001). Therefore, the increase of population density is also a major threat to biodiversity, which is usually overlooked.

Many authors agree to say that we are on the way of an environmental crisis (Ehrlich & Mooney 1983, Ceballos et al. 2002, Pereira et al. 2010), confirmed by a recent article of Ceballos et al. (2015) stating that current extinction rates are far higher than the natural average background rates in Earth’s history. These erosions are not limited to a sharp decrease and to a homogenization (Clavel et al. 2010) of the species distribution (endemic species extinction and exotic species introduction, Mack et al. 2000, Mooney & Hobbs 2000) but also lead to the degradation of ecosystem functioning in their wholeness (such as dynamic of fire, carbon sequestration, biogeochemical cycles, Estes et al. 2011). This can, in turn, affect the services provided by the Nature to Humanity, such as the use of biodiversity for medicinal purposes, feeding and non-feeding resource supply or energy production; the esthetic, ethical or spiritual value of Nature which are an important aspect to motivate people to protect Nature; the ecological value of biodiversity. Ecosystems can become unbalanced and functionally altered (such as poor nutrient recycling, poor resilience) (Schröter et al. 2005), at different degrees depending on the ecosystem type (Thuiller 2007) and sensitivity. In this context, scientists try to understand at which scales the changes happen, its origins, its maintenance and try to predict the evolution of systems taking into account the past and actual states, notably to bring facts, ideas and elements of decisions for policy-making processes (Thuiller 2007).

1.2 From community ecology to functional ecology

a) Describing the communities

The first steps of ecology have been characterized by descriptive and classification tasks. What is a species? How can we classify them? How many species are living in a given place?

The word "species" has received considerable attention in biology for hundreds of years. It all began with the idea of classifying and giving names to plants, animals, etc in order to make oneself understood and to communicate, but also to get a more comprehensible pattern of the diversity observed in Nature and to order it. At the beginning, the species concept did not require any precise definition and all the animals that looked like a sheep were called a sheep. Then, with the discovery of new unidentified organisms, things started to get more complicated. It called for precisely define what a species was. But since the word "species" appeared in the scientific literature, its meaning has been evolving into a multitude of definitions (24 species concepts, Mayden 1997). The biological species concept (BSC) has been introduced by Mayr in 1957. It is still the most used and popular concept: a species is defined as a "group of interbreeding natural populations that are reproductively isolated from other such groups". Moreover, offspring have to be fertile. The main problem with BSC is that most of the life on the planet does not reproduce sexually but asexually (cloning, vegetative reproduction) (Ereshefsky 2010) and inter-specific hybridizations are common, e.g. within plants. Following the BSC concept of species, asexual organisms would actually not form species. The phylogenetic species concept (PSC) is complementary as it is not only used to sort organisms but also consider their evolution. Many other species concepts are found in the literature. We could see this pluralist approach as sterile discussion among scientists, but it actually illustrates the multitude of research approaches and the points of view used to approach the organization of living organisms. Each concept has its limits and weaknesses, but the main question is: "What does best fit the biological question?" Those old concerns are still questioned and some researchers keep working on the way of sorting living organisms (de Queiroz 2007). As stated above, one of the old questions in ecology also deals with the evaluation of biodiversity. Species are considered as one of the fundamental units in ecology. With the definition of the "biodiversity", we can easily conceive why. The term "biodiversity" has been defined as "the variability among living organisms from all sources including, inter-alia, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems" (definition from the Convention of Biological Diversity, Rio de Janeiro, 1992). Given the central place given to the species-level, the multitude of species concepts remains problematic in the case of biodiversity assessment: depending on the species definition and the classification we choose, it will give different estimates of biodiversity. Recently, Cadotte et al. (2010) used the two concepts stated above (BSC and PSC) to propose a new assessment method of biodiversity index based on phylogeny. They integrated the species richness (number of species in a community), their abundance and their evolutionary ecology. Consequently, they assumed that a community composed of three closely related species would be less diverse than a community composed of three phylogenetically distant species. In addition, different indices can be used to estimate the diversity: the species richness (number of species in a community), the Gini-Simpson index and the Shannon index (both take into account the richness and the evenness), all grouped into the Hill numbers considered as a general approach to measure diversity (Hill 1973, Chao et al. 2014). Finally, the scale of the taxonomic diversity measurement has been discussed by Whittaker in 1960, who proposed different measurements, such as the local diversity (α-diversity), regional diversity (γ-diversity) and the between site diversity index (β-diversity). The choice of the classification, the index and the scale of diversity measurements can influence the estimation of diversity, and these questionings are still at the heart of community ecology studies.

b) Characterizing the assemblage of species

The following questions concern the assemblages of species within communities. Why are there more species in some places than in others? How do species interact and coexist within a community? Does one facilitate the development of another? Is there competition? What are the relative influences of temperature and soil characteristics in the complexity of plant communities? How does composition evolve temporally?

Box 1 – Ecological niche

Ecological niche is defined as a hypervolume with n-dimensions (Hutchinson 1957) which holds all the environmental conditions that allow a species to have a positive growth rate (Grinnell 1917). This complete hypervolume is called the "fundamental niche", however it cannot be estimated as it is not possible to test all the conditions where the species could persist (Panzacchi et al. 2014). The niche that we observe is the "realized niche" and is shaped by the biotic interactions and the limitations of dispersion. Therefore, the realized niche can fluctuates with changes in the environment. Other concepts are linked to the ecological niche. The "Grinnellian niche" (Grinnell 1917) refers to the species requirements essential for its survival, while the "Eltonian niche" (Elton 1927) refers to how a species impacts its local environment (the "function"). In both cases, the concept of resources is central, whatever the niche definition.

The aims of community ecology as a scientific discipline are to answer those questions and to elucidate the processes underlying the composition pattern of communities. In this context, approaches mainly focus on the ecological interactions among organisms and with their abiotic environment. The interactions among organisms (competition, facilitation, predation, parasitism, symbiosis, mutualism, neutralism, commensalism) happen on a single or several axis of the species ecological niche (box 1) such as food, time or space.

Species can compete on the spatial axis, but not on the food axis if food resources used by the species are not limiting. Facing the global environmental changes discussed above, species need to adapt their habitat, diet selection or their activity rhythm; or to move or to die. Similarly to the ecological niche, interactions among species can be summarized as a hypervolume with n-dimensions, where *n* represents the number of interactions a species maintained with the *n* other species. During this thesis, I mainly focused on the dietary (or feeding) niche of species. Without additional information, the word “niche” should be interpreted as “dietary (or feeding) niche”.

c) Finding general rules in community structuration

More recent questions have emerged to understand how the assemblage of species works. What are the functions of the species in the community? How does a certain assemblage of species influence the ecosystem processes? How can we generalize our local conclusions to more general pattern at a wider scale?

The taxonomic vision does not reflect the function of organisms and does not allow to give general principles about community assembly (Cornwell & Ackerly 2009, Spasojevic and Suding 2012, Mason et al 2012), neither to predict the abundance of species (Shipley et al. 2006, Laughlin et al 2012), nor to understand the influence of organisms on ecosystem functioning (Diaz & Cabido 2001, Lavorel & Garnier 2002). About 25 years ago, the functional approach of communities has been introduced (Lavorel & Garnier 2002, Cornelissen et al. 2003, Violle et al. 2007) in a context where ecologists were wondering if universal laws could also govern ecology (Lawton 1999, McGill et al. 2006).

Based on individuals, the functional ecology describes the organisms with their biological characteristics (e.g. vegetative height, specific leaf area, root density) and their functions (e.g. light interception, resource intake, nutrient and water absorption) within their environment instead of describing them with their taxonomic identity (Calow 1987). Following the review of “traits” definitions given by Violle et al. (2007), that details how the meaning of the term “trait” varies among studies, we used the definition of traits at the individual-level following Garnier & Navas (2013), i.e. “a trait is any morphological, physiological or phenological feature measurable at the level of individual only, from the cell to whole-organism level, without reference to the environment or any other level of organization”. According to this definition, a trait is not influenced by environmental factors or other level of organization (Violle et al. 2007). Species that are taxonomically different can actually be similar in terms of functions and biological characteristics (morphological, chemical, phenological, biomechanical measurements). These features that have a direct impact on the fitness (survival, growth or reproduction) are called functional traits (Lavorel et al. 1997, Violle et al. 2007). The value of a functional trait is the result of compromises among the different functions of the plants (Diaz & Cabido 1997). The use of independent functional traits allows describing general plant functional strategies useful for the understanding of ecosystem functioning (Lavorel et al.

1997). For example, leaf dry matter content (LDMC) is negatively correlated with specific leaf area (SLA): species with strong LDMC (weak SLA) are composed of a low density of foliar tissue, a low photosynthetic rate not allowing a high resource intake but a high conservation ability, and in turn a slow growth rate. These species are called "conservative" species. The opposite are the "exploitative" species and are dominant in fertile environment (Grime et al. 1997, Reich et al. 1999).

In absolute terms, taking into account the individual variability would theoretically allow completely overcoming the species concept (Albert et al. 2010, Albert et al. 2012). However, this requires a huge amount of work and because a species trait is usually the mean trait value measured from some individuals, it does not overcome the species concept. The use of well-chosen functional traits can however reveal general functions and strategies not determined with the single taxonomic approach. However, nowadays, the importance of intra-specific variability is highly studied (Albert et al. 2012, Violle et al. 2012, Albert et al. 2015) and its omission could lead to misinterpretations of ecosystem functioning. This is discussed hereafter in *1.3*.

The functional approach is useful as indicator of population/community structure, dynamics and assembly at local (Kraft et al. 2008, Angert 2009) and biogeographic scales (Swenson 2010, Siefert 2013), to quantify functional diversity of communities (de Bello et al. 2009), to describe the relationships between traits (Reich et al. 1997, Wright et al. 2004, Onoda et al. 2011), to describe the distribution of traits according to environmental gradients (Thuiller et al. 2004, Albert et al. 2010), to relate functioning of ecosystems and services associated (Diaz et al. 2007a), to explain the relationship between traits and fundamental/realized niche (McGill et al. 2006), to mechanistically understand trophic network (Ibanez et al. 2013a) or to predict community response to disturbance (Deraison et al. 2015). For example, plant functional traits such as plant height, or leaf mass, are well correlated to herbivory pressure (Diaz et al. 2001). Although the relationship between traits and herbivory pressure is usually non-linear, it is possible to predict the response of easily measurable plant traits to grazing, even in communities that are taxonomically diverse. Indeed, cattle grazing tends to favor annual over perennial plants, short plants over tall plants, rosette and stoloniferous rather than tussock architecture, prostate rather than erect forms (Diaz et al. 2007b). Consequently, the functional approach allows a more mechanistic understanding of the forces shaping the communities and their dynamics, and to generalize results across organisms and ecosystems (McGill et al. 2006).

Nowadays, researchers are trying to reveal general ecological theories of community assembly (Pavoine & Bonsall 2011) through the combination of indices of diversity based on traits (functional richness, functional evenness, functional divergence, functional dispersion, Mason et al. 2005, Villéger et al. 2008, Laliberté & Legendre 2010), taxonomy and phylogeny (Pavoine & Bonsall 2011 and references therein). Especially, several studies tried to relate the diversity of traits with species diversity (Mayfield et al. 2005, Holdaway & Sparrow 2006, Grime 2006, Villéger et al. 2010). Some of these studies demonstrate the absence of relationship between trait and species diversity (Mason et al. 2008), which emphasizes their complementary use. In this thesis, we particularly used the twofold taxonomic and functional approach in the study of the coexistence between chamois (*Rupicapra rupicapra*) and mouflon (*Ovis gmelini musimon*) on the feeding axis of the ecological niche (paper II). Indeed, knowing the plant species eaten by two species is helpful to study the inter-specific competition, as the food limitation acts at the plant species level. If two primary consumers compete for the same plant species, according to the competitive exclusion concept, they can be forced to feed on different plant species (taxonomic niche), but reach the same energy requirements (functional niche), which would not impact their dynamic. The complementary use of these two approaches at different scales could sharply change our vision of community structure.

1.3 Downscaling ecological studies at the intra-specific level in order to better understand the dynamic of communities and ecosystem functioning

Most of the studies on niche in community ecology focus on the mean trait of species, suggesting that individuals behave in the same way (Layman et al. 2015). For example, when investigating the inter-specific interactions between chamois and sheep, La Morgia & Bassano (2009) limited their overlap measurement to the mean diets of species. However, as already stated by Darwin (1859), individuals can differ because of genetic diversity or phenotypic plasticity (Byars et al. 2007), or because biotic interactions alter their trait value (e.g. competition, Gross et al. 2009). For example, in the case of plant species, the inclusion of intra-specific variability can help to distinguish populations that differ in their trait values along environmental gradients (Albert et al. 2010). Summarizing data with species-mean values overestimates the contribution of rare species (Paine et al. 2011). Therefore, the omission of intra-specific variability can lead to misinterpretation of community functioning (Jung et al. 2010). For instance, aboveground net primary productivity (ANPP) increased with plant genotypic diversity because of higher niche complementarity, in an experimentally low diverse community (Crutsinger et al. 2006). If the objective of a study is to determine the factors influencing the ANPP, then the omission of intra-specific variability could prevent a correct interpretation of results. In the study of La Morgia & Bassano (2009), if the overlap measurement had been measured between all pairs of individuals instead of between the mean diets of chamois and sheep, they could have been able to determine whether only a subset of chamois individuals were affected by sheep. This information can be particularly important to solve management problems and change our vision of species conservation (Bolnick et al. 2003). Indeed, protecting the habitat of a species based on the mean habitat preferences whereas the species displays a strong among-individual variation is not adapted.

Because natural selection, and then adaptation, acts at the individual level, studying the intra-specific variability is essential to understand how populations adapt to their environment and figure out the evolution of their realized niche (Tinker et al. 2008, Pires et al. 2013, Salvidio et al. 2014). When food resource decreased in autumn, salamander populations increased their population niche breadth thanks to a strong diet specialization of individuals on alternate food items (Salvidio et al. 2014). Without this multi-level approach, authors would have not been able to explain the mechanism responsible of the population niche breadth increase. These improvements could also help to better predict how a population or a species would numerically, spatially and behaviorally respond to environmental changes (Bolnick et al. 2011). For example, if one of the resources used by an herbivore population with a high among-individual variability decreases, only a subset of individuals would be impacted. Without among-individual variation measurement, predictions about the evolution of the population would have led to suggest that all the individuals suffered from the decrease of the resource, and we would have predicted a decrease of the whole individual's fitness instead of only some individuals. Hence, including the intra-specific variability in models describing the population dynamic could help to improve the predictive power of the study (Bolnick et al. 2003).

Intra-specific variation can also affect ecological interactions and in turn community assembly (Hughes et al. 2008, Bolnick et al. 2011), both in low diversity communities (Crutsinger et al. 2006, Hughes et al. 2008) and in more diverse systems (Cornwell & Ackerly 2009, Jung et al. 2010, Paine et al. 2011). For instance, the increase in the resource diversity available to herbivores increased the arthropod richness thanks to associations between particular herbivores and particular host-plant genotype, hence favoring the number of ecological interactions between plants and herbivores (Crutsinger et al. 2006). In a context of increasing spatial overlap among species due to an increase of population size, a stronger inter-specific competition could differentially impact the individuals of a targeted species according to its degree of among-individual variation. Indeed, it is only a subset of individuals (fig.1a) or all the individuals (fig.1b) that could be affected by an overlapping species (in red in fig.1). Hence, intra-specific variation promotes species coexistence by limiting similarity with competing species and by adjusting the trait values of individuals and species to their abiotic requirements (environmental filtering, Jung et al. 2010). Individual-level data appear as a more sensitive indicator of niche differentiation and environmental filtering than species-mean data (Jung et al. 2010).

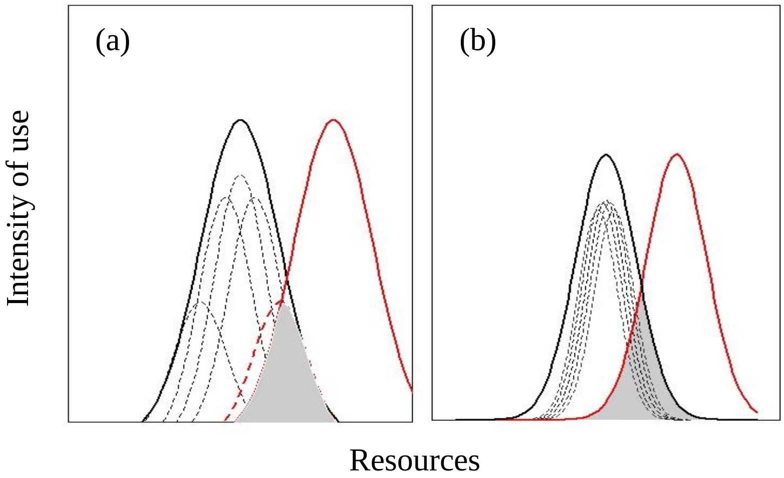

Figure 1. Schematic representation of the impact of a potential competitor (in red) on two populations (in grey, a and b) contrasted in their degree of inter-individual variation. Dotted lines represent the individuals within each species. Inter-individual variation is higher in the left case (a).

Given the importance of intra-specific variability in communities response to environmental changes, in biodiversity assemblage or in network functioning (Dupont et al. 2014, Willmer & Finlayson 2014, Tur et al. 2015), an increasing number of researchers try to take it into account.

For example, Tur et al. (2014) downscaled the understanding of plant-pollinator network at the intra-specific level and showed that the different parameters (linkage density, connectance, nestedness, interaction diversity) describing the structure of networks significantly changed in response of a high degree of individual specialization.

Including the intra-specific variability within ecological studies is not only useful to explain spatial or fine-temporal community composition variation, but also to explore evolutionary processes at a larger temporal scale. Indeed, in an evolutionary perspective, because environmental filters act at the individual-level, different survival, growth and reproduction can be observed among individuals leading to changes in allele frequencies, which in turn may modify the evolution of the population through natural selection (Bolnick et al. 2003).

Chapter II: Theoretical context

2.1 Large herbivores as a good study model

a) Their central place in ecosystems

Large herbivores are of economic, social, cultural and ecological importance (Gordon et al. 2004) and their study and management is therefore of special interest. In an economical perspective, herbivores are also of hunting interest for sport and trophy hunters and generate annually large economic benefits (Palazy et al. 2012). Diversity and emblematic aspect of some herbivores also favor tourism (Cederna & Lovari 1985). Also, large herbivores bring a cultural component to ecosystem services by the maintenance of several cultures (for example, Sami people from Scandinavia still rely on reindeer domestication).

Given their intermediate position, densities of large herbivores are controlled by the resource availability ("bottom up" effect), predators (natural and human predation) ("top-down" effect), illness ("top-down" effect) and competitors ("transversal" effects). Larger herbivore species which require greater plant abundance are more prone to be limited by food availability, whereas smaller herbivore species which require higher plant nutrient content would be more sensitive to predation (Olff et al. 2002, Hopcraft 2010). In predator-free environments, environmental stochasticity (Saether 1997) and density-dependence (Skogland 1985, Coulson et al. 2000) acting partly through food limitation, but also maternal care (Loison et al. 2004) and cohort effect (Gaillard et al. 2003), play an important role in the complex dynamic of herbivore populations.

In addition to be regulated by these factors, herbivores can strongly impact them (resource availability, predators and competitors) through feedback effects.

As herbivores as a whole consume over 20% of the annual net primary productivity (Agrawal 2011 and references therein, different rates of damage by large herbivores in forest for specific trees in Danell et al. 2006) and have a strong impact on the biomass of primary producers in terrestrial and marine ecosystems (Poore et al. 2012), they play a major role in the regulation of plant diversity and ecosystem functioning (Olff & Ritchie 1998, Belovsky & Slade 2000). However, predicting the consequences of herbivores on plant diversity is difficult as studies lead to contrasting results, ranging from positive (Belsky 1992, Collins et al. 1998) to negative (Milchunas et al. 1998, Wardle et al. 2001) or neutral effects (Stohlgren et al. 1999, Adler et al. 2005). Indeed, different parameters are involved in the impact of large herbivores: feeding ecology (grazer/browser gradient), intensity of herbivory pressure and type of physical disturbance (e.g. trampling, rooting behavior, fraying with antler, Latham 1999). Besides, site characteristics such as differences in productivity among locations (Bakker et al. 2006) and the evolutionary history of grazing (Milchunas et al. 1988) also modulate the response. For example, grazer herbivores, supposed to be less selective, should impact dominant species (Milchunas & Lauenroth 1993) and increase plant diversity at higher productivity but decrease diversity at low productivity (Bakker et al. 2006). This is the case of the bison (*Bos bison*), which maintains plant diversity in productive systems in meadows of North-America (Collins et al. 1998). Moreover, the predictions are not straightforward as the relationship between herbivory pressure and plant diversity is non-linear. A moderate grazing pressure has been shown to enhance a higher plant diversity than a high and low grazing (Hobbs & Huenneke 1996, Rooney & Waller 2003, Boulangeat et al. 2014, Ganjurjav et al. 2015), which corresponds to the intermediate disturbance hypothesis explaining plant diversity (Connell 1978) even if the theoretical base of this hypothesis has been questioned recently (Violle et al. 2010).

By their grazing and browsing action, herbivores are a useful tool for landscape management. They can speed up or slow down successional processes, for example by maintaining open habitats and preventing forest establishment (Menoni et al. 2008), or enhancing the forest settlement by promoting the selective grazing on particular plant species (Prins 1998). Hence, domestic herds can be used to restore brushwoods grasslands (Garnier & Navas 2013) and avoid the closure of open areas. For example, in the Bauges Massif (our study site), cows are taken up to the Armene pasture in summer to prevent the spread of the green alder. A good adequacy between the knowledge of the functional structure of the vegetation and the grazing diet, is important for the success of operations of herbivore introduction (Dulphy 1995, Garnier & Navas 2013). Indeed, the introduction of a specific herbivore is not possible everywhere, especially because they can have negative effects on plant diversity in unproductive area (Bakker et al. 2006) or in area that are not used to recent strong grazing pressure (Milchunas et al. 1988).

Aside from the direct energy and material flows between plants and herbivores or predators and herbivores, herbivores also generate trophic cascade through vegetation changes on invertebrates (Martin et al. 2010), small mammals (Smit et al. 2001) or birds (Cardinal et al. 2012). For example, changes in density of forest cover through intensive browsing by white-tailed deer (*Odocoileus virginianus*) lead to the homogenization of songbird community (Cardinal et al. 2012). Herbivores also influence indirectly ecosystem processes such as alteration of nutrient cycles (Wardle et al. 2004, Garibaldi et al. 2007), influences on net primary production (Wardle et al. 2004), modification of abiotic disturbance such as fire (Hobbs 1996), promotion of ground-level light availability in grassland ecosystems through the removal of plant biomass of superior competitors (highest plant species) (Borer et al. 2014).

These effects can act at different spatial and temporal scales (Hobbs 1996) and have in turn different consequences. For example, herbivores can favor the development of grazing-resistant or avoided plant species which in turn reduces the diversity of the plant communities at the landscape-scale, whereas the nutrient release by faeces should improve nutrient cycling and increase the diversity at local-scales (Crawley 1997).

b) Large herbivores in Europe

Rapid increases in large herbivore densities (Putman et al. 1996, Loison et al. 2003, Milner et al. 2006, Maillard et al. 2010, IUCN red list) observed during the last thirty years in Europe led to a large increase of studies on plant-ungulate relationships (Coulson 1999, Côté et al. 2004, Ward 2005, Shelton et al. 2014). In order to draw a parallel with the beginning of the introduction, we are going to specifically address the main factors involved in these variations of population densities. First, alpine and Nordic environments are specifically affected by lower snowfall, early melting and decrease of vegetal productivity (Hamel et al. 2009). These warmer winters lead to the decrease of animal winter mortality while early springs reduce the critical period of search for food (Mysterud et al. 2007, Pettorelli et al. 2007). However, these consequences should be viewed cautiously, given that a same cause can have multiple, and sometimes opposite, consequences. Early springs are not necessarily beneficial for animals because of the asynchrony between the peak of vegetation biomass and the time to build up fat reserves (Pettorelli et al. 2007, Post et al. 2008). This mismatch in timing has also been demonstrated for herbivorous mammals and food plants (Inouye et al. 2000), parasitoids and their host insects (Van Nouhuys & Lei 2004) or insect pollinators with flowering plants (Visser et al. 2005, Harrington et al. 1999). Altitudinal displacement of tree line at the highest elevations, caused by climate warming and by changes in land use during the 20th century (Gehrig-Fasel et al. 2007), increases the availability of high quality vegetal biomass, which can be beneficial to sustain energetic requirements and improve fitness. In addition, the decrease of predator densities and the changes in the way population are managed (Apollonio et al. 2010), through hunting plans or species introduction, largely contribute to the increase of ungulate populations in France and Europe. This contrasts with the overall decline of large herbivores at the global scale (Hopcraft et al. 2010, Ripple et al. 2015). Luo et al. (2014) demonstrated that the modifications of environmental components used by ungulates, such as plant availability, resource quality or other habitat parameters, dramatically altered the spatial distribution of species on the Tibetan Plateau. Modelling results show that species could lose more than fifty percent of their habitat range but the percentage varies with species and location (18% of range contraction in African mammals, Thuiller et al. 2006), whereas some of them might occupy new distribution area through dispersal (Luo et al. 2014).

c) The motives that lead us to initiate this work

Following the increase of large herbivore distribution area in Europe (Loison et al. 2003, Milner et al. 2006, Maillard et al. 2010, IUCN red list), spatial overlap among species – including domestic herds – increases and can lead to changes in intra- and inter-specific interactions. If competition appears or strengthens among individuals within a species and among species, individuals could suffer a decrease of fitness that could lead to changes in population dynamics. For example, this could be problematic for native species suffering the consequences of increasing densities of introduced species (Forsyth & Hickling 1998, Lovari et al. 2014, Ferretti et al. 2015). In parallel, their increase can also become an issue because of a stronger impact on composition, structure and dynamic of vegetal communities (Hobbs & Huenneke 1996), and can also lead to agricultural and forest damages. In order to better understand the structuration of herbivore community, the impact of large herbivores species on ecosystems and give cues to population and habitat management, it appeared necessary to determine how spatially co-occurring herbivores select and partition food at the intra- and inter-specific level. To achieve these goals, we focused our work on the large herbivore community of the Bauges Massif where four ungulate species can be found (chamois, roe deer, deer, mouflon) including one introduced species (mouflon in 1950s, Darmon et al. 2007).

2.2 Diet as a linkage between two trophic levels

a) A matter of spatio-temporal scale

Diet of animals is the last step of a multiple spatio-temporal scale selection process (Johnson 1980, Senft et al. 1987). The selection by an animal requires that a resource be over or under-consumed relatively to its availability in the environment.

Species or populations occur within a distribution area (1st-order selection), where organisms define their home range (2nd-order selection) and select feeding station (vegetal communities) (3rd-order selection) in which they select item (4th-order selection) (fig.2). The selection at each scale impacts the selection at the lower-scale.

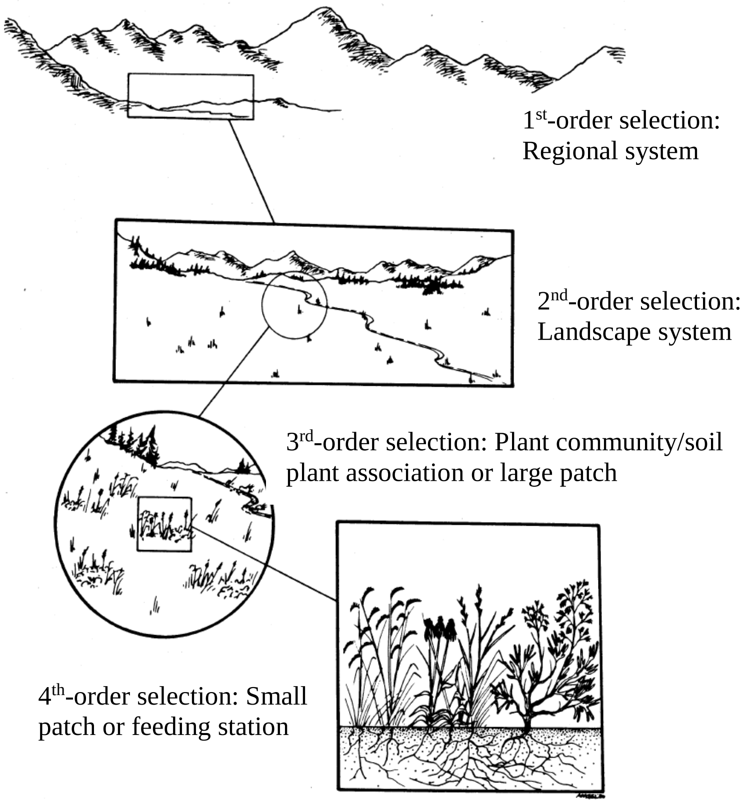

Figure 2. From Senft et al. (1987) and Johnson (1980), Ecological hierarchy of foraging by large herbivores.

Predicting the feeding behavior of animals have been and is still a major goal in ecology (Pyke et al. 1977). One of the most famous theories is the “optimal foraging theory” (OFT), firstly developed by McArthur & Pianka (1966) and then approached by several other authors (Pyke et al. 1977, Stephens & Krebs 1986). Originally stated for carnivores, it predicts that individuals should maximize their energy intake per time unit while minimizing the costs related to searching, handling and digestion processes. Ruminants have to make decisions on a gradient opposing two behavioral options: maximize the time of searching behavior to maximize energy gained (“energy maximizers”) or minimize the time of searching and be less selective for forage in order to save time for other tasks (“time minimizers”, Schoener 1971, Bergman et al. 2001, Fortin et al. 2003). With this vision, trade-offs are consequently required between choosing an optimal diet (in terms of quantity and quality), and lose less energy as possible with displacements and forage handling, and allocate the right time to patches (Searle et al. 2005). Hence, this theory includes different scales of selection and different constraints related to the animal features (temporal, energetic and cognitive). This theory of optimal foraging has been described in an environment where the only constraint was the heterogeneous distribution of resources. However, abiotic and biotic constraints such as inter- and intra-specific interactions, predation (Grignolio et al. 2007, McAthur et al. 2014) and disturbance are known to play a major in the animal decisions. Moreover, this principle may not be specific to energy but also to other plant biomechanico-physico-chemical characteristics (Chapin et al. 1980, Massey et al. 2009, Dostaler et al. 2011, Zweifel-Schielly et al. 2012). Hence, these additional factors should be included in the analyses to better fit to the "real" environment encountered by species.

The temporal variability in the diet selection is also an important aspect of ecological interactions (Wam et al. 2010), as the quality and quantity of forage fluctuates over the year (Duncan 2005). In addition to habitat changes, herbivores are also constrained by their annual cycle and their concurrent requirements (Kaske & Growth 1997) during gestation, lactation, growth of young or fat storage before winter. For example, some studies suggest that herbivores should select proteins in summer for body growth and digestible carbohydrates in winter when the thermoregulation is high (Berteaux et al. 1998, Dostaler et al. 2011).

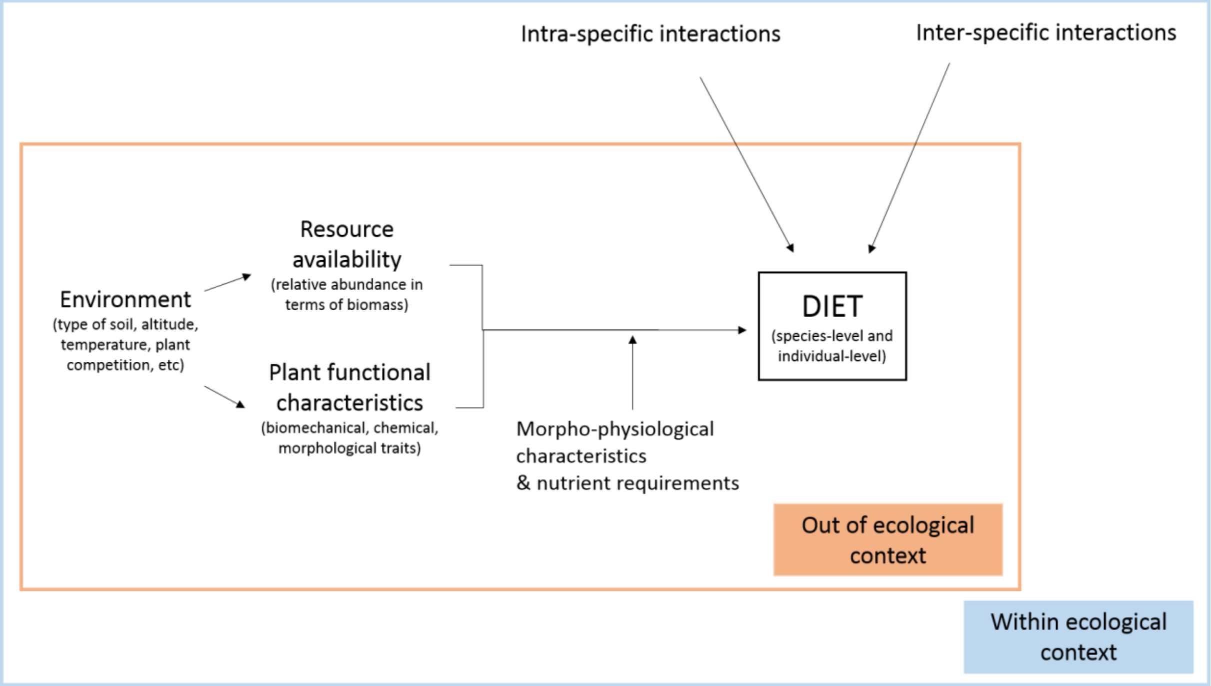

Figure 3. Illustration of the factors influencing the diet of animals.

In this work, we focused mainly on the item scale, and we also used information of available resources at the scale of vegetal communities when we analyzed the scale of diet selection. Habitat selection at broader scale was the topic of Gaëlle Darmon's PhD (Darmon 2007) on the same study site, and is currently pursued by Antoine Duparc for his PhD. While other factors such as animal characteristics (morphological, physiological, cognitive and social traits), the permanent presence of predators, the knowledge animals have gained about their previous diet (Provenza 1995) and the precise spatial distribution, organization and accessibility (Dumont & Petit 1998) of plants are important in the decisions of individuals to choose where to forage, we focused on local foraging decisions and local characteristics of plant abundance and traits that influence those decisions (fig.3). We also incorporated the temporal dynamic in our analyses.

In the following paragraphs, I will specifically describe the factors involved in plant assemblages in individual diet (fig.3).

b) Animal morpho-physiological characteristics and nutrient requirements

Herbivores have to face the paradox of living in a green world (box 3) without having the morpho-physiological characteristics enabling them to feed on all available plant species (Hofmann 1989, Polis 1999, Clauss et al. 2003b). In general, plants are low in nutritional value and hard to digest, because of the tough fibrous thick cell wall (lignin, cellulose, hemicellulose) and/or toxicity due to secondary compounds. Herbivores differ in their ability to cope with these constraints. They are therefore exposed to exert a trade-off between nutrient requirements and digestive constraints, in order for them to meet the nutritional demands required for growth, survival and reproduction (Hanley 1997).

In this work, we will focus on the group of the ungulates belonging to the large herbivores (box 2) (Asher & Helgen 2010). Ungulates represent a highly diversified guild. The highest diversity is found in Africa (Fritz 1994, Fritz et al. 2002) and has been widely studied in community ecology (duToit & Cumming 1999, Fritz & Loison 2006). Especially, we will work on the foregut fermenters, more commonly referred to ruminants (Artiodactyles). Contrary to hindgut fermenters (e.g. horses, rhinoceros, micro-mammals, rabbits) for which the digestive process is monogastric (one stomach chamber) and where the microbial fermentation happens in the large intestine and caecum, cellulose digestion of ruminant diet (foregut fermenters) through microbial fermentation occurs in the reticulo-rumen composed of four stomach chambers. This physiology gives them digestive and nutrient absorption advantages as micro-organisms in the rumen of foregut fermenters can break down the plant material before it arrives in the small intestine where nutrients are absorbed (Feldhamer 2007). On the contrary, food goes directly to small intestine in hindgut fermenters, without being well degraded, and these animals consequently have to forage in large quantities. In environments where the quantity of food is limited, ruminants are more adapted as they have a more efficient digestive system (Feldhamer 2007).

Box 2 – What is an herbivore?

An herbivore is an animal that gets its energy from eating plants. Herbivores can be found in different classes such as mollusks, insects, birds, reptiles, fish, marsupials and mammals (Hopcraft et al. 2010). Herbivores can be divided (artificially) into two groups relatively to their size. Large herbivores are defined as having a body weight > 2kg (Fritz & Loison 2006), which includes mostly ungulates and marsupials, but also some large rodents or birds.

Ruminant species differ on many aspects: the size, musculature and composition of their rumen, the size of the salivary glands, the type of salivary binding proteins, the size and strength of their jaw, their body size (Hofmann 1989, Clauss et al. 2008a). All these morpho-physiological characteristics play a role in the demarcation of their feeding niche, which explains how they coexist on the dietary axis and share resources. For example, the two most employed ruminant classification ranks them on two gradients: the first one describes the resource they use (grazer/browser, Hofmann 1989, fig.4), the second one describes the morpho-physiology of their rumen (moose-type/cattle-type, Clauss et al. 2003b). Browsers, such as roe deer, are selective animals feeding mainly on lignified plant organs (fruits, seeds, buds) and forbs and are able to deal with toxic component and anti-nutrients. Their rumen ("moose-type") is less adapted than the "cattle-type" (see hereafter) to digest fiber (Clauss et al. 2010b). Their salivary glands contain certain proteins able to bind with tannins. It allows the animals that feed on highly nutrient rich plants having high anti-herbivore deterrents (high polyphenol content as tannins) to digest the plant crude protein (measured as nitrogen content, CP=6.25*nitrogen content), without they form indigestible complexes with tannins released from vacuole during chewing (Verheyden et al. 2011). Grazers, such as mouflon, have a diet rich in grasses (Hofmann 1989), and are supposed to favor quantity rather than quality. The high capacity and strong musculature of their rumen ("cattle-type") allow them to overcome the physically resistant diet by being efficient to digest fiber and cell wall (Clauss et al. 2008a, 2010). The size of their salivary gland is smaller than the ones of browsers suggesting a smaller need for the synthesis of salivary tannin-binding protein and a lower ability to digest lignified plant rich in tannins. This is in agreement with the low content of tannins in grass species (Shipley 1999). (This is discussed in the Note). Finally the intermediate feeders, such as chamois, are able to adapt their strategy between the two extremes of the gradient. This diversity in diet categories and diet morpho-physiologies may contribute to the diversity and coexistence of large herbivores.

This simplified vision of ruminant classification could lead us to think that the cattle-type has to adopt a grazer behavior. However, this is not always the case, as it has been demonstrated for the mouflon (Marchand et al. 2013).

The evolution of ruminants can be related to the type of habitat in which they occured. Paleontological studies showed that the main driver of the speciation of new feeding type would have been the increase of the availability of open habitats (Perèz-Barberia et al. 2001). The oldest common ancestor of large herbivore reported so far is a browser inhabiting the forests of the middle of Oligocene era (-34 to -23 millions of years) (Perèz-Barberia et al. 2001). Emergence of meadows inside forests after climate warming events would have opened the way to the evolution of intermediate feeders, then grazers (Perèz-Barberia et al. 2001).

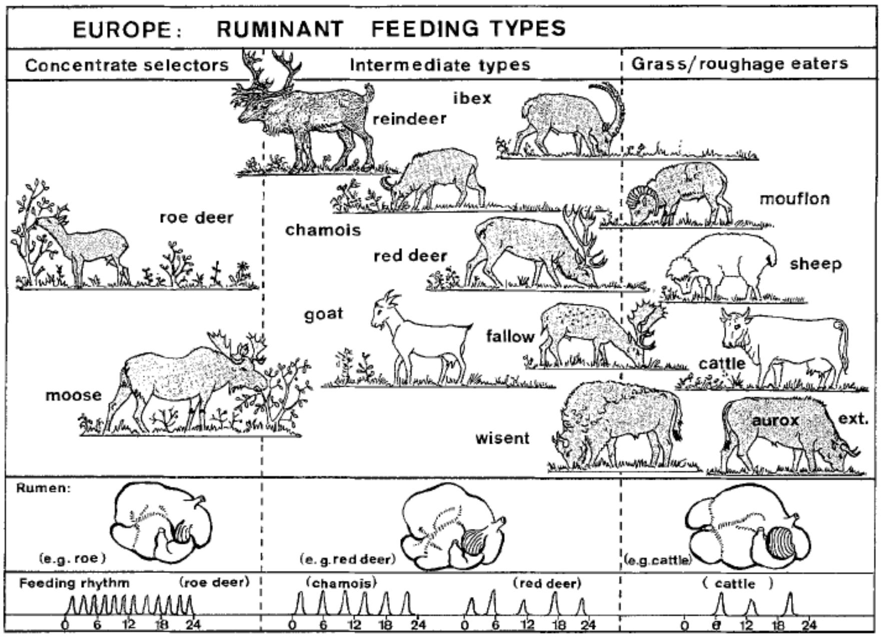

Figure 4. From Hofmann (1989), classification of large herbivores according to their feeding type and rumen morpho-physiology, and their consequences on activity rhythm.

As evoked hereinabove, herbivores also differ in the number of plant species they are able to ingest. They are ranked on a gradient going from generalists, which include many plant species in their diet, to specialists, which only feed on a few plant species (Freeland 1991, Shipley et al. 2009). The low number of specialists species among mammals has been suggested by two hypotheses: one plant cannot provide all the required nutrients ("nutrient constraint hypothesis") and the detoxification system of mammalian herbivores cannot detoxify a high concentration of secondary compounds present in a single plant species ("detoxification limitation hypothesis") (Dearing et al. 2000). A distinction between "obligate" and "facultative" specialists or generalists allows to differentiate the cases where specialization is due to an evolutionary process and is the result of behavioral and/or morphological adaptation ("obligate"), or if specialization is the result of local availability of resources, and the time and spatial temporal scale used ("facultative") (Shipley et al. 2009). Those variations in the dietary specialization play a role in the explanation of the dietary diversity in herbivores and hence their ability to coexist.

In addition to be determined by the morpho-physiological characteristics, we stated that diets of animals were also constrained by their nutrient requirements. The nutrient requirement depends mainly on the body size of animals. Indeed, the metabolic rates are higher for a small herbivore than for a bigger one (Demment & Van Soest 1985, White & Seymour 2003). Consequently, small herbivores have to focus on diets of high quality in order to quickly reach their needs. On the contrary, larger herbivores can use forage of lower quality (Demment and Van Soest 1985) due to their reduced relative energy requirements and their longer passage rates and therefore thorough digestion (Clauss et al. 2003a). To compensate the low quality forage that is low in nutritional value, they ingest larger quantity of food thanks to their larger gut size. Many authors tried to relate the body size directly with diet. However, conclusions are diverse and still debated (McArthur 2014). Whereas some studies find a relationship between body size and percentage of grass intake (Jarman 1974, Demment & Van Soest 1985, Gagnon & Chew 2000), others contradict these predictions (Hofmann 1989, Mysterud et al. 2001, Codron et al. 2007d). Conclusions of several studies stress the need to realize further tests on relationships between plant physical properties and functional morphology (Codron et al. 2007d) or include other animals factors such as the intake and pre-digestion food processing (Steuer et al. 2014).

The trade-off between morpho-physiological constraints and nutrient requirements is consequently reflected by a trade-off between resource quantity and quality. Although spatially co-occuring herbivores rely on the same food resources, they can face different digestive and metabolic constraints that lead them to differentially use the resources, and allow the coexistence. We describe hereafter the importance of resource availability, plant functional characteristics and ecological factors (intra- and inter-specific interactions) in the diet selection by herbivores.

c) Resource availability (relative abundance in terms of biomass)

According to the optimal foraging theory (OFT) described hereinabove, the morpho-physiological constraints and the nutrient requirements, animals have to exert a trade-off between forage quantity and quality. Given that the most nutritious plants tend to be the least available (Hansen et al. 2009), preferences for plants of high quality requires more searching time. In turn, lower energy is needed for the digestive process. On the contrary, a focus on quantity does not require to spend energy for searching plant but requires energy to digest high biomass plants of low quality plant.

In order to determine how large herbivores compose their diet, we need to define to which extent food availability influences the choice. Here, we define plant availability as the relative abundance of the plant in terms of biomass. If herbivores favor quantity rather than quality, we should observe a linear relationship between the relative abundance of a plant in the diet and the relative abundance of that plant in terms of biomass in the environment.

Few studies examine the response of free-ranging large herbivores to available relative abundance of plants in terms of biomass (Alm et al. 2002, Forsyth et al. 2005). Forsyth et al. (2005) showed that deer avoided the most abundant species, and preferred the low abundances in terms of relative biomass. Other exploration has been done with experimental trials on sheep (Parsons 1994) but conclusions were not straightforward as many other factors other than resource availability (in terms of percentage of covered area) influenced the selection (e.g. plant composition, previous diet, preferences).

To our knowledge, most of the studies that reported resource availability to be important in the field focused on the patch-scale or higher scale to explain the spatial distribution of animals (Bergman et al. 2001, Fortin et al. 2003, Fryxell et al. 2004, Zweifel-Schielly et al. 2009, van Beest et al. 2010). A multi-scale approach has been used in Bee et al. (2008) where they showed that red deer selected vegetation patches according to the patch quality, and then selected plant species within this patch. However, no studies clearly reported the multi-scale approach of diet selection in the field by taking into account the real relative abundance of plants in terms of biomass and not the general quality of the patches. Consequently, we are not aware of the importance of the relative abundance of a plant in the field on the diet selection process at a fine-scale (i.e. selection of an item within the feeding patch), and if the strength of the selection is the same as at a coarse-scale (i.e. selection of a patch within seasonal home range). We could assume different alternative hypotheses: (1) animals exert a strong selection for a patch where the preferred resources are highly abundant and then feed on these plants according to their relative abundance within the patch (no selection within the patch), (2) animals select a patch according to other characteristics (e.g. safety, temperature) and are highly selective for the preferred resources within the patch. This requires that the food availability is heterogeneously distributed. In the case of a homogeneous distribution of the resource, (3) no selection would be observed for a patch, but animals could be selective within the patch for preferred plant species. This question has been approached by Dupeyras (2014) and is detailed in the *Summary of results*. Additional information about the selectivity of chamois and mouflon are given in paper II and III.

d) Plant functional characteristics

If herbivore do not forage according to resource availability, then a selection could be observed for certain plant species. For there to be a selection, it requires that plant species differ in their physical, chemical and nutritional characteristics, thereafter affecting their handling and processing rate by herbivores (Pyke et al. 1977). Therefore, the functional approach is the appropriated way to define the diet selection criteria through chemical, biomechanical or physical functional traits (the usefulness of the functional approach has been described in the chapter I). Nowadays, standardized protocols are available to allow robust comparisons among studies (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013) and we used them for our measurements.

Animals must acquire five major nutritional categories from their environment in order for them to grow, survive and reproduce (Robbins 1983). These are energy, protein, water, minerals and vitamins (Robbins 1983). Proteins are important constituents of the animal body (e.g. cell wall components, enzymes, hormones, lipoproteins in fat transport, antibodies) and are involved in the growth and reproduction of individuals (Robbins 1983). Their content in plants is measured through their nitrogen content. When multiplied by 6.25, the nitrogen content is termed the crude protein content (Robbins 1983). The other most limiting nutrients for herbivores are digestible energy which plays role in metabolism and thermoregulation (Robbins 1983).

As animals need to reach a certain threshold of energetic requirements for growth and reproduction (Robbins 1983), it is easily conceivable that the selection should go toward plant traits that satisfy their metabolic requirements. For example, 14-18% of crude protein has been estimated as the optimum percentage for maximum body growth of deer (French et al. 1956, Magruder et al. 1957). For the female elk, 8% of crude protein were required (Van Soest 1994, Cook 2002).

However, plants constrain the use of all these optimal resources by defensive traits usually deterrent for herbivores (box 3), such as lignin which reduces cell wall digestibility or secondary plant compounds that can be toxic (terpenoids, alkaloids, phenolics compounds, Robbins 1983, Tixier et al. 1997, Sauvé & Côté 2007). Hence, large herbivores have to cope with different plant defense strategies and make a trade-off between nutrient intake and plant defenses to get a balanced diet that satisfy their nutritional needs.

Other chemical traits, such as the alkaloid content in plants synthetized by endophytic fungi can also strongly impact the large herbivore growth and survival through intoxication (Vicari & Bazely 1993, Miles et al. 1998). To our knowledge, those traits have never been tested in dietary choices experiments, but only studied because of their impact on animals (Miles et al. 1998).

Box 3 – Green World Hypothesis (Hairston et al. 1960) and "Plant Self-Defense Hypothesis" (Terborgh 2005)

Herbivores encounter a large plant diversity but are not able to feed on all the green biomass available. The "Green world hypothesis" (Hairston et al. 1960) states that herbivores are mainly kept in check by predators, parasites or pathogens ("top-down" control), preventing herbivores to strongly damage the vegetation. At the same time, the discovery of plant secondary compounds (such as phenolics, alkaloids, terpenoids, glycosides) led to the statement that such costly investments were involved in anti-herbivore defenses. The "Plant Self-Defense Hypothesis" (Terborgh 2005) consequently argues that the world is green also because plant can defend themselves against herbivores through chemical or physical (spines, thorns) properties ("bottom-up" control).

While we explained that herbivores should achieve a trade-off between plant quantity and quality, the diet selection could also be influenced by other factors such as the plant visibility, the mechanical ease of plant harvesting and chewing, and the plant digestibility.

First, visibility can be measured through plant height; size, number and color of inflorescence; and plant spatial distribution. The hypothesis that visibility could play a role in diet selection led us to include these plant functional trait measurements in our field work (see *Material & Methods*). Few studies have been realized on the importance of inflorescence in diet selection criteria by large herbivores. The ones that we found focused on specific plant species (Gomez et al. 2000, Gomez et al. 2003): ibex (*Capra pyreneica*) tend to prefer *E. mediohispanicum* with a higher number of flowers (Gomez et al. 2003). However, there seems to be a lack of work on larger plant communities. In addition, we hypothesized that herbivores could be more attracted by plants with large colorful flowers as they could be easier to spot. Finally, we suggested that the distribution of plants measured by their sociality could favor the forage intake of some plant species: as individuals of social plants are grouped, they could be more easily visible and attract animals.

Secondly, we hypothesized that the mechanical ease of plant harvesting and chewing, and the plant digestibility could influence the diet selection. These three mechanisms are mainly influenced by plant fiber composition (Searle & Shipley 2008). Because grasses contain higher fiber content than non-woody browses, herbivores should spend longer time chewing and digesting a unit mass of grass than non-woody browse (Choong et al. 1992). Similarly, even though ruminants are able to extract energy from plant cell wall composed of cellulose and hemicellulose, thanks to the microbial fermentation in the rumen (Hofmann 1989), highly fibrous plant reduce digestibility. In turn, this can influence the food retention time in the gastro-intestinal tract and the plant intake rate (Hanley 1982). Species could have evolved to maximize energy intake in order to allow a higher level of metabolism which gives competitive advantages (McNab 2006). As energy maximization is permitted by a high food intake or a high digestive efficiency (Clauss et al. 2010b), the estimation of digestibility of eaten plants could give information about the animal digestive strategy. During this work we used biomechanical traits (tensile strength and leaf punch toughness) as proxy of leaf harvesting and chewing. These biomechanical traits could actually also be involved in the assessment of plant quality as a plant easy to harvest, chew and digest would allow the herbivore saving energy and would allow an easier nutrient release from vacuole valuable for animals.

Finally, the question of digestibility could be explored at the plant-level and not only at the leaf-level, as previously described. The percentage of dry weight twig/leave on total dry weight could also play a role in diet selection if the animal is not able to feed on the most nutritious and digestible part of a plant, i.e. the leaves. For instance, the proportion of green leaf in the sward can modify the intake of green leaf by wildebeest and topi in Africa: the higher the proportion of green leaves in sward, the higher the proportion of green leaves in diet and the higher the intake rate (Murray & Illius 2000). Consequently, we suggested that a plant allocating more energy to the leaves instead of twigs could be preferred as digestibility of the whole plant would be increased.

The questions of diet selection have been experimentally approached with insects (Coley 1983, Choong 1996, Perez-Harguindeguy et al. 2003, Ibanez et al. 2013a) and some large herbivores (white-tailed deer *Odocoileus virginianus*: Berteaux et al. 1998, Sauvé & Côté 2005, Dostaler et al. 2011; roe deer *Capreolus capreolus*: Verheyden-Tixier & Duncan 2000, Pollock et al. 2007; fallow deer *Dama dama*: Bergvall & Leimar 2005; domestic sheep: Cingolani et al. 2004, Massey et al. 2009, table 1) for which experimental studies allow a controlled design of traits. However the mechanisms of diet selection are poorly understood for wild animals as it requires precise information on diet, on resource availability and a large plant traits database. The studies that tried to demonstrate the factors influencing the herbivore choices in the field dealt with red deer (Forsyth et al. 2005, Verheyden-Tixier et al. 2008, Lloyd et al. 2010, Zweifel-Schielly et al. 2012) or eland (Watson & Owen-Smith 2002). Often, previous works focused on either chemical or physical plant functional traits such as protein and carbohydrates (Chapin 1980, Berteaux et al. 1998), silica (McNaughton et al. 1985, Massey 2009), spines and thorns (Cooper & Owen-Smith 1986) or plant secondary compounds (Bergvall & Laimar 2005). In other cases, a higher number traits were combined, but they were analyzed separately in order to determine which ones were positively or negatively correlated the plant eaten (Tixier et al. 1997, Forsyth et al. 2005, Zweifel-Schielly 2012). However, plant functional traits measured are generally correlated, which might confound the relationship of an independent variable on the response variable (Smith et al. 2009, Ray-Mukherjee et al. 2014, Ruffell et al. 2015). In order to identify the direct and indirect effects of plant functional traits in the process of diet selection, we tested the validity of causal models relating plant functional traits and diet using path analysis (Wright 1921). Especially, we tested whether biomechanical (plant toughness) and chemical (LDMC, nitrogen content) had direct or indirect effects on diet selection, and whether the selection varied between season and species (chamois and mouflon in spring, summer and autumn). Hypothesis, results and discussion are described in the paper III, and in the *Summary of Results*.

Today, the understanding of regional-scale ecosystem functioning is becoming an important topic in ecology (Sutherland et al. 2013). However, large scale studies lack extensive and intensive data that would allow to unify the different parts of ecosystems at different temporal and spatial scales. Hence, it appears necessary to find cost-effective, rapid and accurate methods to deal with plant functional trait measurements with large sample size. For the study of plant nutrient stoichiometry, the NIRS method appears as one of the promising methodology to overcome the problems stated above: (1) time and cost efficient method which overcomes the wet chemistry methodological limitations, (2) the ability to cope with large sample size that would allow the increase of the sampling scale of studies. However, it remains to test the transferability of the method in different geographical regions and for different plant nutrients. This question is studied in the *Summary of Results* and in the *Synthesis, perspectives and directions*.

Table 1. Review of selected traits by wild and domestic large herbivores (SLA: Specific Leaf Area). Asterisks "*" refer to the traits measured in the thesis. Their measurement method is described in chapter IV, section *4.2*.

	References	Herbivore	Selection toward…	Others traits tested
Plant structure *	Holt et al. 1994	Not specified	The superior resource competitor for height	
	Cingolani et al. 2004	Domestic sheep	Short plants	Height, SLA, leaf toughness
	Pollock et al. 2007	Red deer and goats (experimental trial)	Large leaf area for both species, leaves with low stem strength and low divaricating index	Divarication index, leaf area, stem strength, stem phenolics
Nutrient*, sugar and silica content	Tixier et al. 1997	Roe deer	Plants rich in soluble sugars	Digestibility, nitrogen, fiber, soluble sugars and silica content, phenolic and terpenes compounds
	Berteaux et al. 1998	White-tailed deer (experimental trial)	Diets high in energy and low in protein in winter	
	Massey et al. 2009	Domestic sheep (experimental trial)	Plants with low silica content	
	Verheyden-Tixier et al. 2008	Red deer	Diet rich in soluble sugars	Nitrogen, fiber and tannins content
	Dostaler et al. 2011	White-tailed deer (experimental trial)	Plant rich in nitrogen in summer and autumn	Fiber content, nitrogen content, dry matter digestibility (DMD)
	Zweifel-Schielly et al. 2012	Red deer	Plants rich in protein and with a high protein:fiber ratio in summer	Water, protein, tannins, fiber, content

Fiber content	Tixier et al. 1997	Roe deer	Plant low in fiber content	Digestibility, nitrogen, fiber, soluble sugars and silica content, phenolic and terpenes compounds
	Watson & Owen-Smith 2002	Eland	Diet low in fiber content	Nitrogen, phosphorus, calcium, magnesium, potassium, fiber, total phenols, condensed tannins content
	Forsyth et al. 2005	Red deer	Plants with low fiber content in winter (hemicellulosis, cellulosis, lignin)	Nitrogen, phosphorus, fiber, condensed tannins content, SLA
	Sauvé & Côté 2005	White-tailed deer (experimental trial)	Plants with low fiber content in winter	Crude proteins, total phenols, fiber, condensed tannins content
	Zweifel-Schielly et al. 2012	Red deer	Plants with low fiber content in spring and summer	Water, protein, tannins, fiber, content
Specific leaf area	Lloyd et al. 2010	Red deer and domestic sheep (experimental trial)	Deer: Plants with high SLA Sheep: Leaf tensile strength, SLA, leaf nitrogen content	SLA, tensile strength, nitrogen and phosphorus content, mass of phytoliths (as a proportion of leaf dry weight)
	Mkhize et al. 2014	Goat (experimental trial)	Plants with broad-leaves with long shoot and no spines	Broad/fine leaves, long/short shoot, nitrogen, condensed tannins, fiber content
Leaf toughness*	Cingolani et al. 2004	Domestic sheep	Plants with high toughness until 5 N mm^{-1} and then selectivity decreases with low toughness	Height, SLA, leaf toughness
Secondary compounds	Bergvall & Leimar 2005	Fallow deer (experimental trial)	Food of low tannins concentrations	
	Sauvé & Côté 2005	White-tailed deer (experimental trial)	Plants with low condensed tannins content in winter	Crude proteins, fiber, total phenols

e) Inter-specific interactions

Positive, negative or neutral interactions for a resource can occur between large herbivores. These ecological factors can modify the niches of animals and in turn structure the community. We describe them hereafter. As we work on the feeding axis of the niche, we will limit our examples and explanations to the food resources. However, resources can also be spatial, temporal or climatic for example.

Positive interactions describe the positive effect of a species on another. For example, grazing facilitation has been observed in different cases: among wild large herbivores (Wegge et al. 2006, Waldram et al. 2008), and between wild and domestic ungulates (Gordon 1988, Hobbs et al. 1996, Odadi et al. 2011). Facilitation can occur through increased resource access or quality of resources (Arsenault & Owen-Smith 2002). For example, the grazing by cattle during winter on the Isle of Rum enhances the proportion of green biomass, and these areas are preferred by the red deer in the following spring (Gordon 1988). Also, the presence of white rhinoceros (*Ceratotherium simum*), by its grazing activity on tall grass swards, facilitated the short grass grazers (impala, wildebeest, zebra) use (Waldram et al. 2008).

Negative interactions describe the adverse effect of a species on another. The competition is considered as the major driver of herbivore community organization (Schoener 1983, Gordon & Illius 1989, Arsenault & Owen-Smith 2002). If two species spatially co-occurring are competing for a limiting resource, the subordinate species would be excluded, as the niches of two species cannot completely overlap (except if resource is abundant enough). This has been called the "principle of competitive exclusion" (Gause 1934, Hardin 1960). Competition can be direct, called "interference", when the presence of one species directly impacts the behavior of another species through visual or acoustic disturbance. For example, a species (chamois) can shift its feeding station if a superior competitor (mouflon) is present (Chirichella et al. 2013). Herbivores can also compete at the patch scale indirectly through changes in plant composition and diversity ("exploitation") (Huntly 1991, Murray 2000). As we are interested in the item scale, competition can occur at the plant species or plant part level. By pre-empting the resources of another species, the superior competitor can lead native animals to feed on lower quality resources (Jenkins and Wright 1987), to spend more time searching for food (Kie et al. 1991), or to decrease the quantity of resources ingested (lower food intake rate, Lovari et al. 2014). This could result in changes in individual growth, survival and reproduction (Lindström et al. 1999, Lummaa et al. 2002, Pettorelli et al. 2007, Richard et al. 2010, Ferretti et al. 2015) which in turn could influence the population dynamics of the inferior competitor (Sinclair & Norton-Griffiths 1982, Forsyth & Hickling 1998, Forsyth 2000, Mishra 2004).

Positive and negative interactions can therefore modify the dietary niche of a species through niche expansion/shrinkage or niche displacement (fig.5). Even if competition occur on the dietary axis, the shift can also be done on others axis of the ecological niche (temporal or spatial) and enhance coexistence. On the opposite, competition can also make disappear the inferior competitor through a degradation of fitness.

Neutral interactions can also occur when the resource is not limiting and/or because species niche are partitioned on other unmeasured variable. For example, two species can feed on the same plant species but at different period of the day, and consequently prevent interference competition. Darmon et al. (2012, 2014) demonstrated that mouflon had no effects on the spatial and temporal (activity rhythm) niche axis of the chamois, in the Bauges Massif. Indeed, as daily activity rhythm were species-specific, mouflon had no behavioral interference on chamois. Besides, even if chamois and mouflon were occupying the same pasture in spring, they choose different plant communities (preference for the meadows dominated by *Carex furruginea* for mouflon, and fallen rocks and meadows dominated by *Sesleria* and *Carex sempervirens* for chamois). However, even though mouflon did not have negative impact on the spatial and temporal niche of the chamois, we could hypothesize an exploitative competition for forage between both ungulates, as they both track high quality food. The coexistence on the dietary niche axis is explored in the paper II.

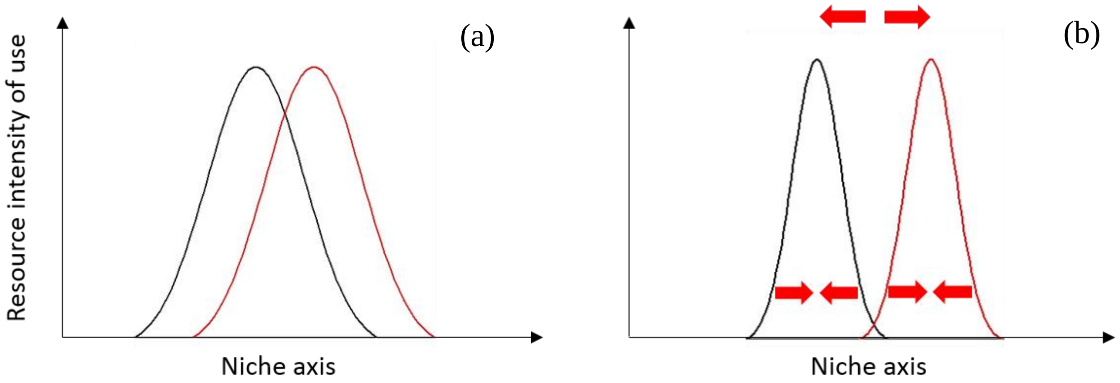

Figure 5. Illustration of the niche dynamics. (a) Overlap of the niches. If resource is not limiting, species can coexist. If resource is limiting, inter-specific competition can be enhanced. (b) To avoid competition, species niche of one or both species can narrow and/or shift.

The overlap measurement has been widely used to measure the strength of inter-specific interactions (Jenkins & Wright 1987, Homolka 1993, Singer & Norland 1994, Bertolino et al. 2009). However, a high overlap of resources can indicate competition if resource is limiting, or an absence of competition if resource is abundant enough. The best option to quantify the strength of interactions is to compare the studied population in two conditions between two similar environments: a site where it lives in allopatry or in sympatry with another species. This setting has been used in the paper II for the study of the impact of mouflon on chamois.

f) Downscaling the study of diet at the individual-level

All the previous description has been done at the species-level to explain how different factors can influence the diets of species, as the inter-specific differences on the dietary axis of the ecological niche play a major role in the species assemblage in a community. The same factors can impact the diets of individuals within a species. This statement implies that individuals can potentially differ one from another. Indeed, Charles Darwin, in its publication of *On the Origin of Species* (Darwin 1859), already stated that a high variability could be observed among the individuals of a species and it was its one requirement for the natural selection to occur. The study of the diet of each individual in itself is not particularly relevant. However, studying the degree of among-individual variability and how it varies with intrinsic species characteristics (e.g. body mass, sex, experience) or ecological factors (such as intra- and inter-specific interactions, environmental heterogeneity) can help to improve our understanding of population dynamic and community structure (Hughes et al. 2008). The interest of including individual specialization in community ecology studies is explained in the chapter I. In this section, I describe how the factors of fig.3 influence among-individual variation (see Araujo et al. 2011 for a complete review on the ecological causes of individual specialization).

Bolnick et al. (2003) have brought up to date the inter-individual differences by defining the “individual specialization” (mainly called among-individual variability or among-individual variation in this work). It can be measured with different indices (Bolnick et al. 2002) and define an individual as a specialist if its niche is narrower than the population niche for reasons not attributable to the sex, age, or discrete morpho-physiological characteristics (fig.6, Bolnick et al. 2003). This definition was used to exclude obvious classifications such as in case of sexual dimorphism (Layman et al. 2015). However recent studies (Smith et al. 2015, Snowberg et al. 2015) showed that subtle differences between sexes or morphological variants can be important determinants of individual specialization (Layman et al. 2015). Hence, different hypotheses arose in the literature to explain the drivers of diet variability and feeding strategy among individuals.

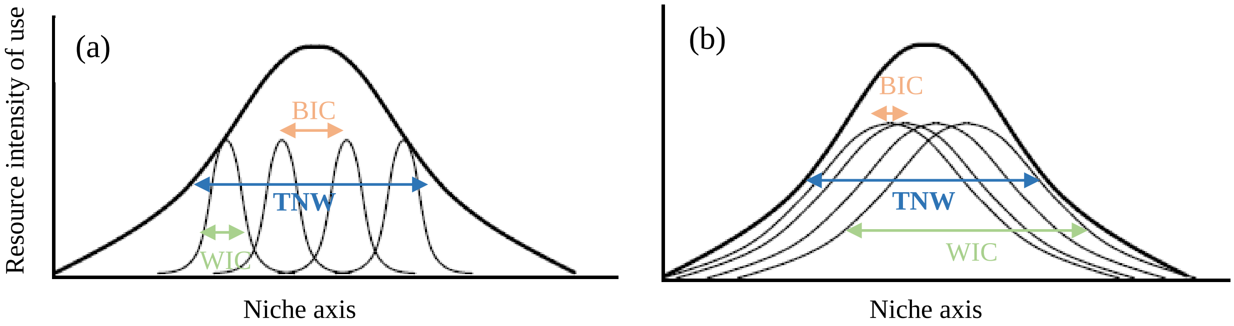

Figure 6. Illustration of two possible degree of among-individual variation with (a) strong among-individual variation, (b) low among-individual variability (inspired from Bolnick et al. 2003). TNW, WIC and BIC are described in the box 4 hereafter.

Box 4 – Parallel with α, β and γ-diversity

The total niche width (TNW) of a population or a species refers to the γ-diversity as it measures the diversity of the diet of the mean population. The within individual component (WIC) refers to the α-diversity as it measures the average of individual niche widths, calculated as the diversity of the diet of each individual. The between individual component (BIC) refers to the β-diversity as it measures the variance in mean resource use among individuals (Bolnick et al. 2003). (TNW=WIC+BIC, fig.6)

Intrinsic factors such as body mass (Luna et al. 2013), sex (Smith et al. 2015), reproductive status (Belovsky & Jordan 1978), age (Dostaler et al. 2011), physio-morphology (Snowberg et al. 2015), experience (Provenza et al. 2003) or dominance (Goss-Custard & Durell 1988) can influence the nutrient requirements of each individual and its ability to detect/handle/digest optimal resources. As described above at the species-level, these characteristics will lead individuals to make a trade-off between resource availability (relative abundance in terms of biomass), plant quality, plant digestibility or plant visibility.

Ecological factors such as intra- and inter-specific interactions also influence among-individual variation (fig.7).

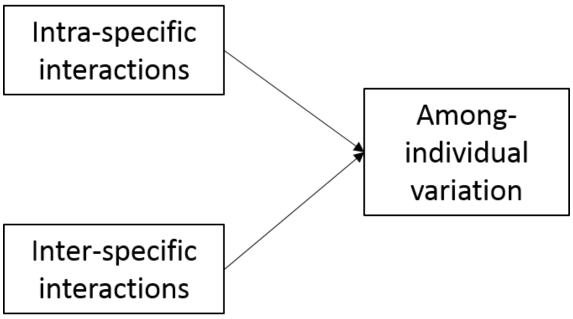

Figure 7. Ecological factors influencing among-individual variation.

The signs of the arrows are not straightforward to predict. In order to facilitate the reasoning, we will take the example of competition as the interaction. We will also limit the explanation to the case of exploitative competition. Indeed, other kind of competition such as interference competition can differently influence among-individual variation (Svanbäck et al. 2011).
The decrease of preferred resources caused by environmental changes, increase of population density or inter-specific competition can lead to different evolution of the degree of among-individual variation according to:

(1) The degree of among-individual variability at time t_0 (or pattern of rank-preference variation, see Araùjo et al. 2011): for instance, if the inter-individual variability is low and the few preferred resources become limiting, some individuals should shift on less-preferred resources which would increase among-individual variability (fig.3.a in Araùjo et al. 2011). On the contrary, if the among-individual variation is high, we can suggest that the decrease of preferred foods would lead the animals to converge on the same alternative available resources, and reduce among-individual variation (fig.3.b in Araùjo et al. 2011).

(2) The plasticity of feeding behavior of animals: individual niche width can be limited by an upper bound if functional trade-offs (cognitive or physical constraints) prevent the evolution of a generalist strategy (Taper & Case 1985, Wilson & Turelli 1986). In that case, if the preferred resources decrease, individuals cannot expand their niche width on sub-optimal resources but can only change their niche position which leads to the increase of among-individual variation (Araùjo et al. 2011). Hence, according to the ability of the animals to ingest a certain number of plant species and to its behavioral and morpho-physiological skills to shift on other resources, the among-individual variability will vary.

(3) The diversity and abundance of available resources: ecological opportunities (diversity and abundance of available resources) are supposed to influence among-individual variation, i.e. higher levels of ecological opportunity favor individual specialization (Roughdarden 1974, Araùjo & Gonzaga 2007, Gerardo Herrera et al. 2008).

Although the evolution of among-individual variation depends on all these factors, conclusions of several studies lead to two general patterns. The increase of (1) intra-specific competition induces among-individual variation through individuals using different subset of resources (Araùjo et al. 2008, Svanbäck et al. 2004, 2007), (2) inter-specific competition reduces niche width though the decrease of variation in resource use among individuals (inverse of ecological release, box 5) (Van Valen 1965, Knudsen et al. 2007, Costa et al. 2008, Bolnick et al. 2010). However, as said before, this need to be taken carefully as inter-specific competition can lead to niche displacement of the focal species and have no impact on among-individual variability for example, or the ecological release can also lead to a decrease of individual specialization because of the increase of individual niche widths for example in Bolnick et al. (2010, box 5).

Out of their ecological context, few studies tried to explain the differences in among-individual variability among different species. Svanbäck et al. (2015) demonstrated with different size classes of Eurasian perch that the trophic position of a population could impact the among-individual variability. However, we found no studies comparing species of the same trophic level differing in their population niche width. In paper I (Bison et al. 2015), we tested two hypotheses: the niche variation hypothesis (NVH, Van Valen 1965) and the sociality hypothesis, to explain the differential diet breadths observed among ungulate species. We extended the NVH to the inter-specific level (because it is originally stated at the intra-specific level) and we tested whether generalist species with wider niche display higher among-individual variability (box 5). The sociality hypothesis posits that other mechanisms could influence the level of among-individual variation: more social species could indeed display lower among-individual variability if all individuals belonging to given social groups share similar diets. The tests of these hypotheses were possible because in our study, the generalist species was the most social, and the specialist species the least social (see fig.1 from paper I for hypotheses).

Having regard to the two last sections (*2.2.c* and *2.2.d*), we highlight that intra- and inter-specific interactions are constantly evolving and interacting before species reach coexistence and stability within a community. In case of competition, as it is considered as a major force structuring community assemblage even if highly debated (Murray & Illius 2000), the niche expansion of a superior competitor can (1) displace the niche of the inferior competitor and/or (2) make decrease the niche breadth of the inferior competitor. In the first case, species can in turn compete with another species. In the second case, it can enhance intra-specific competition, which can lead to increase species niche breadth through individual specialization, or through increase of all individual niche widths (box 5). This niche breadth expansion may in turn cause overlap with another species, and so forth. This dynamic underlines the need to consider the temporal variability, and hence study population niches at different time scales and at the intra- and inter-specific level.

Box 5 – Decoupling of individual and population niche widths

When a population/species is released from a competitor, the total niche width of the population/species can increase through two different paths: all individuals increase their niche width (WIC) by adding new high-value preys to their diet (fig.8 upper path), or between-individual variation (BIC) increases while niche width remain constant (Niche Variation Hypothesis, fig.8 lower path) (Bolnick et al. 2010).

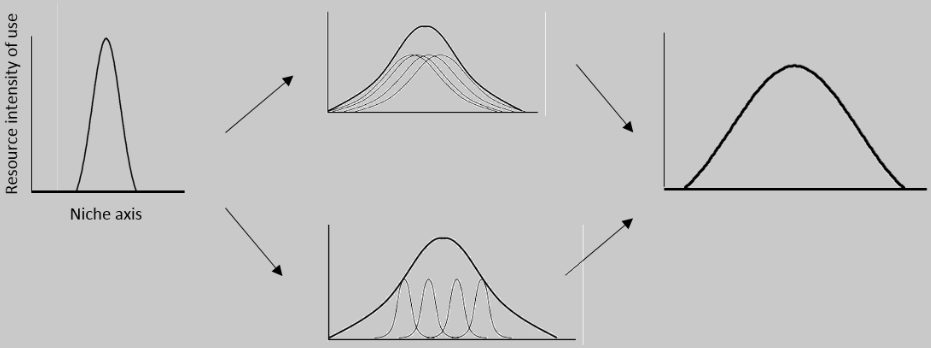

Figure 8. Illustration of the increase of population niche width through two different paths.

Specialization can take a wide range of formats: individuals can be more or less specialized within a population (fig.9a), individuals can be clustered (fig.9b) or nested (fig.9c). In this work, we only explored the clustering of individuals (see Summary of Results *6.1.a*). However, the type of specialization can influence the interactions among individuals and in turn have consequences on population dynamic that remain to be determined (Araùjo et al. 2009). For example, in the case (b), if individuals, e.g. young individuals, form a cluster because of similar requirements, then the decrease of their preferred resource could strongly affect the population dynamic as all the young individuals would be impacted. In the case (c), interactions among individuals would be asymmetric if the resources are limiting.

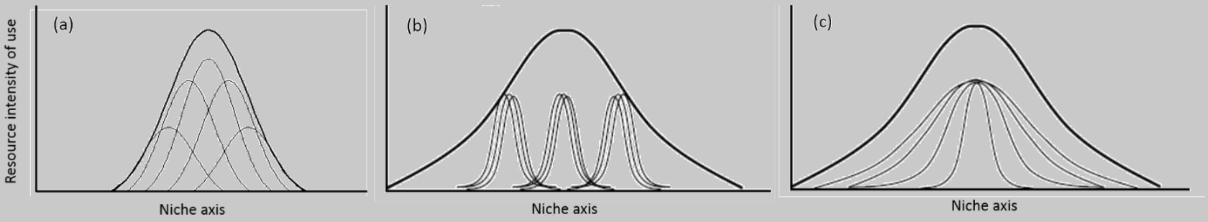

Figure 9. Alternative ways in which individuals can specialize (inspired from Araùjo et al. 2009).

2.3 Objectives

The aims of this three-year work was to improve our understanding on ecosystem structure and functioning through the study of interactions between large herbivores and vegetal communities at the intra- and inter-specific levels (fig.10). At the intra-specific level, we were interested in how sociality affect the feeding behavior of individuals (paper I). At the inter-specific level, we focused on whether introduced species can modify the native community of herbivores by trophic interactions (paper II) and we tried to identify diet selection criteria of large herbivore at relatively fine scale (paper III). Finally, we explored the usefulness of NIRS methodology in ecological studies (paper IV and note).

The results from papers and additional analyses are organized as below:

1) From community to individuals (paper I)
    - Does sociality drive the inter-specific variability of populations?
    - How does intra-specific variability in diet vary with resource availability?

2) The relative importance of food quantity and quality in the large herbivore diet selection (papers II-III)
    - How do large herbivores with high metabolic rate survive in poor environment such as pastures?
    - Methodological considerations
    - At which scale do herbivores make their diet selection?

3) How do introduced species influence plant-herbivore interactions? Are introduced species compulsory harmful for ecosystems? (papers II-III)
    - What is the impact of introduced mouflon on the native chamois trophic niche?
    - How do species coexist?

4) The unexpected importance of biomechanical traits in large herbivore diet selection criteria (paper III)
    - Does plant chemical content better explain diet selection criteria than other traits?
    - Is the relationship between biomechanical traits and chemical traits (C:N ratio, LDMC) consistent across growth forms?
    - What are the traits correlated to leaf punch toughness?
    - What about the relationship between diet and other traits?

5) A bit of methodology: is the use of NIRS relevant and useful for estimating diet and plant quality? (paper V and VI)
   - Are diet quality estimations with NIRS consistent with measurements on plant functional traits ingested?
   - Is the estimation of N, C and P with NIRS as robust as classical methods? Can we create three general calibration models (one for each chemical component) usable for different ecosystems? (paper in prep. not included in the thesis, Ancin Murguzur F.J, Smis A., Bison M., Struyf E., Bråthen K.A.)

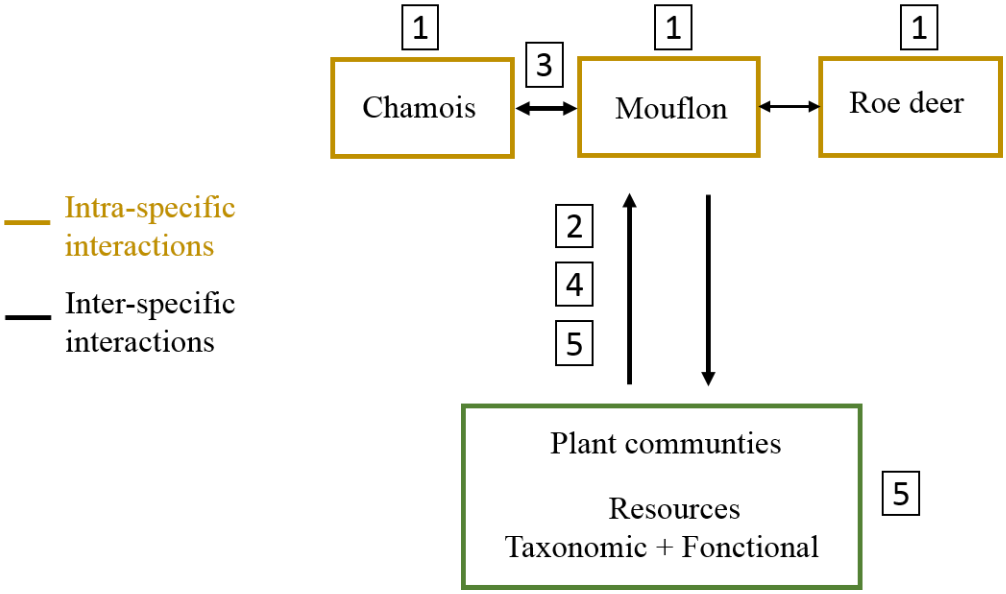

Figure 10. Connections between the topics approached in the thesis. In yellow are the intra-specific interactions within large herbivores. In black are the inter-specific interactions among large herbivores (arrows between boxes of ungulates) and between large herbivores and plant communities. The number corresponds to the questions asked hereabove.

For hypotheses and predictions, see the corresponding papers.

MATERIAL & METHODS 2

Chapter III: Roe deer, chamois and mouflon in the Bauges Massif

3.1 Bauges Massif

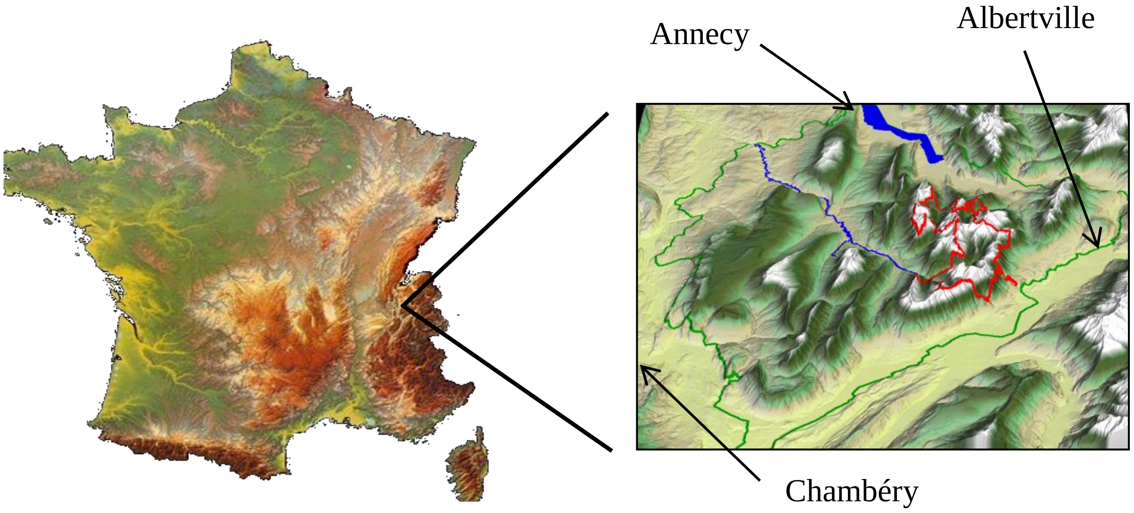

Figure 11. Localization of the Bauges Massif in France. In red is the Bauges Game and Wildlife Reserve.

“Physically, without being as wild and magnificent as the neighbouring alpine Maurienne, Tarentaise and Haut-Faucigny Massifs, the Bauges Massif displays a certain originality in its aspect, its soil composition, its plants, its animals, its climate, its watercourses, its stratigraphic curiosities. It is a world rich in natural gifts and full of appealing beauty”. Translated from Louis Morand (Les Bauges. Histoire et Documents. 1889)

The Bauges Massif (156 km²) is situated between the departments of Savoie and Haute-Savoie. It has a roughly triangular shape, with the towns of Chambéry, Albertville and Annecy as corners (fig.11).

The morphology of the Massif is remarkable with steep rocky cliffs (mostly urgonian limestones) alternating with grassy smooth slopes. Besides being a Natural regional park, it also received the “geopark” label acknowledging his geological features. The altitude goes from 250 to 2217m (sub-montane, montane and subalpine levels), dominated by the Arcalod summit. The mixture of calcareous cracks and old glacial basin that can be found on the Margeriaz slopes, where the wind blows vertically to climb cliffs and falls forward in short vegetation, evoke a fantastic world. During foggy days, the fog fills the empty space delimited by the cliffs of the Armene pasture, and let the rocky knolls appear, as independent towers carrying some vegetation.

Figure 12. Arces summit from the ascent of Armenaz summit. We can see the Belledonne Massif behind the sea of clouds.

There is no gold in the Bauges Massif, or at least, not the gold that we first think about. It's the green gold that we find. Since the last period of glaciation, the massif has been covered by extensive forests where we find the main woody species are fir, spruce, pine, yew, some of them being of economic forestry interest. Deciduous species such as beech, oak, maple, ash, elm, alder, rowan and others grow in the Bauges forests. Pastures harbor specific species from the alpine environment. The Bauges Massif is a wonderful place for botanists with more than 1500 plant species. Regarding animals, there are passing wolves (no pack established so far), and large populations of ungulates such as chamois, roe deer, mouflon, red deer and wild boar. Mouflon has been introduced in 1950s (Darmon et al. 2007) and co-occur in pastures with the chamois, and in forest with the other ungulates. In the Bauges Game and Wildlife Reserve (5,170 ha), chamois and mouflon are the two most abundant species (Darmon et al. 2012) and have no natural predators, except for golden eagles or wolves that may anecdotally depredate new borns and sick animals. Hunting occurs from September to January.

The Bauges mountains constitute a transitional area between the internal Alps and the lowland areas in the west and is subjected to a continental climate with an oceanic influence (Loison et al. 1999) causing large precipitations (> 1850 mm/year) favorable to high plant diversity. Temperature goes from 0°C in winter to 17°C in summer, on average. The green meadows are replaced by the plant yellowing in autumn (September-November) and a thick layer of snow covers the ground in winter (November-April), mostly permanently above 1000m.


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Figure 13. Two different views of the Armenaz pasture in summer.

3.2 This work takes place in an already well-studied ecosystem

The Bauges Game and Wildlife Reserve (~5200ha) is included in the Bauges Massif and is co-managed by three public institutions: National Forest Office (ONF), National Agency for Hunting and Wildlife (ONCFS) and the Bauges National Park (PNR Bauges). The Reserve was first created in 1913 to stop the sharp decrease of chamois populations. Today, one of the main objectives of the Reserve is to improve knowledge on mountain wildlife through applied researches. Especially, four sites (Armenaz and Charbonnet in pastures, Coutarse and Bellevaux in forest) have been targeted to more fully study chamois populations and other ungulates (mouflon and roe deer). They are long-term study sites for chamois population demography studies, as animals have been equipped with collars since 1985, and with GPS since 2003.

Different projects have been hold on ungulates from the Bauges Massif, for example about genetic of populations (Cassar 2007, Loison et al. paper in prep), epidemiology (Loison et al. 1996, Pioz 2006, Pioz et al. 2008), demography (Loison et al. 1999, Garel et al. 2009, 2011, Bleu et al. 2014, 2015), movement (Loison et al. 2008, Gaudry et al. 2015, Tablado et al. in prep.), colonization process of the introduced species (Darmon et al. 2007), habitat and diet selection (Darmon et al. 2012, Redjadj et al. 2014), species niche partitioning (Darmon et al. 2012, 2014), or human disturbance effects (Tablado et al. in prep).

Studies focusing on the spatial axis of the ecological niche demonstrated that chamois and mouflon living in the same pasture could coexist by choosing different plant communities, at least in spring (Darmon et al. 2012). As for spatial studies, mouflon did not behaviorally interfere with chamois when the activity rhythm was studied, thanks to GPS equipped with activity sensor recording motion data (i.e. animal's head movements) (Darmon et al. 2014). These studies suggest the absence of competition between chamois and mouflon, partly allowed by species-specific requirements and behavior. It is in this context that we were consequently interested in testing whether and how ungulates could coexist on the dietary axis of the ecological niche, at the inter- and intra-specific levels. Indeed, spatial distribution and habitat selection of ungulates can fluctuate over the year, and chamois and mouflon could be more prone to be spatially aggregated in some seasons (strong spatial overlap in July contrary to august for example, Darmon 2007). This could lead to exploitative competition for food resources, as both species track high-quality plants. Approaching those questions was possible owing to existing databases on ungulates diet. During her PhD, Claire Redjadj (2010, Redjadj et al. 2014) determined the evolution of the diet composition and quality of chamois, roe deer, mouflon and red deer over the year, thanks to DNA-metabarcoding and NIRS on faeces samples (Rayé et al. 2011), and micro-histology and NIRS on rumen samples. C. Redjadj and A. Duparc (then in Master 2) also estimated the biomass, phenology and composition of plant communities on two pastures of the Bauges Massif, in order to include resource availability in the studies (Duparc et al. 2012, Redjadj et al. 2012). Hence, these huge databases have been the starting point of my PhD.

All these results and databases provided a framework particularly useful for my thesis to continue the exploration of trophic interactions between large herbivores and plant communities at the intra- and inter-specific levels, and are also relevant for the other ongoing PhDs.

Indeed, the current PhD of Antoine Duparc aims at determining the impact of human activities and degree of inter-specific coexistence on the spatial occupancy of ungulates in mountain. These questions about human disturbance take part in a bigger project which led to an additional partnership with the laboratory of environment, dynamics and mountain lands (EDYTEM) in order to understand the sociological and ecological aspects of human-wildlife interactions, e.g. during the practice of winter sports, but also during hunting or other recreational activities in the Bauges Massif. Finally, the PhD of Tiphaine Lefebvre aims to explore the impacts of herbivory (chamois and cows) on the biomass and quality (nitrogen, carbon, phenols, lignin) of alpine plant communities, and on the soil through the decomposition rate of litter.

Besides, the Reserve takes part in the “Zone Atelier Alpes” (ZAA) which aims at understanding the climate-human-environment dynamics, through long-term studies on several topics such as the dynamic of biological diversities in the Alps, the ecosystem functioning and the provided services, the inter-relationships between ecological systems and human activity system.

3.3 Studied species

The studied species are of high interest as they are range on the browser-grazer, specialist-generalist, and solitary-gregarious gradients (table 2).

Because population sizes of ungulates in open and forest areas are difficult to estimate with precisions, we prefer to not give estimates of population size that could be wrong, but we can say that there are more chamois (>2500) than mouflon, red deer and roe deer. Monitoring methods, based on repeated censuses (Loison et al 2006) are aimed at identifying populations trends, and indicate that populations of chamois may have reach a plateau since 1990 (based on abundance index), mouflon are increasing and roe deer are stable (pers. comm.).

Mouflon have been introduced in 1950’s from the zoological park of Chambord (see Darmon et al. 2007 for the mouflon colonization, and Marchand 2013 for details on mouflon phylogeny).

Chamois and mouflon are physiologically adapted to steep slopes of open areas. However, mouflon is not well-adapted to snow cover because of the absence of a membrane between the two fingers of the foot, unlike chamois which hoofs act as a snowshoe. While mouflon migrate in the valley during winter, chamois can stay all year round in pastures. Yet, some chamois also occupies the forest (see the thesis of Claire Redjadj 2010), and for most part, seem to stay in the forest all year round (ongoing analyses, Duparc PhD). Roe deer mainly inhabits forest (see fig.14 for the localization of studied sites and faeces sampled).

Sexual dimorphism differ between ungulate species. Sexual dimorphism can be assessed by differences in body mass or physical attributes sex-specific.
It is not easy task for inexperienced observers to visually differentiate male from female chamois. Indeed, male and female have horns and the difference between sexes is based on the angle of the horn's hook. In addition, even if the body mass is heavier for males than females (Garel et al. 2009), the difference is not high enough to easily differentiate them from a considerable distance. Additional cues such as the general stature of the animal (such as neck and head size) and its behavior (such as calves following their mother, lactation, urination) can help the identification.
Visually, it is easy to differentiate female and male roe deer during the period when males have antlers. When they lose them in autumn, it becomes more difficult as the body mass ratio between male and female is also low (1.10 for Trois Fontaines population, Gaillard et al. 1993).
Finally, the sexual dimorphism is more pronounced for the mouflon. Females do not have horns (or little ones), contrary to males. The sexual dimorphism in terms of body mass is important as females weigh between 25 and 35 kg whereas males weigh between 35 and 50 kg (Vallance 2007).

For most sexual dimorphic ungulates, sexual segregation occurs outside the mating season (Cransac et al. 1998, Bonenfant et al. 2004 and references therein). This spatial segregation could be explained by different responses to the predation risk ("predation risk hypothesis"), different energetic requirements ("forage selection hypothesis") or different activity rhythm ("activity budget hypothesis") (Main 1996, Ruckstuhl & Neuhaus 2002).

The "predation risk hypothesis" predicts that females with calves should make a different trade-off between patch quality and security than males. Females with calves are more vulnerable to predation. Hence, they should choose secure sites (for example steep areas) of lower quality to ensure the calves survival (breeding success, Main 1996), which would in turn decrease their diet quality. On the contrary, because the breeding success of males is related to their body mass, they would be more prone to choose sites of higher resource quantity and quality to increase their body growth and secondary sex characteristics development (Main 1996). In addition, habitat segregation should peak during calving, when calves are more subject to predation (Bonenfant et al. 2004).
Males and females, even subtly (see hereabove), differ in their body mass. The "forage selection hypothesis" describes the consequences of sex body mass differences, and in turn physiological requirements, on habitat segregation and hence on diet quality (Main 1996, Ruckstuhl & Neuhaus 2002). Indeed, as females have a smaller body size and body mass than males, they have higher energetic requirements and they should be more selective in terms of resource quality than quantity, and choose high quality food habitats (Main 1996) (see section *2.2.b* for allometric relationships between energetic requirements and gut size). However, this "forage

selection hypothesis" has been questioned as several studies show no differences in habitat quality used by both sexes (Ruckstuhl & Neuhaus 2002 and references therein).

The "activity budget hypothesis" do not predict habitat segregation but social segregation. Because of body size dimorphism, males and females could differ in their activity budgets. For example, as males are bigger than females and supposed to feed on lower quality plants, the time dedicated to rumination should be higher than for females. A mixed group would be less synchronized because of differences in activity budgets between sexes. This would led to less stable groups because neighbors would compromise the optimal activity of each individual (Conradt 1998). Hence, the best strategy would be that animals with similar activity budgets form groups, which would also be efficient to decrease predation risk in open areas (Ruckstuhl & Neuhaus 2002).

Consequently, by impacting the habitat selection, sex can influence the diet selection and hence diet quality. In this thesis, we did not take into account any sex effect. However, further analyses should explore the differences in diet quality between males and females at different periods of the year and try to determine which hypotheses could explain these differences.

Domestic species (cows) occupy the studied pastures of Armenaz and Charbonnet in summer and beginning of autumn (june to September) since 2004, partly to prevent the spread of the green alder in the pasture. They can occasionally physically interact with chamois when they come through enclosures.

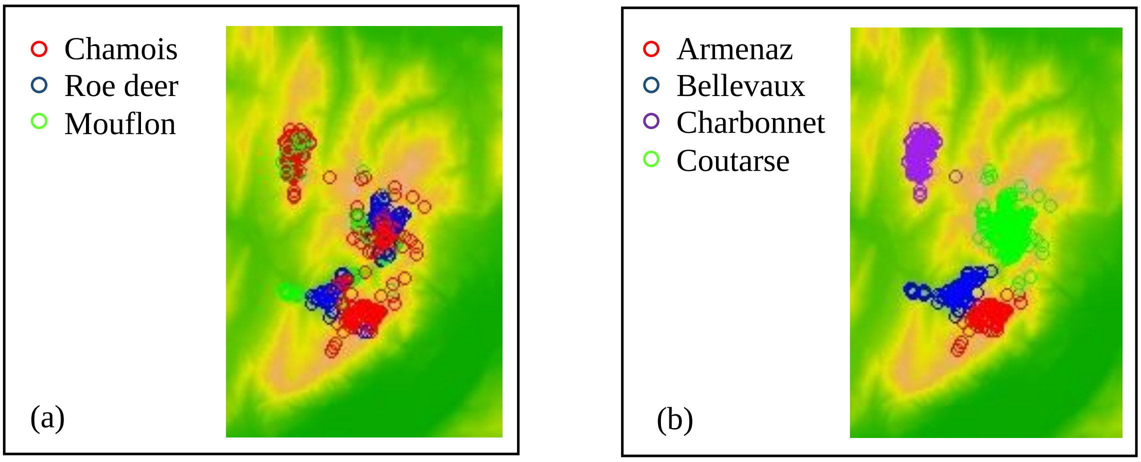


Figure 14. (a) Localization of chamois, roe deer and mouflon faeces sampled in the Bauges Game and Wildlife Reserve in 2007 and 2008, (b) Localization of the sites where the faeces of the three ungulates have been sampled in 2007 and 2008.

Table 2. Ecological and biological characteristics of studied animals.

	Roe deer *Capreolus capreolus*	Chamois *Rupicapra rupicapra*	Mouflon *Ovis gmelini musimon*
Family	Cervidae	Bovidae	Bovidae
Sub-family	Capreolinae	Caprinae	Caprinae
Artiodactyle/ Perissodactyle ?	Artiodactyle	Artiodactyle	Artiodactyle
Number of youngs	1-3	1	1-2
Habitat	Forest	Pasture	Forest and pasture
Sociality	Solitary	Social (low stability)	Social (high stability)
Body mass	15 to 35 kg [a]	35 to 60 kg [a]	35 to 60 kg (according to the sex) [a]
Masseter muscle	44.2 ± 11.6 g [b]	58.9 ± 4.0 g [b]	143.2 g [b]
Diet category	Browser [c]	Intermediate [d]	Grazer/ Intermediate [e]
Digestive morpho-physiology	Moose-type [f]	Intermediate [g]	Cattle-type/ Intermediate [h]
Niche breadth	Specialist [i]	Intermediate [i]	Generalist [i]

(a) ONCFS, (b) Clauss et al. 2008a, (c) Hofmann 1989, Tixier et al. 1996, Redjadj et al. 2014, (d) Hofmann 1989, Garcia-Gonzalez et al. 1996, Bertolino et al. 2009, La Morgia et al. 2009, Redjajd et al. 2014, (e) Hofmann 1989, Cransac et al. 1997, Marchand et al. 2013, Redjadj et al. 2014, (f) Kamler 2001, Clauss et al. 2009, Clauss et al. 2010b, (g) Clauss et al. 2010a, (h) Kamler 2001, Clauss et al. 2009, Clauss et al. 2010a, (i) Hofmann 1989, Clauss et al. 2003b, Bison et al. 2015

Chapter IV: Overview of databases

4.1 DNA-metabarcoding as the method to identify the diets (papers I-II-III-Note)

The composition of diet in wildlife can be determined in several ways:

- Through direct field or controlled experiment observation (Tixier et al. 1997, Massey 2009)
- Through identification of herbivory impacts on plant species (browse surveys) (Lembke 2005)
- Through rumen analyses (Staines 1976, Jackson 1980, Forsyth 2005, Redjadj 2014)
- Through faeces analyses (Garcia-Gonzalez & Cuartas 1996, Bertolino et al. 2009)

Two methods can be used to determine the composition of rumen and faeces: microhistology (Jenkins 1987) or DNA-metabarcoding (Taberlet et al. 2007, Rayé et al. 2011, Pompanon et al. 2012).

The morphological diagnosis used for microhistology is tedious. First, it requires a high-level of technical expertise. Second, some plant morphological keys are only usable for specific development stage or specific genous, and the resolution can be difficult below family or genous. There are also some cryptic species that are morphologically indistinguishable. Species identification can be wrong because of the phenotypic plasticity of the used feature. Finally, many fragmented cuticles are so small that they cannot be visually recognizable, which in turn under-estimate the diet species richness (Pärtel 2014).

DNA-metabarcoding method solves a significant part of those issues. The molecular barcoding is a technique which allows, with a small non-damaged DNA sequence, to determine the species in question, crossing the determined sequence with a reference database. This technique has been implement by Hebert in 2003 and was developed to differentiate animal species. Instead of sequencing the whole genome, Hebert and its team discovered that the mitochondrial gene of the cytochrome c oxidase had a strong species discriminative power. Indeed, mitochondria accumulate enough mutations to differentiate species, but do not allow the differentiation of two conspecific individuals. This technique offers an access to the « hidden » biodiversity, i.e. not visible through direct or miscroscope observation. In the case of large herbivores rumen and faeces analyses, DNA-metabarcoding needs to be adapted to plant species differentiation. Taberlet and his team (Taberlet et al. 2007) have used a short chloroplast DNA fragment, the P6 loop of the *trn*L (UAA) intron, as minimalist barcode (Rayé et al. 2011) for plant identification. Thanks to universal primers being capable of binding to the chloroplast intron, it is possible to amplify the DNA signal through PCR (Polymerase Chain Reaction). Then the amplicons are sequenced and compared to a reference database for identification. However, other issues are encountered with DNA-metabarcoding. This is a method which requires time to select the right gene to sequence in order to differentiate the species of interest. Besides, sequenced plants are not always identified or indexed in the database, which makes sequence assignment not always feasible. Finally, sequencing errors can lead to wrong species identification. Still, from a general point of view, it appears to be a powerful tool, that has now been used in many studies (e.g. Soininen et al. 2009, Valentini et al. 2009a, b, Rayé et al. 2011, Ibanez et al. 2013b, Bison et al. 2015, to name only some where LECA is involved as examples) as this is a relatively low-cost method which gives a high taxonomic resolution (Rayé et al. 2011) not necessarily achieved with microhistology. This is particularly useful for the study of trophic networks as it can provide reliable results of diet composition (Rayé et al. 2011). However, biases can be found in the frequency of sequences detected in faeces because of the differential digestibility of plants in the digestive tract, which itself varies with species. Indeed, DNA fragments of some eaten plants cannot be recovered in faeces due to a high degradation (Rayé et al. 2011). To calibrate the results on faeces obtained with DNA-metabarcoding, controlled experiment should be conducted (Rayé et al. 2011). Finally, as dozens of samples with several thousand sequences per PCR product can be directly characterized (Pompanon et al. 2012), it a useful approach for broad temporal and scale studies.

In this work, DNA-metabarcoding method has been applied on faeces samples. DNA extraction and taxonomic identification of plants found in faeces have been realized by Claire Redjadj between 2007 and 2011, during her PhD – see the thesis Redajdj 2010 for a detailed description of faeces sampling and Taberlet et al. 2007 for detailed DNA-barcoding method.

4.2 Plant functional traits measurements (papers II-III-Note)

In order to determine the diet selection criteria of large herbivores, we measured different plant functional traits that we classified in different categories (table 3): ecological traits influencing the visibility of a plant and the ease for an herbivore to find it (e.g. reproductive and vegetative height, number, size and color of inflorescence, distribution through sociality), quality traits related to animal nutrient requirements and the ease of plant harvesting, chewing and digestion (chemical traits: leaf nitrogen content, leaf carbon content, leaf phosphorus content, leaf dry matter content, biomechanical traits: punch toughness, tensile strength).

a) Sampling design

Plants have been sampled in the Bauges Massif on the Armene pasture at altitudes ranging from 1700 to 2000 m and in the Bellevaux forest at altitudes ranging from 700 to 1000 m.

The pasture consisted of eight vegetal communities (Duparc et al. 2012, Appendix 4). A total of 87 plant species have been sampled in spring after snow melt (beginning of June), in summer during the vegetation peak (mid-july) and in autumn during senescence (mid-September) (fig.15).

Plant biomass and specific composition of the plant communities of the Armene pasture have been estimated between 2007 and 2010 with the BOTANAL method (Lavorel et al. 2008, Redjadj et al. 2012).

Plant species have been sampled according to their abundance in the different vegetal communities: (1) when the abundance of a species in each community was less than 10%, we sampled the plant species in the community where it was the most abundant; (2) when the abundance of a species in each community was more than 10%, we sampled the plant species in each of those communities. We assumed that the abundance of a plant in a community is the result of environmental pressures. Hence, we considered that the more a plant is abundant in a community the better it is suited to the local environmental biotic and abiotic conditions optimally expressing its traits (Vile et al. 2006, Cingolani et al. 2007). Hence, each plant species has been sampled in one or two communities and each plant community has been visited.

For each community, one GPS point has been firstly drawn randomly at the average altitude of the community, if possible outside the cow pens. Then, individuals were sampled in a 90 m² quadrat around the GPS point. When possible, the distance of 5 meters was respected to avoid clones or genetically close individuals. Two communities were situated inside the cow pens. Sampling therefore occurred in this area. The same locations have been used for each sampling season. Because of the difficulty to find targeted plant species in forest, sampling locations have been based on a Bauges Forest Inventory and not on random GPS points.

Figure 15. Pastures in (a) spring (June 2013), (b) summer (July 2013), (c) autumn (September 2013).

b) Traits measurements

- Visibility traits

Vegetative height

The vegetative height was defined as the distance between the ground and the highest point of the highest leave, without taking into account an exceptional branch (fig.16). It has been measured on 15 individuals using a tape measure to the nearest 1cm.

Special case for basal plant rosette: for plants whom most of the leaves were basal rosette, with proportionally few photosynthetical area on the twig, we measured the vegetative height as the distance between the ground and the top of the rosette. For plants with one third of rosette leaves and two third of twig leaves, we measured the vegetative height as the distance between the ground and the highest leave of the main twig.

Reproductive height

The reproductive height, or flower height, was defined as the distance between the ground and the highest point of the flower (fig.16). It has been measured on the same 15 individuals as for the vegetative height, using a tape measure to the nearest 1cm.

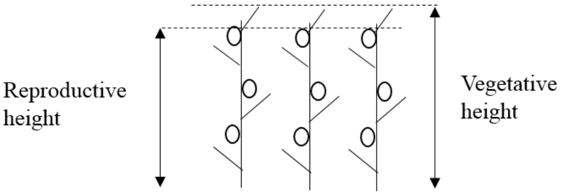


Figure 16. Schematic view of the reproductive and vegetative height measurements.

The following term « inflorescence » meant bud, flower or fruit, depending on the phenology.

Inflorescence size

The length, width and height of 10 inflorescences per species have been measured to the nearest 1mm using a caliper (fig.17). During flowering period, only open flower were taken into account. During fruiting period, only fruits were measured. If the inflorescences were individualized or not closely clustered, the length, width and height of a medium inflorescence was quantified, and the volume was multiplied by the number of inflorescences of an individual. If they were clumped, the whole inflorescence was measured.

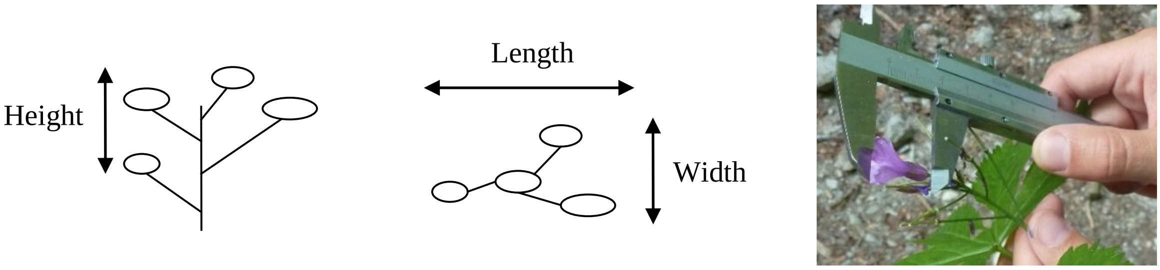


Figure 17. Schematic view of the inflorescence length, width and height measurements, and a picture of height measurement.

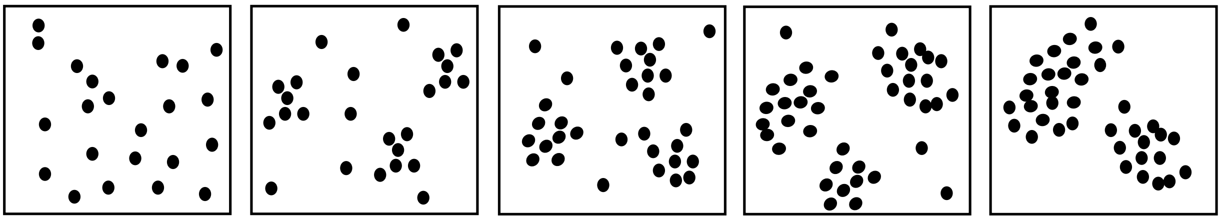
Color of inflorescence

The colors of 10 inflorescence per species have been recorded from a human visual perception, in a crude-way (yellow, red, green, brown, purple, white).

Sociality

The sociality has been defined at the population-level, contrary to the others traits that were measured at the individual-level. This measure did not fit the definition of traits given above, but for the sake of simplicity, we kept this information here.

Sociality was defined as the spatial distribution pattern of individuals on the studied area (Braun-Blanquet et al. 1952): 1-isolated individuals, 2-individuals spread in small isolated groups, 3-individuals in tighter groups, 4-individuals in more or less dense colonies, 5-individuals in compact settlements (fig.18).



1-isolated individuals

2-individuals spread in small isolated groups

3-individuals in tighter groups

4-individuals in more or less dense colonies

5-individuals in compact settlements

Figure 18. Illustration of the different levels of sociality.

- Quality traits: Chemical traits

For each plant species, we sampled 10 young leaves (i.e. the most relatively new and developed leaves) on 10 robust and well-developed individuals. Damaged plants by herbivores or pathogens were excluded.

Leaf Dry Matter Content (LDMC)

Limbs were kept in wet tissue from the field study site to the lab, in order to keep them hydrated. They were weighted to obtain the fresh mass. Then, they were stored in a 60°C oven for 48h, and weighted again to obtain the dry mass. The ratio between dry and fresh mass gave the leaf dry matter content (inverse of leaf water content).
This operation has also been done on the twigs and petiole to determine the twig dry matter content (TDMC) and petiole dry matter content (PDMC).

The 10 limbs were distributed in 3 eppendorfs (3 individuals in the first, 3 in the second and 4 in the third) and grinded with tungsten balls. Leaf veins were not taken off except for the species which main rachis was well-apparent (*Heracleum sphondyllium*, *Rumex arifolius*, *Rumex alpinus*). The choice of keeping veins was motivated by our wish to mimic as closely as possible the leave uptake from a large herbivore that cannot avoid veins.

Leaf Nitrogen Content (LNC) and Leaf Carbon Content (LCC) (estimated with classical method)

Between 3 and 5 mg of grinded dried plants were put in aluminium cups. The cups were placed in the elementary scanner (Elementary sensor, Flash EA 1112, Thermo Electron Corporation in the LECA Grenoble) and underwent a "Flash" dynamic burning (combustion). The gaz produced went through a catalytic oxidization and then, the NOx was reduced in N_2 through a reduction column. The oxygen and SO_2 in excess were trapped. Then, the elements were separated in a chromatography column. $H_2$0 was trapped. Gaz detection was performed with a catharometer (universal sensor). The output values were obtained in % of N and C and were then weighted by the dry mass in order to obtain the C and N absolute values in the measured organ.

Leaf Phosphorus Content (LPC) (estimated with classical method)

Quantitative analysis of phosphorus content in leaves with molybdate blue has been done in the Center of functional and evolutive ecology (CEFE) in Montpellier. First, the dried plant sample was weighted and then mineralized. Then, the phosphorus in the sample associated with the molybdate to create a phosphomolybdic complex in a highly acidic environment. This complex was reduced by ascorbic acid giving the blue coloration. 880 nm was the appropriate wavelength for the optic density measurement. The relationship between absorbance and phosphorus concentration followed the Beer-Lambert law. The optic densities obtained were proportional to phosphorus content. Phosphorus concentrations were expressed in µg/ml.

NIRS estimations

Leaf nitrogen, carbon, phosphorus and silica content were also estimated with Near-InfraRed Spectroscopy (NIRS) to study the NIRS applicability (See *Material and Methods: NIRS measurements* for details). Calibration has been done through the Bauges plants for nitrogen, carbon and phosphorus. Silica measurements had to be cautiously interpreted as calibration has been done with Norwegian plants. Moreover, forbs had usually low amounts of Si, and the predictions were not highly reliable. Except for Alchemilla alpina, which could have reasonably high values, the rest of the forbs had Si concentrations below 0.5 (as a general rule). See *Material and Methods: NIRS measurements* for the calibration and validation models, and the transferability of calibration models from sub-arctic to temperate ecosystems.

Percentage of inflorescences/leaves/twigs dry weight on total dry weigth

Three entire individuals per species have been sampled and directly dried. Inflorescences, leaves and twigs have been separately weighted to obtain the percentage of inflorescences/leaves/twigs dry weight on total dry weigth. This measurement was done to evaluate the energy allocation in plant.

- Quality traits: Biomechanical traits

Among the techniques commonly used in ecological studies that include biomechanics (Sanson et al. 2001), we used the punching and tearing tests, which are respectively considered as tests of compression and tension.

We used a sophisticated machine (Instron 5942, Canton, MA, USA) from the LEHNA (Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, Puijalon S.) in Lyon. For the punch trial (fig.20, fig.21), a flat-ended cylindrical steel rod (2 mm diameter) was mounted onto the moving head of the machine, and went through a stationary base with a hole setting the leaf. For the tearing trial (fig.20, fig.21), two pliers were mounted both on the moving head and at the base of the device to maintain the leaf. For both trials, the force was applied at a constant speed (10 mm s^{-1}), irrespective of the resistance.

Punch strength

It corresponds to the leaf hardness: maximum force per unit punch area required to punch a hole through the leaf lamina (in N m^{-2}, fig.19, fig.20, fig.21). The specific punch strength is the ratio of punch strength to leaf thickness (Read & Sanson 2003, in N m^{-2} m^{-1}). This measure has only be done on the lamina part of the leaves.

Punch toughness (Work to punch)
It corresponds to the energy required to punch a hole through the leaf lamina or, the total work required to fracture a leaf per unit punch area (in J m^{-2}, fig.19, fig.20, fig.21). The specific punch toughness is the ratio of punch toughness to leaf thickness (Read & Sanson 2003, in J m^{-2} m^{-1}). This measure has only be done on the lamina part of the leaves.

The punch toughness is preferred to punch strength as it takes into account how the material deforms and breaks (Sanson et al. 2001).

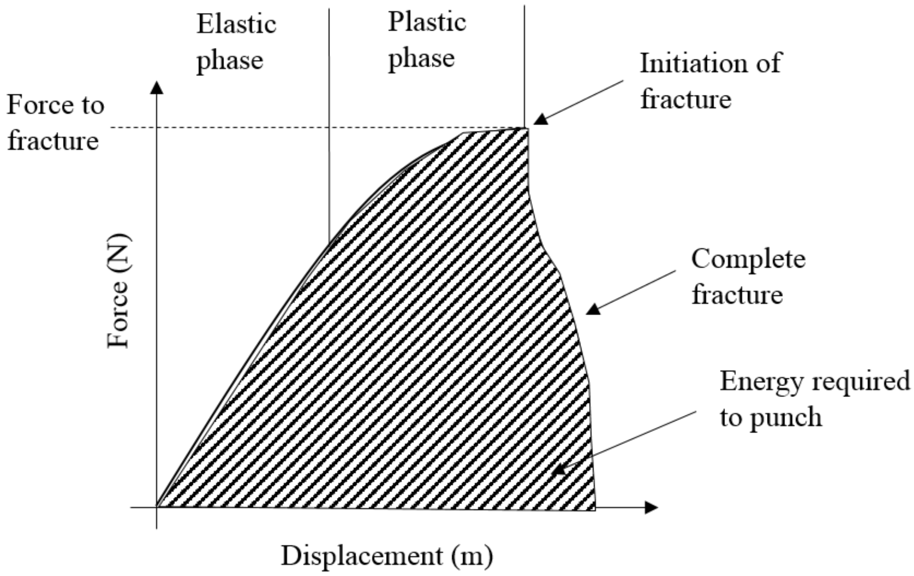


Figure 19. Evolution of the force in function of the displacement. During the elastic phase, the material return to its original dimensions if the force is removed. During the plastic phase, the material will deform permanently. The figure and the legend are inspired from Sanson et al. 2001.

Tear strength
It is the strength at which the sample breaks corrected by the cross-sectional area (in N m^{-2}, fig.20, fig.21). It describes the robustness of the material. This measure has been done on the leaves (without the veins on big leaves) or on the stems, depending on the stature and height of the plant. In order to mimic the plant intake by herbivores, we considered that an animal should not be able to feed on small leaves of short plants (e.g. *Helianthemum nummularium*) and we therefore did the tearing test on the twig. On the contrary, we supposed that on tall plants with big leaves, animals were able to physically discriminate the leaves from the twig and we only did the tearing test on leaves (e.g. *Veratrum album*).

Young modulus
It describes the stiffness of the material (i.e. resistance to distortion).

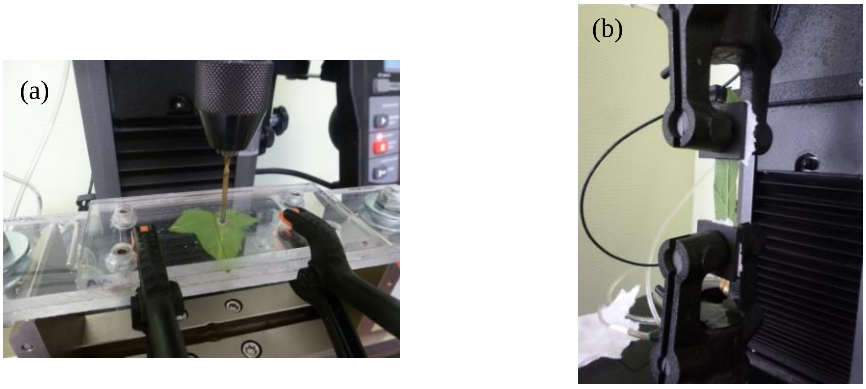


Figure 20. Pictures of the "torturometer" device, (a) punching test, (b) stretching trial.

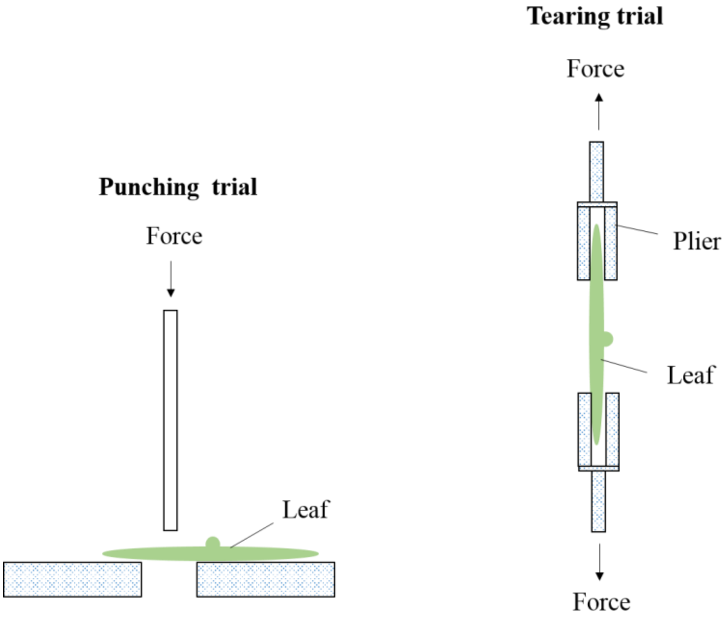


Figure 21. Schematic view of the punch and tear trials realized on a leaf.

- Others

Phenology

We identified the phenology on 10 individuals: 1-vegetative form, 2-flowering (defined as soon as one flower is opened), 3-mature (fruit and autumnal yellowing).

Spinescence/pubescence

The presence of spines or hairs on the leaves, twigs or inflorescences has been specified.

Table 3. Summary of measured traits on the field or in the laboratory.

Category	Traits	Type of data	Unity/level
Visibility	Vegetative height	Continuous	cm
	Reproductive height	Continuous	cm
	Inflorescence* size	Continuous	cm (height, length, width)
	Number of inflorescences	Continuous	
	Color of inflorescence	Categorical	Yellow, White, Brown, Red
	Sociality (population-level)	Categorical	1, 2, 3, 4, 5 (low to highly social)
Quality (chemical traits)	LDMC	Continuous	Ratio leaf fresh matter (FM) content/dry matter (DM) content
	PDMC	Continuous	Ratio petiole FM/DM
	TDMC	Continuous	Ratio twig FM/DM
	C	Continuous	%
	N	Continuous	%
	P	Categorical	% weak, medium, strong
	% of flower/leaf/twig dry weight on total dry weigth	Continuous	% (weight of the dry flow/weight of the whole individual)
Quality (biomechanical traits)	Punch strength	Continuous	N
	Punch Toughness	Continuous	$J m^{-2}$
	Break strength	Continuous	N
	Tensile strength	Continuous	N
	Young modulus	Continuous	N
Others	Phenology	Continuous	Between 1 et 3 (vegetative, flower, fruit)
	Spinescence	Binary	yes/no = 1/0
	Pubescence	Binary	yes/no = 1/0

* “inflorescence” means bud, flower or fruit, according to the phenology

4.3 NIRS measurements (papers IV-Note)

NIRS measurements have been done on faeces from the ungulates of the Bauges Massif after calibration with a reference laboratory analysis (Redjajd 2010) to measure the total nitrogen, and fiber content (ADF, NDF, ADL) (Redjadj 2010).

NIRS has also been applied on 84 plant species of the Bauges Massif and on 23 plant species from Finmark to evaluate the ability of NIRS to correctly estimate nitrogen, carbon and phosphorus content, but also to evaluate the transferability of calibration models between two different geographic areas. This study was conducted by Francisco J. Ancin Murguzur and Kari-Anne Bråthen from the department of biology from the University of Tromsø, and I took part of it. As I did not include the paper in preparation (Ancin Murguzur F.J, Smis A., Bison M, Struyf E., Bråthen KA) in the thesis, I describe hereafter the main points of material and methods explained by Ancin Murguzur F.J. in the paper in prep.

All plant species were sampled at different seasons and samples measured with NIRS consisted of green non-woody parts of the leaves, in order to avoid light interference with big pieces of veins that could not be perfectly ground. Plant samples were dried at 60°C for 48h and grinded into powder using a ball mill. The powder was pressed into tablets (Ø 16mm, 1mm thick) using a hydraulic press. Tablets were dried again. A portable NIRS spectrometer has been used to scan the samples (range of 350-2500 nm wavelengths). Leaf carbon, nitrogen and phosphorus content were previously analyzed with classical methods (described in *4.2* for France analyses).

The first aim was to estimate the applicability of the NIRS method. To answer this question, calibration and validation models testing the relationship between NIRS measured and classical chemistry values have been developed for each plant constituent and each region. The most parsimonious calibration models were determined based on a high correlation coefficient (R^2), given a number of wavelength (k) and low root mean square of the error of the calibration (RMSEC, error between predicted and measured constituents). Each calibration model was tested against its respective validation set (25% of the total samples). The same parameters as for calibration models have been calculated to evaluate the robustness of the validation.

The second objective was to assess the transferability of each regional model to the other region. This has been achieved by predicting the nutrient contents of one region with the model of the other region. R^2, RMSEP and bias of the linear relationship between NIRS measured and classical chemistry values were also calculated.

The third objective was to test whether a single global model including the data from both regions could be enough robust to correctly estimate C, N, P content of both regions. R^2, RMSEP and bias were also used to estimate the robustness of the calibration and validation models of each constituent.

4.4 Resource availability (papers II-III)

Available plant diversity and biomass has been described at the scale of plant communities. Given the GPS position of faeces, available resource at the scale of 48h and seasonal home range has also been calculated.

a) Within plant communities

Thirtheen plant associations (homogeneous plant unities) have been mapped by photo-interpretation across the Bauges Game and Wildlife Reserve, and photosociological relevés allowed to determine them by using the CORINE biotope database as typology reference (Boissier 2005, CBNA 2005, European community commission 1991) in 2001. We assume that changes in relative area of plant communities were marginal between 2001 and 2007 (first faeces sample date). Previously, we wrote that the pastures consisted of eight vegetal communities. Here, thirtheen vegetal communities are described as forest areas are taken into account (mixed forest, coniferous, riparian forest, pre-forest semi-lignified, meadow).

Table 4. Relative abundance (in %) of each plant association within the Bauges Game and Wildlife Reserve of the Bauges Massif (data from the report of P.A Dupeyras 2014).

Plant association	Relative abundance (%)
Mixed forest	49.3
Lawn of *Sesleria*	19.3
Scree	8.6
Mountain forage	6.0
Coniferous	3.3
Meadow	2.8
Megaphorbiaie	2.8
Lawn of *Carex ferruginea*	2.7
Alnus	2.6
Lawn of *Nardus stricta*	1.0
Heathland of *Rhododendron*	1.0
Riparian forest	0.7
Pre-forest semi-lignified	0.2

Maps of plant communities in the pastures have been validated during Claire Redjadj’s PhD. Qualitative and quantitative estimation of available resources in pasture has been done on the Armenaz and Charbonnet sites in 2007, 2008, 2009 and 2010, by Antoine Duparc and Claire Redjadj (Redjajd et al. 2012) by using the BOTANAL method (Tothill et al. 1992). The “quadrat 3D” method (or “Botacube”) (Saïd et al. 2005) has been used in forest and shrubby areas (Coutarse and Charbonnet sites) to estimate biomass per strata and per plant species. These two protocols allowed to obtain data on plant composition, phenology and biomass per plant community.

300 plots have been randomly distributed within these four sites (Armenaz, Charbonnet, Coutarse and Bellevaux), which sampling resulted in the identification of 296 plant taxa. On the pastures, plant composition and biomass have been estimated during two period: between

mid-May and mid-June, and between end of June and end of July (Durparc et al. 2012). Relative abundances of plant species were not significantly different between the two periods and we always used the summer period data (end of June to end of July 2007) in our analyses, in order to fit with the hypothesis of Manly et al (2002) assumption that plant species proportion availability should not vary across the studied period.

b) Within the 48h home range

Since our goal was to identify selection criteria at a fine scale, we determined the plant characteristics in the close vicinity of each faeces. Plant found in the faeces are likely summing up several meals depending on the digestibility of plants. We considered (see Rayé et al. 2011, Steuer et al. 2011) that plants eaten during the last 48 hours were most likely to be found in the faeces. Therefore, we estimated plant availability in an area around the faeces which size amounted the average 48 hours home range of chamois and mouflon. The latter was estimated based on GPS-fixed from marked chamois and mouflon. This was the topic of P.A. Dupeyras master in 2014 (appendix 1 of paper II).

Given that faeces are not expected to be at the center of the last 48 hours home range, the relative proportion of vegetal community around faeces has been calculated as the mean relative proportion through the bootstrap method with 1000 samplings from 100 buffers randomly located around the faeces GPS location (fig.22). Consequently, each buffer has a centre more or less shifted relatively to the corresponding faeces location. Radiuses of 48h-home range buffers (r) were randomly sampled from the radius value distribution of 48h-home ranges of the summer season (fig.22).

Then, we estimated the relative proportion of plant species around faeces given the relative proportion of vegetal communities around faeces and the plant proportion within each vegetal community.

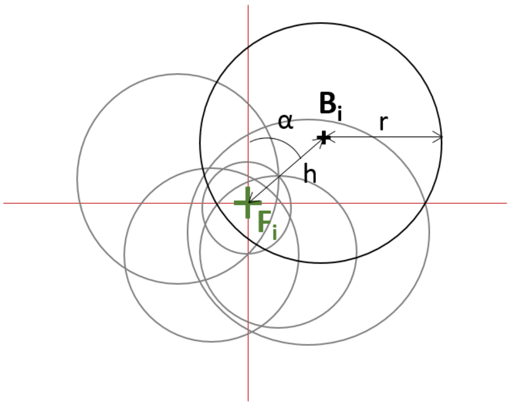


Figure 22. Visual representation of the method to estimate resource availability at the individual scale. F_i is the localisation of the faeces, B_i is the center of a buffer, with a radius r, staggered from a distance h and an angle α (from Dupeyras 2014).

c) Within seasonal home range

A minimum convex polygon (MCP) of faeces on both pastures was used to determine a theoretical zone corresponding to the seasonal areas occupied by the animal shaving produced the sampled faeces. This MCP has been enlarged by a buffer whose diameter was equal to two size the maximum radius calculated from areas values of 48h home range of each species (rmax=645m for chamois and 890m for mouflons). A visual check from GPS data of individuals equipped with GPS in the same sites allowed to validate a potential zone used by the animals (Dupeyras 2014).

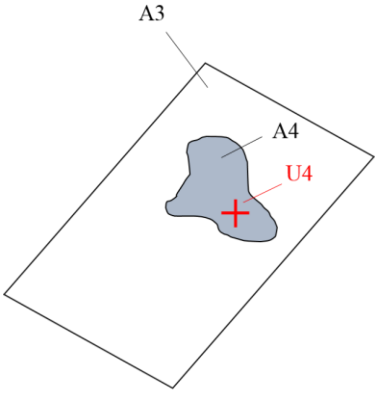


Figure 23. Schematic view of the different spatial scales surrounding an individual. A3: Relative abundance of available resources within the seasonal home range (*4.4.c*). A4: Relative abundance of available resources within the 48h home range (*4.4.b*). U4: Relative abundance of used resources measured in the faeces (*4.1*). Red cross corresponds to the GPS localization of the faeces. Selection at the 4th-order corresponds to the ratio of U4 to A4. Selection at the 3rd-order corresponds to the ratio of A4 to A3 (from Dupeyras 2014).

4.5 Synthetic view of the databases used for each analysis

In the first paper, we only used the information of taxonomic diets of the three ungulates (chamois, roe deer, mouflon, fig.24) to study the among-individual variation.

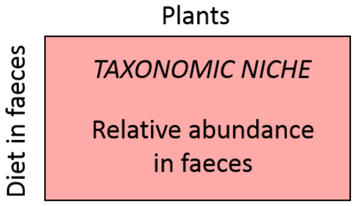


Figure 24. Database used in the article I (Upscaling the Niche Variation Hypothesis from the intra- to the inter-specific level).

In the second paper, we used the taxonomic and functional information of diet and habitat to study the coexistence between chamois and mouflon (fig.25).

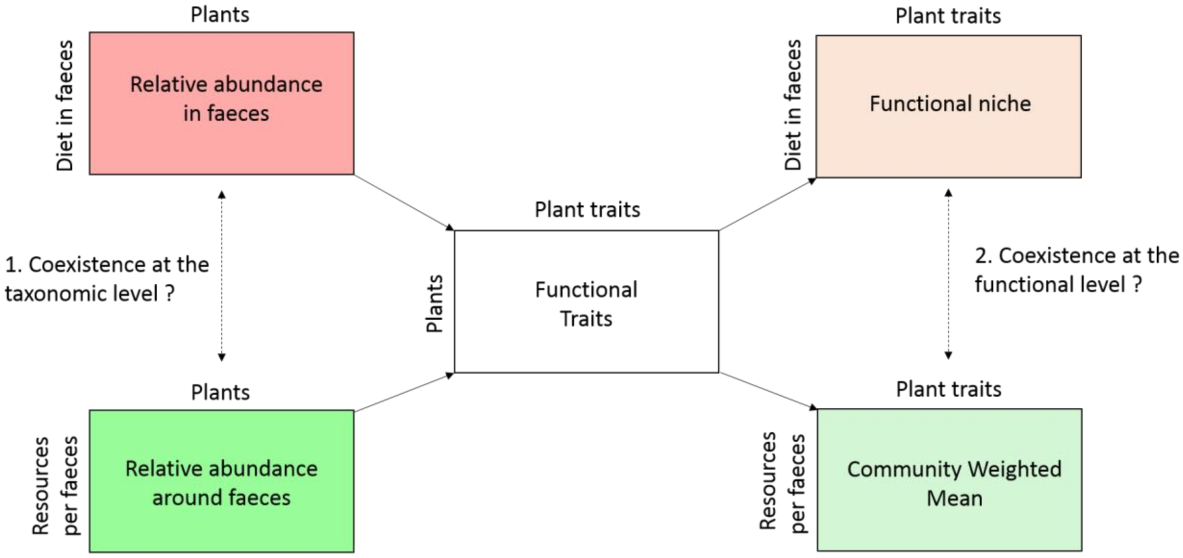


Figure 25. Overview of the databases and methods used. The Functional Niche (FN) and Community Weighted Mean (CWM) are calculated from the equation: $\boldsymbol{CWM} = \sum_{i=1}^{n} \boldsymbol{p_i} \times \boldsymbol{trait_i}$, where n is the total number of plant species in the diet or habitat, p_i is the relative abundance of species i in the diet or habitat and $trait_i$ the trait value of species i. Questions 1 and 2 are solved with the coupled analysis of diet and habitat data, respectively at the taxonomic and functional level.

In the third paper, we used the functional niche of diet and habitat community weighted mean to determine the degree of selectivity; and the taxonomic diet of ungulates and the database of plant functional traits to determine the diet selection criteria over the year (fig.26).

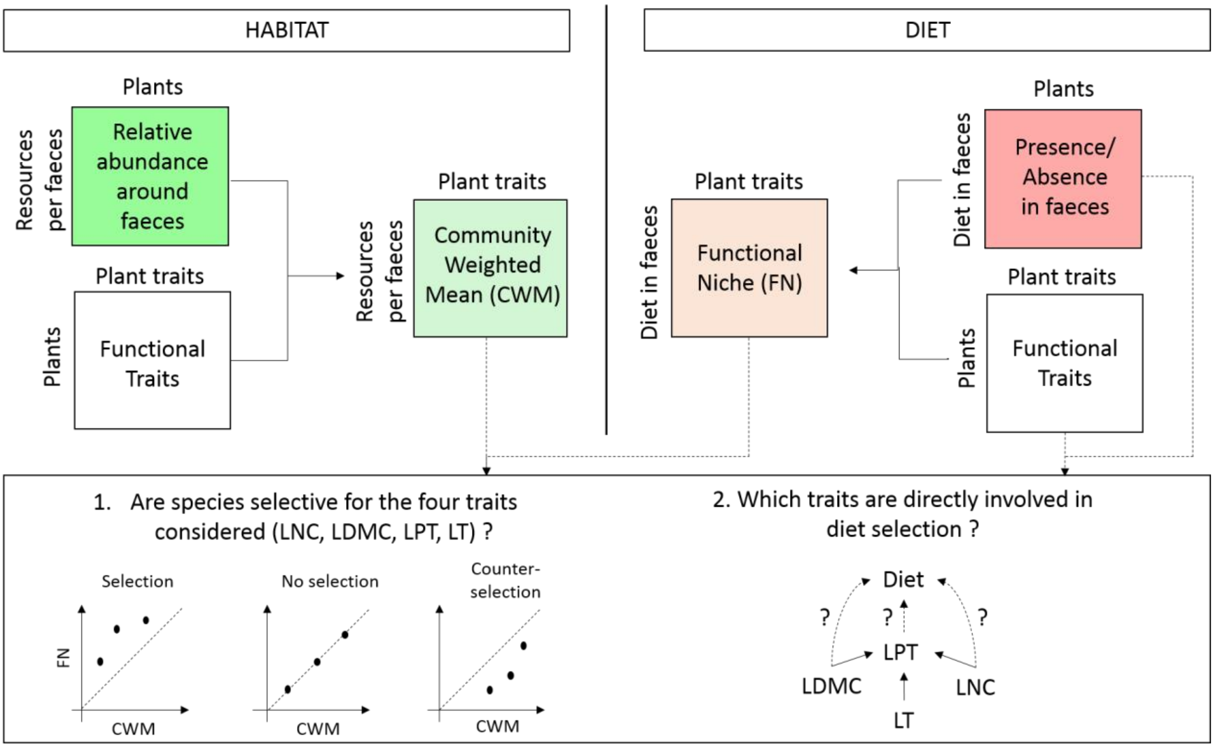


Figure 26. Overview of the databases used and questions asked. The Functional Niche (FN) and Community Weighted Mean (CWM) are calculated from the equation: $\boldsymbol{CWM} = \sum_{i=1}^{n} \boldsymbol{p_i} \times \boldsymbol{trait_i}$, where *n* is the total number of plant species in the diet or habitat, p_i is a proportion and is the same for each plant species *i* in the faeces (if a faeces is composed on 10 plants, then each plant will have a proportion of 1/10),or p_i is the relative abundance of plant species *i* in the habitat and $trait_i$ the trait value of plant species *i*.

In the analysis of resource selection at multiple scale (Dupeyras 2014), we used the taxonomic diet of chamois and mouflon, the relative abundance of plants around faeces and at the pasture-scale (fig.27).

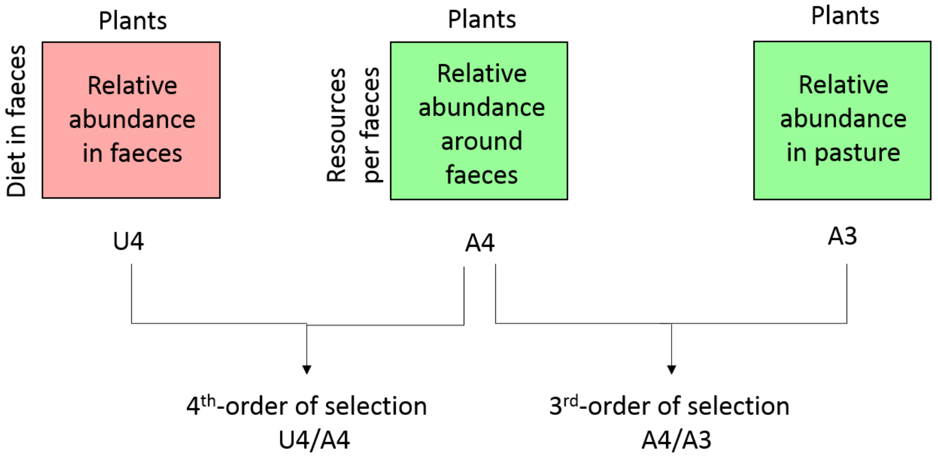


Figure 27. Databases used to determine the scale of resource selection.

In the fourth paper, we used the results from NIRS measurements and classical method measurements of French and Norwegian plants to determine the transferability of calibrations from a sub-arctic to temperate ecosystem (fig.28).

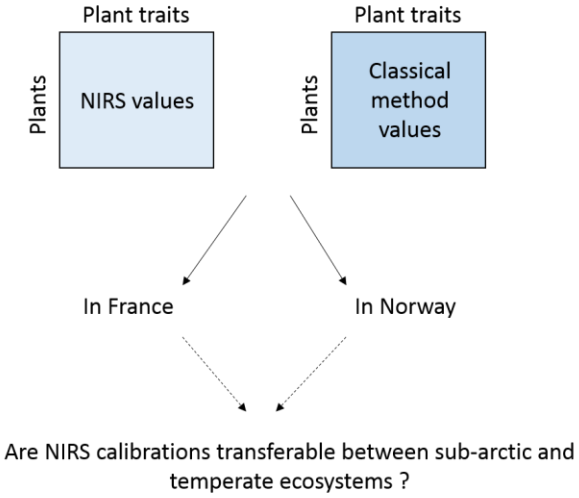


Figure 28. Databases used for NIRS calibrations in France and Norway.

In the note, we used the NIRS measurements on faeces and the functional niche of diets estimated from the plant functional trait database and the taxonomic diet database (fig.29).

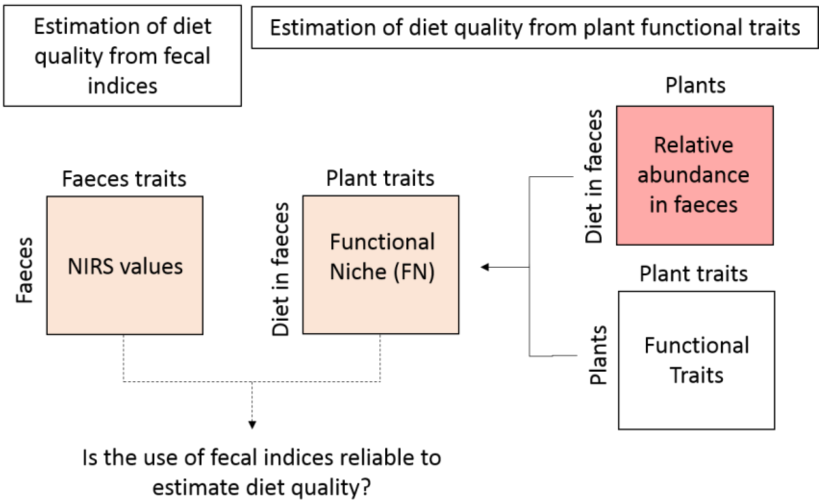


Figure 29. Databases used for different diet quality estimations comparison.

3

SUMMARY OF RESULTS

Chapter V: General information about the diets

5.1 Database information

1076 faeces have been sampled in the Bauges Game and Wildlife Reserve, including 659, 205 and 212 faeces of chamois, mouflon and roe deer respectively. The sexes of all species, but roe deer, was identified. Faeces of chamois come from 339 females and 284 males, and faeces of mouflon from 115 females and 66 males. We did not use this information in the work presented here, but it could be used for further analyses as males and females can differ in their nutrient requirements (difference in body mass, antler and horn growth, gestation and lactation, see *3.3*).

5.2 Plant species identified in faeces

Respectively 326, 281 and 250 plant taxa were respectively identified in chamois, mouflon and roe deer faeces in the raw database.

After having removed plant species whose proportion was under 2.5% of DNA sequences in a faeces; 96, 79 and 70 plant taxa were respectively left in the faeces of chamois, mouflon and roe deer (see appendix 1 for the plant present in the faeces and their associated mean frequency of sequence and frequency of occurrence over the year; table 5 and table 6, and appendix 3 for rarefaction curves). Under this threshold, the sequence was considered as a barcoding mistake or as an occasional resource (Bison et al. 2015). All the analyses have been performed based on this cleaned-up database.

Table 5. Mean frequency of sequence (FS, %) and frequency of occurrence (FO, %) over the year of growth forms present in the diets of chamois, mouflon and roe deer (as rosodae are important in the diet, we let it in the table even if it is not a growth form denomination).

	Chamois (FS, %)	Chamois (FO, %)	Mouflon (FS, %)	Mouflon (FO, %)	Roe deer (FS, %)	Roe deer (FO, %)
Deciduous shrub	4,81	21,85	2,04	20,00	2,96	17,45
Deciduous tree	1,58	12,59	4,69	28,29	3,66	28,77
Evergreen shrub	29,49	65,10	6,04	32,68	5,96	11,32
Evergreen tree	2,08	16,84	8,75	27,80	4,04	24,06
Fern	0,14	0,30	0,00	0,00	0,00	0,00
Forb	21,02	82,25	12,81	59,02	19,23	64,15
Grass	0,43	4,70	1,33	16,10	0,08	0,47
Leguminous	18,82	67,37	29,35	62,93	5,56	20,28
Rosodae	16,97	47,80	24,18	63,41	53,46	92,45
Sedge	0,04	0,46	0,00	0,00	0,01	0,47
Others	4,61	4,60	10,81	5,92	5,03	4,72

Table 6. Overview of the sample size, mean number of eaten plant species per individual, and number of plants in the mean diet for the three ungulate species during each month (the other months were not included because of a too low sample size).

		April	**May**	**June**	**July**	**Aug.**	**Sept.**	**Oct.**	**Nov.**
Chamois	Sample size	11	71	116	120	118	74	133	16
	Mean number of eaten plant species/indiv.	3.2 Min: 1 Max: 5	5.2 Min: 1 Max: 11	6.5 Min: 2 Max: 11	6.4 Min: 2 Max: 12	6.3 Min: 2 Max: 11	5.2 Min: 1 Max: 13	3.6 Min: 1 Max: 10	2.2 Min: 1 Max: 4
	Number of plants in the mean diet	12	47	53	64	53	46	48	10
Mouflon	Sample size	16	20	19	61	16	8	34	31
	Mean number of eaten plant species/indiv.	4 Min: 1 Max: 7	4.35 Min: 1 Max: 9	6.7 Min: 3 Max: 10	4.6 Min: 1 Max: 11	5.1 Min: 1 Max: 8	7.6 Min: 6 Max: 10	6.4 Min: 1 Max: 9	3.4 Min: 1 Max: 8
	Number of plants in the mean diet	20	23	26	27	17	17	53	30
Roe deer	Sample size	13	63	6	22	17	27	46	18
	Mean number of eaten plant species/indiv.	1.7 Min: 1 Max: 4	5 Min: 1 Max: 11	4.7 Min: 3 Max: 7	4.5 Min: 2 Max: 8	5.3 Min: 1 Max: 9	4 Min: 1 Max: 10	3.1 Min: 1 Max: 10	3 Min: 1 Max: 7
	Number of plants in the mean diet	5	48	11	17	30	28	41	24

Chapter VI: Results from papers and additional analyses

6.1 From community to individuals (paper I)

a) Does sociality drive the inter-specific variability of populations?

The sociality hypothesis (SH) positing that in social species, individuals may have a more similar diet than individuals of solitary species as all individuals feed close to each other with the same resource availability, was not supported with our data. On the contrary, the niche variation hypothesis (NVH), predicting that populations with wider niche should display higher among-individual variability, was supported at the inter-specific level (fig.2 in paper I).

We conducted additional analyses at the within species-level to determine if groups of individuals having similar foraging behavior could be identified, assuming that we were likely to find clusters of individuals with similar diets in social species (chamois and mouflon). We measured the degree of clustering with the clustering coefficient proposed by Araùjo et al. (2008). However, no clusters were found in the populations of chamois, roe deer and mouflon. The idea that we should find clusters of individuals feeding on the same plant species within the mouflon population as it is a social species where individuals spatially aggregate, and to a lesser extent the chamois population, was therefore not supported.

b) How does intra-specific variability in diet vary with resource availability?

Our results showed that the total niche width (TNW) of all populations declined with resource availability. TNW was the lowest in winter, and the highest in summer for chamois and roe deer as the highest plant diversity occurred during this period. Mouflon had the largest niche width in autumn when it shifted from pastures to forests, resulting in a diet composed of various plants from these two environments (fig.2 in paper I).
In addition, the response of inter-individual variation to seasonal variation in TNW supported the niche variation hypothesis (NVH) at the intra-specific level, which meant that the more diverse the available resource, the higher the TNW and the higher the inter-individual variation (fig.2 in paper I).

6.2 The relative importance of food quantity and quality in large herbivore diet selection (papers II-III)

a) How do large herbivores with high metabolic rate survive in poor environment such as pastures?

The question of the use of food resources by large herbivores in relation to their availability is a recurrent question in ecology (Wam et al. 2010). It opposes two hypotheses: the forage-abundance hypothesis where ungulates feed in response to the abundance of forages and the selective-quality hypothesis where the selectivity of feeding depends on the nutrient quality of forages (Weckerly 1994).

➔ Taxonomic niche

According to our results from paper II, diets of chamois and mouflon appeared to be conservative, at least for the main plant species making up the diet in spring and summer, within the daily home range. By the word "conservative", I mean that whatever the availability (except 0) the proportion of plant intake (but not the selection!) was constant (fig.30). Moreover, no significant relationship were found between the proportion of plants in the diet and the local plant availability. Our results also underlined the strong avoidance of chamois and mouflon for the most abundant plant species occurring in the pastures, i.e. *Carex sempervirens* and *Sesleria caerulea*. On the contrary, they focused on rare evergreen plant species, such as the evergreen shrub *Helianthemum nummularium* or on leguminous rich in nitrogen and easily digestible such as *Onobrychis montana* or *Lotus corniculatus*.

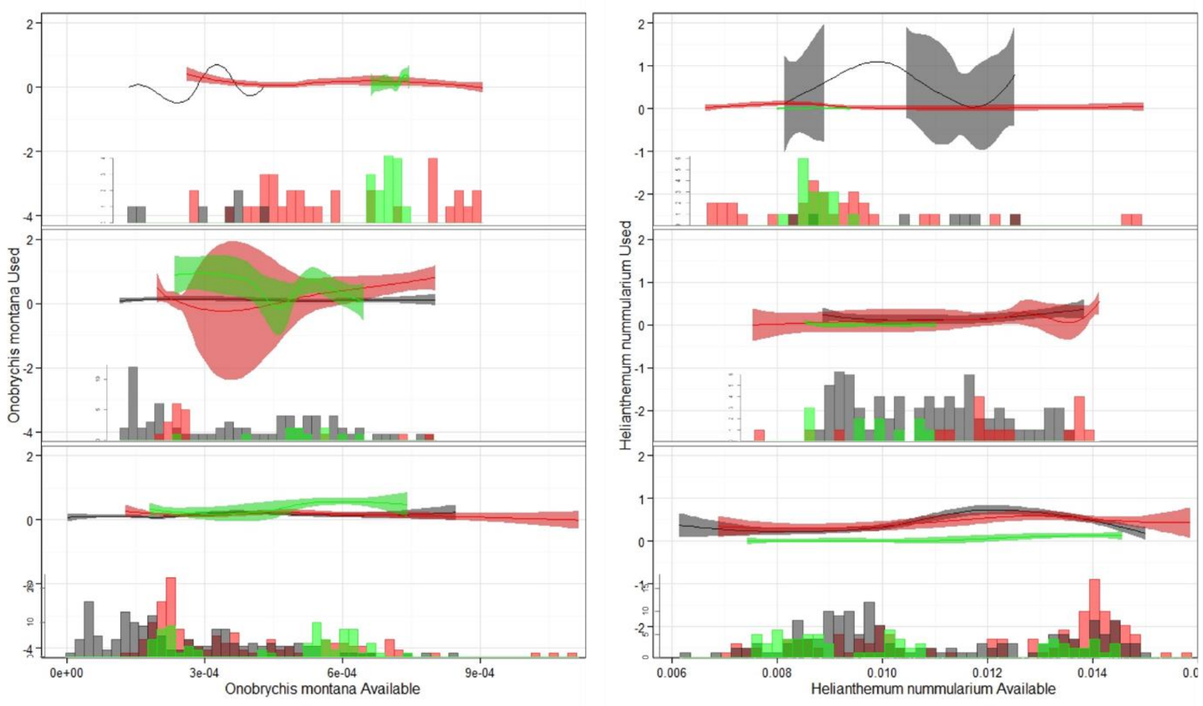


Figure 30. Effect of plant availability (relative abundance in terms of biomass in the field) on proportion in the diet for two of the most abundant plant species in the diets of chamois and mouflon (*Onobrychis montana* on the left and *Helianthemum nummularium* on the right). In green: mouflon population, in red: chamois in sympatry, in black: chamois in allopatry.

This selectivity observed both for chamois and mouflon was not completely in agreement with previous studies. Indeed, La Morgia & Bassano (2009), Bertolino et al. (2009), Garcia-Gonzalez et al. (1996) recorded that diets of chamois (*Rupicapra rupicapra* for the two first studies, *Rupicapra pyreneica* for Garcia-Gonzalez et al.) were composed of a large proportion of grasses (respectively about 30.2% in August to 46.9% in September, 48% in autumn to 67% in spring, 13.7% in autumn) in addition to forbs, in line with the "intermediate feeder" chamois diet type. Like in our study, both La Morgia & Bassano (2009) and Bertolino et al. (2009)

underlined the presence of Cistaceae (the family of *Helianthemum nummularium*) in the diets, but in lower proportions.

Even though mouflon have been classified as grazers in many studies (see references in Marchand et al. 2013), our study confirmed the non-compulsory grassy diet of mouflon as demonstrated in Marchand et al. (2013) (fig.31). In the Bauges Massif, their diet in pasture was mainly composed of forbs, with a low proportion of grasses (*Dactylis glomerata* especially). Hypotheses about the unusual diet compositions of chamois and mouflons are given in the *Synthesis, perspectives and directions*.

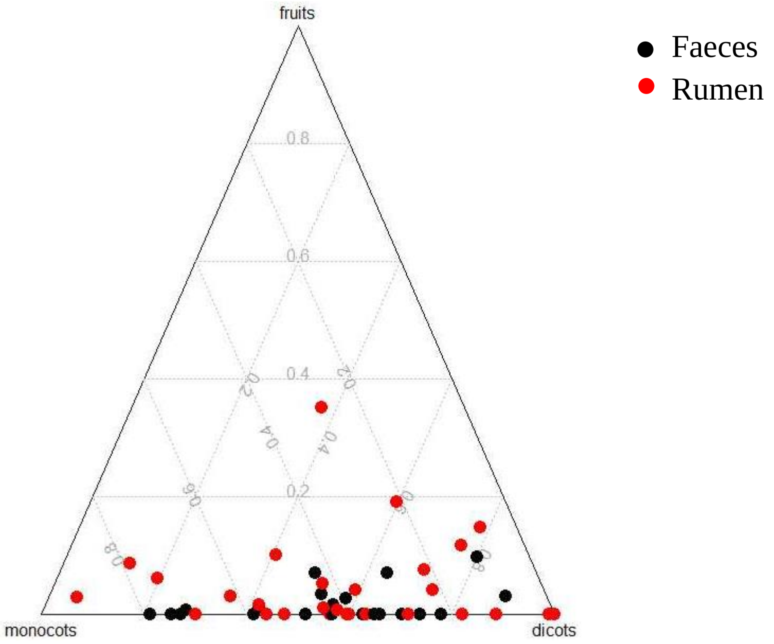


Figure 31. Ternary plot of the diet compositions of mouflon populations reviewed in Marchand et al. 2013.

➔ Functional niche

Functional niche of diets was described with the analogous of the CWM (Community Weighted Mean) metric, using three plant functional traits in relation with diet quality (nitrogen, phosphorus and leaf dry matter content). It also reflected the weak importance of functional availability (CWM available). Indeed, whatever the available nitrogen, phosphorus or water, animals were able to build their functional niche in a constant way, in spring and summer (fig.3 in paper II). In autumn, availability influenced the functional niche, but we hypothesized that during this period, selection could not compensate for the general decrease in the quality of plants available (fig.3 in paper II).

As stated in the introduction, 14-18% of crude protein has been estimated as the optimum percentage for maximum body growth of deer (French et al. 1956, Magruder et al. 1957). In our study, the diets of chamois and mouflon contained from 14% in autumn to 24% in spring of crude protein, which was greatly above the threshold of the deer. It suggested that chamois and mouflon, with their high metabolic rate, due to their low body mass (Demment & Van Soest 1985, White & Seymour 2003) selected for and found enough of a high quality diet. Hence, chamois and mouflon were able to reach their energy requirements whatever the availability. Moreover, we showed that they were able to survive in poor environments such as pastures mainly composed of grass species by selecting rare plants of higher quality than the average available vegetation (diet rich in nitrogen, rich in water, easily digestible; fig.2 in paper III).

➔ Functional diversity

Although the preferences did not depend on the environment (CWM of the diet independent of the available CWM), we wondered whether the functional diversity (variation of functional trait value) of the diet depended on the functional diversity of the environment (48h home range around faeces). For that, we calculated the functional dispersion index (FDis, Laliberté & Legendre 2010), which estimates the mean distance between species trait and the CWM. For each season, we tested the relationship between the FD of the diet and the available FD, as in paper II for the CWM.

Except for LDMC in autumn where there was a positive relationship (slope=0.91, p<0.05), the functional diversity of the diet estimated with functional dispersion did not longer depend on the functional diversity of the available plant in the environment (fig.32, p>0.05).

<u>Main result:</u>

Chamois and mouflon fed on plants of high quality rather than on plants of high biomass and of low-quality. We assumed that it allowed them to reach their energetic requirements for growth and reproduction.

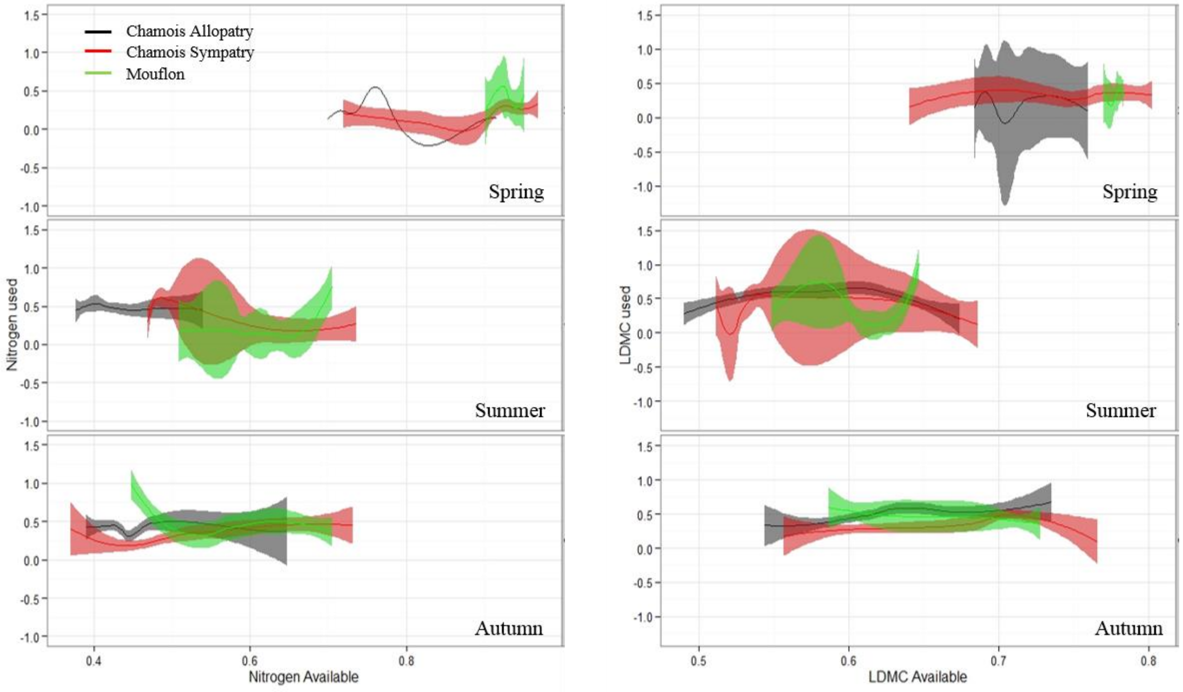


Figure 32. Effect of habitat FD (calculated as functional dispersion) on diet FD for nitrogen content (on the left) and LDMC (on the right).

b) Methodological considerations

In this work, the carbon content in plants had a relatively low coefficient of variation compared to nitrogen, phosphorus and water content. Consequently, even if Elser et al. (2000) advise the use of nutrient ratios, we decided to not include the C:N and C:P ratio in our analyses as their variations tracked the N and P variability. Moreover, we thought that the interpretation of single components was easier, as we are not aware of optimum ratio values required for chamois, mouflon and roe deer growth and reproduction.

In addition, the carbon content measured with the CHN analyzer included the indigestible and digestible carbohydrates. As the carbohydrates on which herbivores rely on are the digestible ones, which constitutes the proxy of energy, the total carbon content value does not give precise information on what is really used by the animal. Indeed, the lignin, considered as deterrent for herbivores as it is indigestible (Robbins 1983), is highly composed of carbon and could explain a large proportion of the total carbon content. The carbon content measured was not adapted to test the hypothesis that in winter, ungulates (white-tailed deer) would focus on plant rich in energy (Berteaux et al. 1998). For their part, they estimated the energy through the percentage of dry matter digestibility in food.

Finally, Elser et al. (2000) advised to use N:P ratio for animal studies. For the same reason as before, we preferred to focus on the two components independently, as we did not know the optimum values that large herbivores need to reach for their development.

c) At which scale do herbivores make their diet selection?

Additional analyses on the feeding selection scale by chamois and mouflon have been realized by P.A. Dupeyras (2014, M2 internship). The hypotheses are detailed in *2.2.c*.

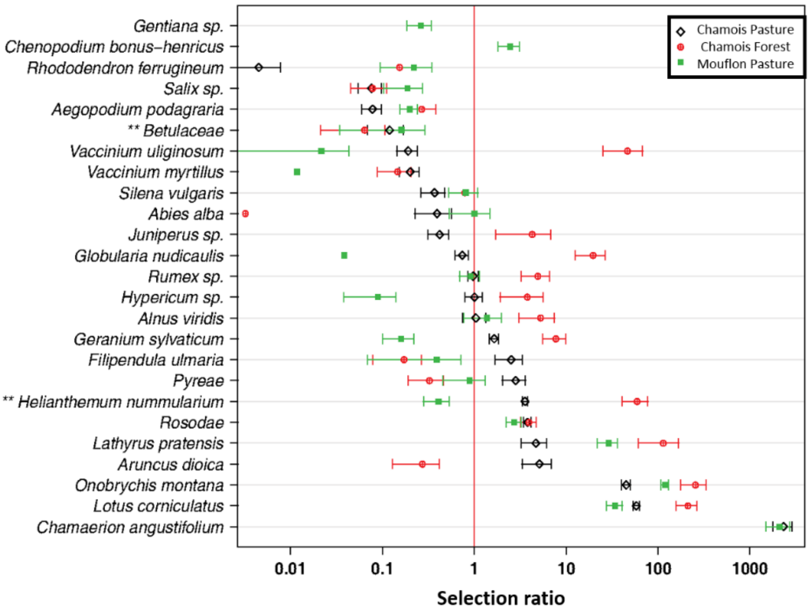
The results showed that a large part of the key-resources (resources on the right of the red axis x = 1 on fig.33) of both chamois and mouflon had a selection pattern similar as “SP1” (selection pattern 1 on the fig.34). Key-resources were selected at the 48h home range (4th-order selection) and not at the seasonal home range (3rd-order selection) (fig.34). Therefore, animals did not choose sites where the preferred resources were abundant (1st hypothesis rejected). The most abundant plant species (*Sesleria caerulea, Carex sp.*) were eaten in low proportion or not eaten and led to pattern “SP2” or “SP3”. Hence, those patterns suggested that the home range selection did not depend on forage resources but on other factors such as sociality, fear or body physiology.

In addition, “SP1” highlighted a strong inter-individual variability in the proportion of key-resources eaten, which was in line with the significant among-individual variation observed in paper I.

<u>Main result:</u>

Herbivores selected their diet at the fine-scale (4th order of selection), i.e. within the 48h home range.

While availability did not seem to be the strongest determinant shaping the diet, the selection of plants should, at least partly, depends on functional traits. We used this approach to determine the plant characteristics involved in the diet selection hereafter (*6.4*).



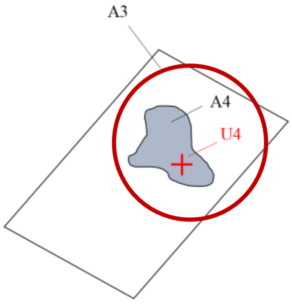


Figure 33. Mean selection ratio for the 25 key-resources in the diets of chamois and mouflons. Vertical red line (x = 1) corresponds to the axis where selection is neutral (from Dupeyras 2014). Selection ratios need to be interpreted carefully as they can be high in two cases: when the resource is rare and highly used, or when the resource is abundant and overused.

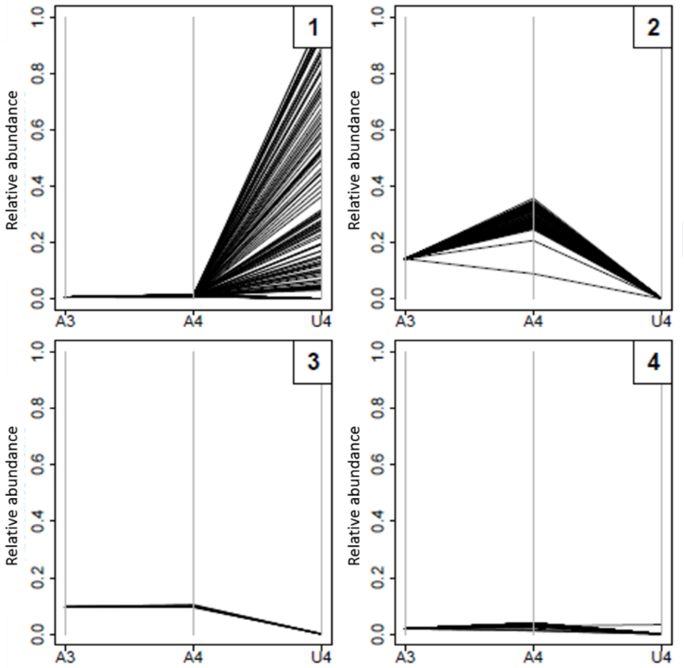


Figure 34. Selection pattern (SP) at the different orders of selection. 1: *Helianthemum nummularium* from chamois in pasture, 2: *Sesleria caerulea* from mouflon in pastures, 3: *Carex sp*. From chamois in pasture, 4: Betulaceae from chamois in forest. A3: Relative abundance of available resources within the seasonal home range (4.3.c). A4: Relative abundance of available resources within the 48h home range (4.3.b). U4: Relative abundance of used resources measured in the faeces (4.1). Each individual is represented by two lines linking the relative abundance of the used resource at two spatial scale (A3 and A4) (from Dupeyras 2014).

6.3 How do introduced species influence plant-herbivore interactions? Are introduced species always harmful for ecosystems? (papers II-III)

a) What is the impact of introduced mouflon on the native chamois trophic niche?

Our results demonstrated a neutral interaction between chamois and mouflon on the trophic axis of the ecological niche. Chamois in sympatry did not remarkably change its taxonomic niche in the presence of mouflon.

The additional analyses on functional diversity (functional dispersion, fig.32) revealed some differences between the two chamois subpopulations. Depending on the season and the traits, functional diversity of the diet of chamois in sympatry was always equal or lower than for the chamois in allopatry. As these differences were not explained by availability, we could hypothesize that the presence of mouflon influenced the diet mixing of chamois.

However, the mean diet quality (calculated with CWM) of chamois in sympatry was always equal or higher than for the chamois in allopatry.

These information were in agreement with previous findings on activity rhythm and habitat selection (Darmon 2012, 2014) for which interactions between chamois and mouflon were marginal. These results confirmed the idea that introduced species are not necessarily harmful for co-occurring species of the same trophic level, even when both species are at relatively high densities.

__Main result:__

Introduced mouflon does not have negative impact on native chamois, neither on the taxonomic (ingested plant species) nor on the functional (diet quality) niches.

b) How do species coexist?

The absence of negative effect of mouflon on chamois dietary niche may be due to (1) species-specific taxonomic and functional dietary niches, (2) non-limiting resource availability, (3) relatively low population density of introduced mouflon compared to the chamois preventing forced competition (Forsyth & Hickling 1998) for food (even though we are not aware of the absolute densities of chamois and mouflon in the pastures, we nevertheless know that chamois densities are similar between the sympatric and the allopatric sites, and the density of mouflon are lower than the density of chamois in the sympatric site), or (4) a spatial partitioning at a fine-scale during the three seasons preventing competition for shared resources. The population density estimates have to be interpreted carefully as population densities are difficult to assess.

(1) Species-specific taxonomic and functional dietary niches?

Our results (paper II) showed that, depending on the season, chamois and mouflon differed more or less in their diets in terms of taxonomic and functional niche position (paper II). Comparisons of the mean scores of chamois and mouflon populations on the first axis of the NSCA (fig.2 in paper II) revealed no differences in spring, but significant differences in summer and autumn, suggesting a partial taxonomic niche partitioning between both ungulates. The differences in functional niches between both species were less visible, but mouflon had a higher diet quality than chamois in autumn.

In spring, the absence of taxonomic and functional niche partitioning could be explained by a lower richness of developed plant species available, leading the animals to feed on the same first plantlets. In addition, as chamois and mouflon were partially spatially segregated during this period (Darmon et al. 2012), exploitative competition would have a weaker effect on populations.

In summer and autumn, the partial taxonomic and functional niche partitioning could be explained by differences in diet selection criteria, but not necessarily. Indeed, ungulates can have the same diet selection criteria (for example leaf nitrogen content) but have different taxonomic niche if they forage on different plant species to avoid competition, and different functional niche if ungulates exploit different range of values depending on their needs (Behmer & Joern 2008). Besides, both species can have different functional niches based on nitrogen, phosphorus and leaf dry matter content (as in paper II), but other plant functional trait could actually act as the main diet selection criteria.

Results from paper III showed that this partial niche partitioning can be partly related to different diet selection criteria between ungulates (see *6.4.a*).

(2, 3, 4) What about the others suggested factors?

Even though a partial niche partitioning was observed between chamois and mouflon, it does not mean that non-limiting resource availability, herbivore density or spatial partitioning (see *6.3.a*) are not acting in the coexistence.

Indeed, as we still observed a taxonomic overlap between both species in autumn and summer, we hypothesize that (1) the shared resources are not limiting and prevent competition, or (2) resources are limiting and there is exploitative competition, but, as they are suboptimal resources, it does not impact chamois diet quality (fig.2 in paper II).

To test the effect of mouflon population density on the strength of the niche partitioning between chamois and mouflon, we should investigate different sites varying in their mouflon population density.

Finally, a partial spatial partitioning of ungulates was observed in spring in Darmon et al. (2012), and it could also be active in summer and autumn and prevent competition on the shared food resources.

6.4 The unexpected importance of biomechanical traits in the large herbivore diet selection criteria (paper III)

“All models are wrong but some are useful” claimed Georges Box 30 years ago. We tried to emphasize some useful models to determine the plant functional traits involved in the food selection by ungulates. As correlation does not imply causation, as multicollinearity can be found between independent variables and might confound the relationship of an independent variable and the response variable (Smith et al. 2009, Ray-Mukherjee et al. 2014, Ruffell et al. 2015), and as relations between variables can be direct or indirect, we tested the validity of causal models relating plant functional traits and diet using path analysis (Wright 1921).

a) Do plant chemical content better explain diet selection criteria than other traits?

The results from paper III highlighted the major role of biomechanical traits in the food selection of chamois over the year (see fig.4 in the paper III). The pattern was slightly different for the mouflon. Indeed, in spring, none of the measured traits were responsible of diet composition, while LNC was preferred in summer and leaf toughness was avoided in autumn (see fig.4 in the paper III). In spring, when the mean leaf nitrogen content of plants is high in average and variability is low (Robbins 1983), selectiveness is likely to be relatively less important than in other seasons (Weckerly & Kennedy 1992). Still, the most abundant plant species did not dominate the diet, and ungulates selected plants on the basis of the four traits considered (Figure 2). Unmeasured traits might drive the selection criteria, or the too low sample size might prevent any significant pattern for the path Leaf Punch Toughness → Diet in spring. In summer, mouflon would select the plants with high nitrogen content in order to support nutritional demands, particularly for yearling growth (Crête & Huot 1993, Parker et al. 2009, Dostaler et al. 2011), horn development and body mass maintenance (Asleson et al. 1997), but also for lactating females that have to meet the protein demand for milk production (Reese & Robbins 1994) and to replenish their body condition before a new breeding cycle and winter (Crete & Huot 1993, Gerhart et al. 1997). Finally, in autumn, as plant quality decreases, mouflon focused on easily chewed plants.

Then comes the question: "Why do we not observe the same pattern of selection for chamois over the year?" Morphological traits of ungulate might be involved in the differences observed in diet selection criteria. Mouflon have more muscular rumen and stronger masseter muscles than chamois (Clauss et al. 2008a). Given these features, mouflon would have a higher ability to overcome the forage resistance both orally (mouth) and internally (rumen). Hence, in summer, when plants are still easy to chew or digest for the mouflon, they prefer to focus on the nitrogen content than on the leaf toughness. On the contrary, as masseter muscle mass of chamois are twice lower than mouflon (Clauss et al. 2008a), we hypothesized that the work required to chew or digest is the most important criteria for the choice over the year. For example, leaf punch toughness and nitrogen content are lower for *Helianthemum nummularium* (preferentially selected by chamois) than *Onobrychis montana* (preferentially selected by mouflon). Each of these plants builds up a large proportion of chamois and mouflon diets respectively and play a role in taxonomic diet differentiation, especially in summer and autumn (Bison et al. in prep).

Our results disclosed the importance of mechanical resistance, a criteria herbivore strongly select against, and therefore could have evolved in plants to protect leaves from herbivory (e.g. Coley 1983, Choong 1996, Wright & Vincent 1996, Pérez-Harguindeguy et al. 2003, Clissold 2007, Ibanez et al. 2013a).

<u>Main result:</u>

In the three seasons for chamois and in autumn for mouflon, biomechanical traits were more directly involved in diet selection than biochemical traits. Such patterns were not able to be detected in other studies because of correlations among traits.

b) Is the relationship between biomechanical traits and chemical traits (C:N ratio, LDMC) consistent across growth forms?

Testing the correlations between traits, we observed that strategies of plants are not as perfectly defined as theory predicts for the leaf economic spectrum (LES). For example, we found a positive correlation between punch toughness and leaf dry matter content during the three seasons, when all growth forms were included in the model (such as found in Ibanez et al. 2013a). However, when focusing on forbs, punch toughness was not related to leaf dry matter content anymore (fig.35) in spring (p-value = 0.18), summer (p-value = 0.08) and autumn (p-value = 0.91). The absence of correlation was already observed in some other studies (Perez-Harguindeguy et al. 2003, Deraison et al. 2015, unpublished data Ibanez S.). When feeding on forbs, this allows the animals making opposite selection toward two traits usually correlated.

The same observation was highlighted for the relationship between LDMC and C:N. While they were generally correlated at large scale (p<0.05 when all the growth forms were included in the analysis) (Wright et al. 2004), they were independent when linear relations were tested for each growth form separately. This resulted in the idea that correlations depend on the scale (Gross et al. 2007) and vary with the pool of species. For instance, Deraison et al. (2015) found no correlation between LDMC and C:N because of a high proportion of forbs in their samples. In such cases, it becomes possible to discriminate the effects of LDMC and C:N on the diet selection process.

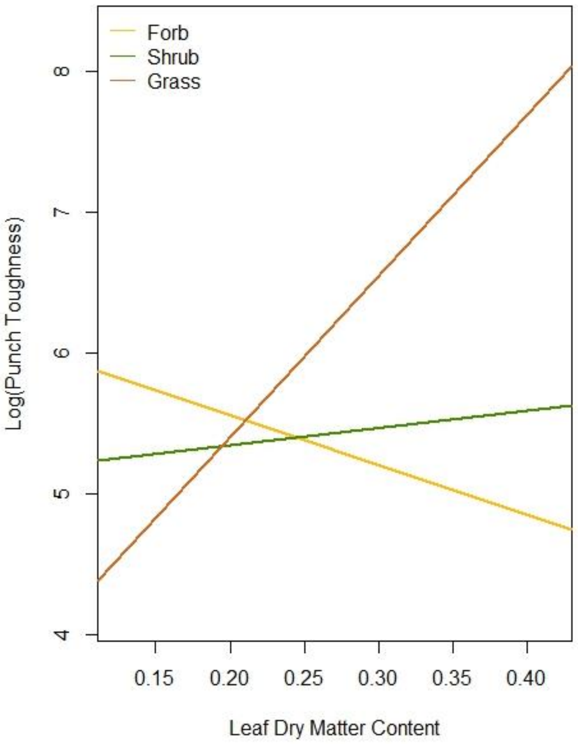


Figure 35. Relationship between punch toughness and leaf dry matter content for three growth forms in July.

c) What are the traits correlated to leaf punch toughness?

About 60% of the leaf punch toughness variability was explained by leaf dry matter content (LDMC), leaf nitrogen content (LNC) and leaf thickness (LT). The remaining 40% could be related to the organization, type and density of fiber content (Choong 1992, Onoda et al. 2011). Indeed, Choong et al. (1992) showed for dicotyledonous trees that the sclerophylly index – proxy of digestibility –, defined by Loveless (1961) as the ratio of crude fiber to crude protein, was correlated with the leaf toughness, particularly for the former.
In addition, fiber content was supported to be a strong diet selection criteria for red deer (Forsyth 2005, Zweifel-Schielly et al. 2012), white-tailed deer (Sauvé & Côté 2005) and eland (Watson & Owen-Smith 2002) as fibers reduce the digestibility of food to ruminants (Van Soest 1994) and makes nutrient access more difficult (Clissold 2007).

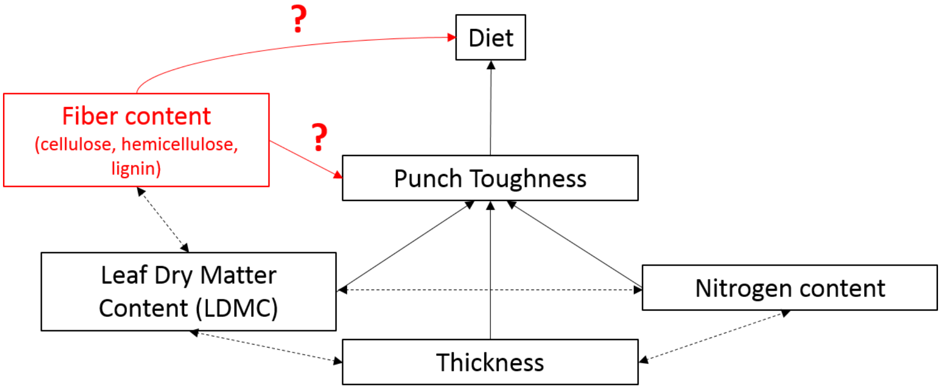


Figure 36. Hypothetical path analysis including plant fiber content as a trait influencing punch toughness.

Even though fiber content is correlated with LDMC (Al Haj Khaled et al. 2006, r = 0.63, p<0.05 for grass species), we hypothesize that fiber content could have a direct effect on diet selection, in addition to an indirect effect through LDMC. Further estimations of fiber content should be done to assess their influence on biomechanical traits measurements and how they impact diet selection.

Other anatomical properties of cell walls, veins organization, and cuticule/epidermis features could also be involved in the toughness measurement (Lucas et al. 2004, Read & Stokes 2006, Sanson 2006, Peeters et al. 2007, Onoda et al. 2008).

<u>Main result:</u>

The leaf nitrogen content, leaf dry matter content and leaf thickness accounted for 60% of variation of biomechanical traits. The remaining percentage could partly be related to plant fiber content.

d) What about the relationships between diet and other traits?

We did not include all the measured plant functional traits in the path analyses for two reasons: first, it would have led to a highly complex path diagram, and second, causal relationships among these other traits and diet are difficult to predict.

In the paper III, we tested the effects of quality traits on diet (biomechanical and chemical traits). In the introduction (*2.2.d*), we proposed that plant traits related to visibility could also influence diet choice. Hereafter we present plots relating the mean frequency of occurrence of plants in the diets of chamois in function of the plant “visibility” traits (vegetative height and inflorescence volume). We did not present the boxplot showing the frequency of occurrence of plants in the diet in function of sociality or phenology, as no trends were observed.

To calculate the inflorescence volume of each individual, we first measured the volume of a medium inflorescence (width*height*length) and then we multiplied this number by the number of clusters of inflorescence on the individual. In the case of *Arnica montana* for example, there was one inflorescence and we only measured the volume of this inflorescence. For *Heracleum sphondyllium* for instance, for which flowers are clustered, we first measured the volume of a medium cluster, and we multiplied this number by the number of clusters of inflorescence. Inflorescence means bud, flower or fruit, depending on the phenology.

No strong tendencies were observed between the frequency of occurrence in the diet and either of the two visibility traits (vegetative height and inflorescence volume). We hypothesized that their effects on diet selection of chamois were not major. However, more robust statistical analyses taking into account all the individuals, and not the mean frequency of occurrence of plants in the diets as presented here, should be done. In addition, the inflorescence volume should be interpreted with the information of the percentage of individuals having an inflorescence. Indeed, the inflorescence volume has been calculated from the plants having an inflorescence. Consequently, a plant can display a high inflorescence volume in our database, but as being the only individual amongst the 10 samples to have an inflorescence. This parameter can also play a role in the visibility and should be investigated.

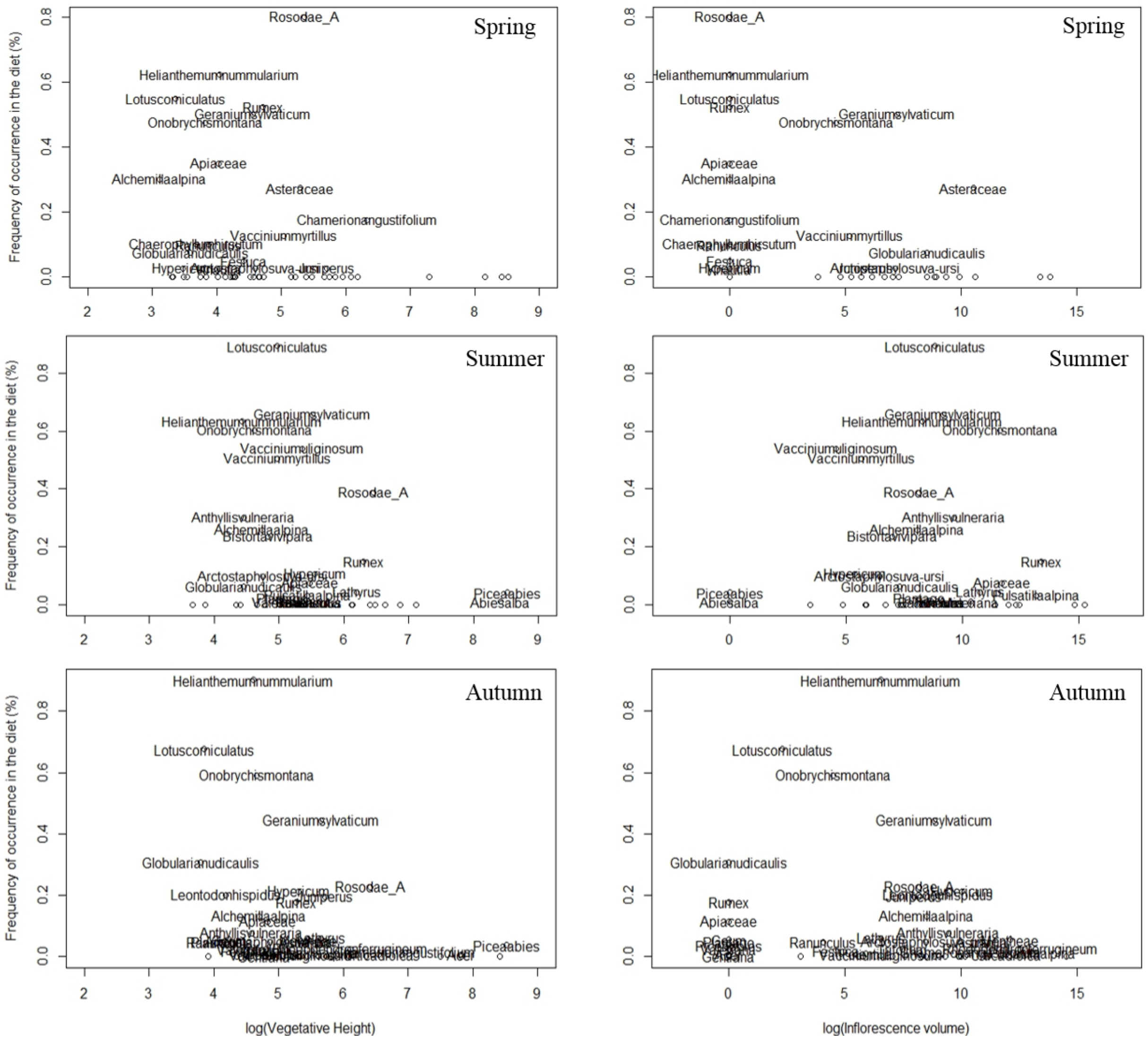


Figure 37. Mean frequency of occurrence of plants in the diets of chamois as a function of vegetative height and inflorescence volume in spring, summer and autumn. Dots without names are the plants present in the pasture but not eaten.

6.5 A bit of methodology: is the use of NIRS relevant and useful for estimating diet and plant quality? (papers IV-Note)

a) Are diet quality estimations with NIRS consistent with measurements on plant functional traits ingested?

In the previous analysis of this thesis, the quality of the diets has been estimated through the plant quality of ingested plants. This required a precise diet database and an extensive sampling and measurement of plant functional traits. In several studies, fecal indices (fecal nitrogen content for instance) appeared as a useful tool to determine the diet quality of populations and individuals. However, the relevance of fecal proxies of diet quality has been questioned by some authors (Robbins 1983, Robbins et al. 1987, Hobbs 1987, Servello et al. 2005).

At the inter-seasonal level, our results showed that FN (fecal nitrogen) cannot be used as a reliable estimator of DN (dietary nitrogen estimated with the nitrogen values of ingested plants) as only 38% and 14% of variation of DN were explained by FN for chamois and mouflon respectively. At the intra-seasonal level, no more significant relationships were observed. Different causes could be at play to interpret the differences in the slopes and intercepts of the relationships between FN and DN between both ungulates: (1) the activity level of tannin-binding salivary protein differ among species, which in turn affects the fecal nitrogen release differently between the two species (see *2.2.b* for the effect of tannin on nitrogen), (2) the diets of chamois and mouflon vary in their tannin content, which in turn, as previously, affects the fecal nitrogen release differently between the two species , (3) as a part of the fecal nitrogen come from undigested microbial nitrogen, the microbial rumen community could diverge among ungulates and differently affect the nitrogen release. Further analysis should be conducted to better detect the causes that are at the sources of the differences in relationships between DN and FN for different ungulates with different feeding types. Diets more rigorously and clearly described in terms of botanical and chemical compositions, in addition to a good knowledge about the digestive and assimilation process of nutrients by ungulates, should bring additional robust conclusions.

As a conclusion, we advised to use fecal nitrogen index for species-specific population at a large time-scale and not to detect small changes in population response to a changing environment, nor to compare the diet quality from fecal indices of different species.

<u>Main result:</u>

Fecal nitrogen estimated with NIRS account for a low proportion of dietary nitrogen variation estimated from functional traits of ingested plants.

b) Is the estimation of N, C and P with NIRS as robust as classical methods? Can we create three general calibration models (one for each chemical component) usable for different ecosystems? (paper in prep. not included in the thesis, Ancin Murguzur F.J., Smis A., Bison M., Struyf E., Bråthen K.A.)

Results demonstrated that the cross-validation and validation models varied in their goodness of fit depending on the nutrient tested (table 7). The best models were obtained for nitrogen (N, table 7, fig.38), as in Meuret et al. (1993), de Aldana et al. (1995), Moron & Cozzolino (2002), Petisco et al. (2005). The estimation of phosphorus (P) and carbon (C) were less accurate. As mineral elements as P do not directly absorb NIR radiation, they are indirectly measured by NIRS (de Aldana et al. 1995, Chodak et al. 2008). The prediction relies on association with organic or hydrated inorganic molecules (Clark et al. 1987). As the proportion of forms in which P exists in plants (phytate, phospholipids and nucleic acids) may vary among season, species and location, the reliability and consistency of calibration models are weak (Foley et al. 1998), relatively to nitrogen. In addition, the low range of P content values contained in plant could increase the error measurement and bias the models, explaining the low accuracy of P calibrations. Finally, as the coefficient of variation obtained for P with classical reference method was high, it could be additionally responsible for the unsatisfactory NIRS models. The use of NIRS data to estimate P should be suitable for studies not requiring high accuracy (Petisco et al. 2005).

The predictive ability of a region-specific model transferred toward another region was limited for all the three nutrients (C, N, P, table 7).

We suggested different hypotheses to explain this low transferability. First, same plant species exposed to different environments would have different biochemical structures which would absorb NIR radiation at different wavelengths. Hence, the wavelengths used to build specific-location models were different, leading to less reliable estimations when predicting sample values from different location. In addition, if a calibration does not include, for example freeze-resistant plant species, then a prediction of freeze-resistant plant constituents would be biased because the model “is not aware” of how much the antifreeze molecules change the spectra. As only ten species were in common between France and Norway, the difference in plant composition between the regions could participate in the low transferability of models. Finally, as the classical methods used to evaluate N, C and P content differed between France and Norway, the low transferability ability could be explained by errors in reference values (high coefficient of variation). Samples from both locations should be analyzed concurrently with both classical methods in order to remove the bias due to the methodology.

However, the global models including the data from both regions showed similar calibration coefficients as both models taken separately (table 7, fig.38). The global model helped to overcome the specificities related to the location, plant growth form, seasonality and methodology used, making more robust the estimation of chemically unknown samples from different location, species or season. Hence, our results suggested that the use of global models should be a useful and accurate predictive tool for extensive and intensive analysis at a large scale.

Main result:

Estimation of nitrogen content (N) with NIRS was as robust as classical methods but models and reference values of carbon (C) and phosphorus (P) need to be improved.

A single global model could be used to estimate leaf nitrogen, carbon and phosphorus content from different ecosystems.

Table 7. From the paper in prep. (Ancin Murguzur et al.). Parameters of cross-validation and validation models for France and Finnmark data for the three plant nutrients (C, N, P). Additional parameters of validation models done with foreign dataset. R^2 cal = R^2 for cross-validation, RMSEC = Root Mean Standard Error of Calibration, R^2 validation = R^2 of the validation set (internal validation and foreign dataset), RMSEP = Root Mean Standard Error of the Prediction, bias = mean error between estimated and measured values.

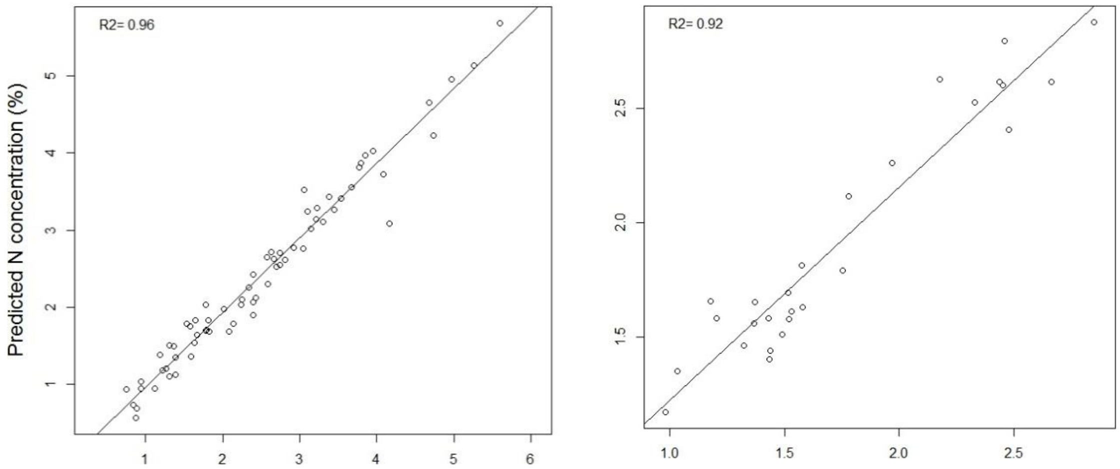
Carbon	k	R^2 cal	RMSEC	R^2 validation	RMSEP	Bias	Intercept	Slope
Global	26	0.83	1.1432	0.88	1.0027	-0.03	2.29	0.95
France	21	0.88	1.0034	0.89	0.8	-0.04	1.99	0.96
Prediction of Finnmark with France model				0.66	1.19	2.0519	18.02	0.59
Finnmark	16	0.83	1.0792	0.87	1.1568	-0.19	3.36	0.93
Prediction of France with Finnmark model				0.7	1.36	2.4295	-3.09	1.09

Nitrogen	k	R^2 cal	RMSEC	R^2 validation	RMSEP	Bias	Intercept	Slope
Global	17	0.93	0.2688	0.95	0.2207	-0.07	0.09	0.99
France	20	0.96	0.2373	0.93	0.2662	-0.03	0.09	0.97
Prediction of Finnmark with France model				0.86	0.28	0.42	-0.19	0.96
Finnmark	18	0.96	0.1583	0.94	0.172	-0.02	0.26	0.88
Prediction of France with Finnmark model				0.88	0.38	0.5657	0.54	0.94

Phosphorus	k	R^2 cal	RMSEC	R^2 validation	RMSEP	Bias	Intercept	Slope
Global	13	0.65	0.0747	0.75	0.0685	<0.01	0.02	0.89
France	6	0.71	0.0675	0.81	0.0565	<0.01	0.05	0.8
Prediction of Finnmark with France model				0.55	0.09	0.1222	-0.02	0.653
Finnmark	10	0.69	0.0672	0.69	0.0714	<0.01	0.04	0.84
Prediction of France with Finnmark model				0.54	0.08	0.1324	0.09	0.97

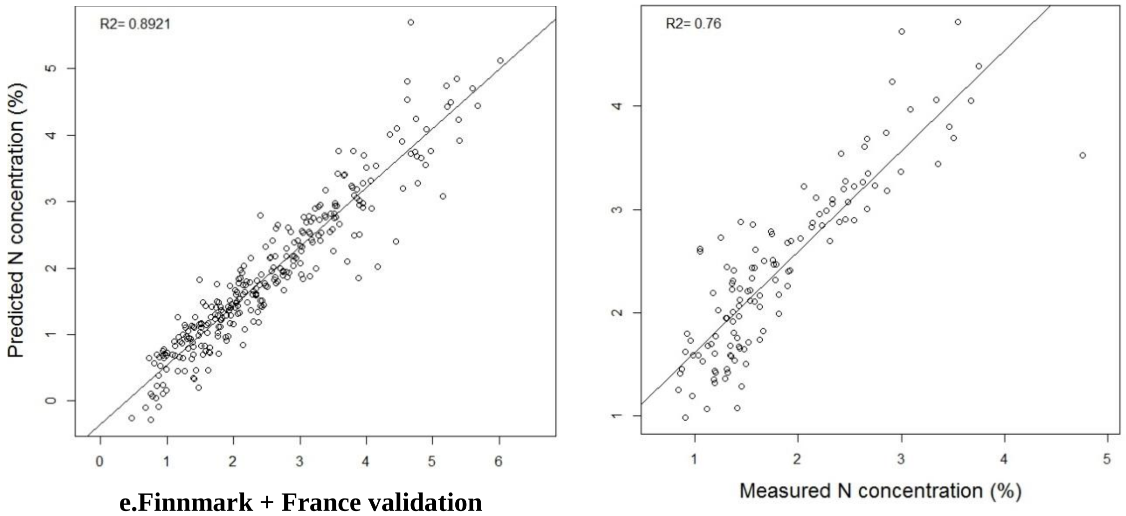
a.France validation model

b.Finnmark validation model



c.Finnmark vs France validation

d.France vs Finnmark validation



e.Finnmark + France validation model (global model)

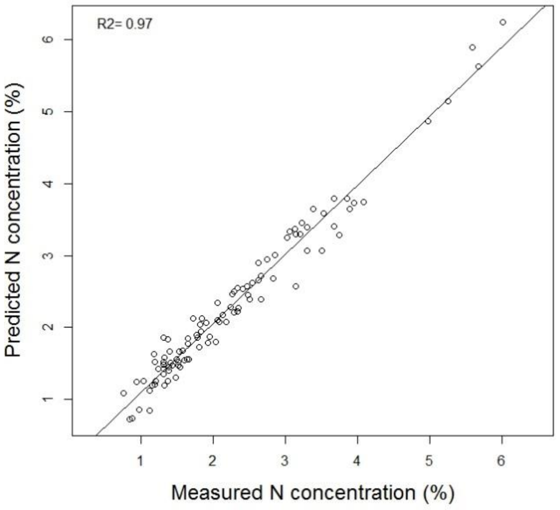


Figure 38. From the paper in prep. (Ancin Murguzur et al.). Validation models testing the correlation between predicted N content (%) from NIRS and measured N content (%) from classical chemistry methods, at each site (a,b), one site vs the other (c,d), for the global model (e).

SYNTHESIS, PERSPECTIVES & DIRECTIONS

4

First, I will address some methodological considerations that should be taken into account in interpreting the results. Then, I will discuss about plant-herbivores interactions in the light of results obtained in this thesis. Finally, I would like to demonstrate that our results, in addition to provide some clarifications about trophic interactions between ungulates and plant communities, could be useful in the field of studies that attempt to predict species distribution in response to climate change.

7.1 Methodological considerations

a) Questioning the reliability of diet estimation from faeces data

Usually assessed from rumen or fecal samples, browse surveys or direct observations (Pompanon et al. 2012), composition of diets can be misevaluated. In the case of fecal samples, the real diet is usually biased because of the differential digestibility among plant species (Verne & Ullrey 1984). Indeed, as plants with low fiber content are more easily digested than high fiber content plants, they are hard to identify and tend to be underestimated (Skinner & Telfer 1974). In this work, grass species that decompose slowly were poorly represented in the faeces, which reinforce our conclusions that grass species are eaten to a low extent by chamois and mouflon. However, the diets described for chamois and mouflon were not always consistent with other studies, as detailed in the summary of results (*6.2*). Different hypotheses about these differences are possible. Firstly, the grass species were under-represented in the faeces even though a large proportion (between 20 and 50% of the diet) was found in the rumen of chamois and mouflon (Redjadj et al. 2014). However, the comparison has to be done carefully as Redjadj et al. (2014) focused on the period from September to January, which has been poorly studied in our work as a very low number of faeces was available in winter. Second, diets obtained from other studies (La Morgia & Bassano (2009), Bertolino et al. (2009), Garcia-Gonzalez et al. (1996)) have been determined by microhistology, a method where the identification of highly digested small fragments is very difficult and which tends to overestimate grass species. We would need to analyze faeces both by microhistology and barcoding to properly compare the discrepancies between the two methods. Third, according to the review of Marchand (2013), diets of mouflon are not restricted to grass species, and the environment influences the diet choices. Hence, it is conceivable that mouflon from the Bauges Massif could prefer a diet rich in dicots. As chamois are classified as intermediate feeders, it was not surprising that their diet contained only few grasses.

b) NIRS experience

One of the challenging topics in ecological studies is the identification of large-scale process driving the structure and dynamics of communities (Sutherland et al. 2013). We therefore have an urgent need for sampling and analytical methods suitable for building large databases of plant chemical functional traits, for example. Devices such as CHN analyzer used for classical chemical analysis, e.g. to estimate plant nitrogen content, are time-consuming, costly and destructive. The use of NIRS methodology is a promising approach as it overcomes the problems of time, cost and sample destruction. Several studies, among which one presented in section *6.5.b,* have demonstrated that NIRS was a useful tool for predicting nitrogen content in plants (Petisco et al. 2005, Moron & Cozzolino 2002, de Aldana et al. 1995, Meuret et al. 1993). Additional measurements need to be done to determine why NIRS is not as accurate for estimating carbon and phosphorus content. Besides, the results showed that a single calibration for sub-arctic and temperate ecosystems gave similar results as specific models for each location for the three studied nutrients (C, N and P). This opens the way to extensive sampling whilst saving time and money: instead of having to calibrate a model for each location, a single global model could give similar results.

c) Fecal indices as poor estimator of diet quality

NIRS was applied on faeces sample to evaluate the diet quality of the animals that produced the faeces. Here, the reliability of NIRS was not tested by comparing it to results obtained from traditional chemical analyses, but we indirectly assessed its relevance to detect diet quality by comparing it to the average nitrogen content of ingested plants (determined by DNA-metabarcoding). The relationship between these two estimates of diet quality was poor suggesting that using NIRS nitrogen estimates was a poor proxy of diet quality at the intra- and inter-seasonal level. Fecal indices could perform poorly because of the effect of tannins on nitrogen release. However, the main shortcoming of our results is that our method to estimate ingested nitrogen from diet composition obtained from barcoding, combined with plant nitrogen, is not yet validated as a reliable method to estimate true nitrogen intake. Experimental trials controlling the initial quality or resource ingested should be used to determine the factors and the methodological bias affecting the diet quality measurements.

7.1 Plant-herbivores interactions

European mountain ecosystems are affected by climate warming, concomitant with the increase of large herbivore densities and changes in vegetation dynamic. In order to predict population dynamic and ungulate interactions, resource characteristics that are important for herbivores need to be determined. This involves identifying the factors explaining diet selection and coexistence among herbivores at the intra- and inter-specific level.

a) Thoughts about diet selection

The results of this work suggested that diets of ungulates living in alpine pasture environments (chamois and mouflon) were affected by food quality rather than quantity (paper II & III), and that the resource selection happened at the fine-scale 48h home range rather than at the broader-scale of the seasonal home range. At this coarse-scale, the selection was driven towards high biomass (and relatively low-quality) plant communities (Duparc, personal communication), and towards areas where preferred resources were locally rare. Those results contradict other studies where ungulates selected patches of high-quality within the seasonal home-range in order to reach their energy requirements for lactation or growth (deer in winter in Zweifel-Schielly et al. 2009, moose in summer in van Beest et al. 2010). It suggested that, in our study, other factors such as sociality, fear (search for refuge sites against predators, Ruckstuhl & Neuhaus 2002) or body physiology (temperature plays a role in the habitat selection, Marchand et al. 2015) motivated the plant community choices. However, within the chosen plant communities, ungulates were highly selective and were able to compose a diet of higher quality than the average available vegetation (paper III).

While we showed that species functional niche position (calculated as CWM) was influenced by food preferences for both chamois and mouflon, we also demonstrated that the variation of functional diversity of each functional trait (estimated as functional dispersion hereabove, Laliberté & Legendre 2010) did not depend on habitat diversity. The level of diet generalization of these ungulates seemed to be species-specific, contrary to grasshoppers where the species niche widths depended on habitat functional diversity (Ibanez et al. 2013b). Even though co-occurring species differ in their niche position, such as chamois and mouflon in paper II, large and overlapping functional niche widths could limit the niche partitioning (Ibanez et al. 2013b).

Our results (paper III) pointed out that plant functional traits may be used as determinants of diet selection and that different choice criteria among ungulates can act as mechanisms at the origin of niche partitioning. Furthermore, our analysis highlighted the importance of biomechanical traits in diet selection, as already observed for insects (Gomez et al. 2008, Perez-Harguindeguy et al. 2003, Ibanez et al. 2013a). Biomechanical plant properties therefore have the potential to act as anti-herbivore defenses (Sanson et al. 2001), even against large herbivores. In addition, our results went one step further as they discriminated the direct and indirect effects of correlated functional traits of diet selection and pointed out that the usual idea that herbivores would focus their selection towards protein intake (Berteaux et al. 1998, Dostaler et al. 2011) was true but not complete: this parameter has not always a direct but an indirect effect on diet selection through biomechanical trait.

- We measured the functional traits of plants, but what about their match with herbivore functional traits?

As large herbivores are able to make a choice based on plant biomechanical features, it suggests that their morphology constrains the use of resources, and/or they are morphologically able to feed on all the resources but have preferences for soft plants. Soft plants indeed require less energy to be digested. In both cases, it involves innate or learning abilities in order for animals to make the appropriate selection (Provenza 1995, Tixier et al. 1998). The importance of morphological associations between resources and consumers has been emphasized in studies of herbivore-plant network (Ibanez et al. 2013a), prey-predator interactions (Song & Kim 2014, Spitz et al. 2014), or plant-pollinator systems (Temeles et al. 1996, Maglianesi et al. 2014). For example, Ibanez et al. (2013) showed that mandibular traits reflected the feeding preferences of grasshopper species, as grasshoppers with higher mandibular strength were able to consume tougher plants. In hummingbird-flower interactions, bird species with curved bills better reached nectar from curved flowers than straight-bill hummingbirds (Maglianesi et al. 2014). These results indicate that morphology can strongly influence resource use, which in turn allows niche partitioning within species assemblages and reduces competition. Different studies demonstrated the link between feeding strategy of large herbivores (browser-grazer) and animal characteristics (such as type of reticulo-rumen: Clauss et al. 2003b, Clauss et al. 2009; shape of muzzle: Gordon & Illius 1988; salivary binding proteins activity: Clauss et al. 2005; teeth size and wear: Williams & Kay 2001, Mendoza et al. 2002; jaw muscle strength: Clauss et al. 2008a). For example, Clauss et al. (2003) showed that grazers are more prone to overcome a diet composed of grass than browsers, as the stronger musculature and the higher capacity of their reticulo-rumen allows digesting fibrous plants in relatively large quantity. Hence, large herbivores with strong masseter and rumen muscles should be able to better feed on tough plants than herbivores with low masseter and rumen strength for example. Those associations are suggested in our paper III. The quantitative confirmation of such associations would be consistent with the optimal foraging theory predicting that a strong match between traits of resources and consumers favors the efficiency of resource use (Pyke et al. 1977). Therefore, one of the next step in plant-large herbivore interactions would be to further explore quantitatively the relationship between the eaten plant characteristics, i.e. not only their proportion in diet, and the intrinsic animal characteristics to determine to which extent functional traits of primary producers and consumers are related and to mechanistically explain the network of trophic interactions (Clauss et al. 2008b). This kind of analysis should be done on a large ungulate community, such as found in Africa, to obtain a wide gradient of herbivore features. However, we are aware that biomechanical traits are not the only traits implied in diet selection, as diet results from a complex set of constraints. Other biochemical traits could exert additional selection pressures on diet selection (Daering et al. 2005, Iason et al. 2005) and lead some animals or species to feed on non-optimal plants in terms of biomechanical traits (Ibanez et al. 2013a). For instance, large herbivores with low jaw and rumen strength could feed on tough plants to avoid secondary compounds negative effect.

Besides, given the selected plant and the herbivore’s anatomy, the cropping and chewing rate would be affected. As grasses are tougher than browses (higher fiber content, higher dry matter content, lower nitrogen content), the chewing and digestion process will take longer time (Robbins 1983, Choong et al. 1992, Wright & Illius 1995), especially if the animals has a reticulo-rumen less adapted to digest fibrous plants (Clauss et al. 2003b). However, the gain of energy animals would win on a relatively fast passage rate permitted by a higher digestibility, would be potentially offset by the loss of energy required to search for non-apparent high quality resources (Pyke 1977, “process 1” in Spalinger & Hobbs 1992).

- Including the spatial distribution of vegetation at a fine-scale in diet selection studies

Even if our results point at the importance of food quality rather than quantity in the diet selection and a frequency-independent food choice, we still need to more precisely evaluate the influence of plant availability on diet choice. A more precise spatial analysis of the available vegetation would be useful to disentangle the relationship between spatial heterogeneity of vegetation (Laca et al. 2008), resource selection and among-individual variation. For example, it has been shown that the plants neighbors can influence the food intake (Palmer et al. 2003, Bergvall et al. 2006, Bee et al. 2008). Field study showed that red deer were less likely to browse plant species when they were surrounded by less palatable plants because herbivores were avoiding low-quality patches, and more likely to browse if they were in a patch of high quality vegetation, in agreement with the “repellent-plant hypothesis” (Bee et al. 2008). On the contrary, the “attractant-decoy hypothesis” predicts that a plant growing among plants of high quality would gain protection from herbivores, as herbivore would also feed on the other high-quality plants, but would lose protection if it is surrounded by lower quality plants (Bee et al. 2008, Bergvall et al. 2006). As, in our study, chamois and mouflon were selecting patch of high biomass where preferred resource were locally rare, we could suggest that the foraging on the preferred plant species was exacerbated by the surrounding plants of low quality, as predicted by the “attractant-decoy hypothesis”. Here, we would like to determine whether such processes influence chamois and mouflon diet choice in the wild. For that, the positions of feeding station of animals and the associated diet, in addition to precise vegetation maps describing the abundance, the spatial distribution and quality of plants at a small resolution would be required, which represents a huge amount of field work. This could help to bring robust conclusions about the relative importance of quality, quantity and spatial heterogeneity of plants in the process of individual diet selection by wild solitary large herbivores.

- Concerns

Different concerns arose from the diet selection criteria study. As we used generalized linear mixed models in the path analyses, we were not able to determine the percentage of variation of the diet explained by the variables included in the models. As the process of food selection is not driven by a single trait, but by a complex set of features, it is likely that other factors or plant functional traits not included in the model explain another large part of the variation that we did not account for. Including other variables in path analysis requires to figure out how traits co-vary. We already have a good knowledge about the relationships between some chemical and biomechanical traits (LNC, LCC, LDMC, leaf punch toughness) and plant structure (specific leaf area, height), but relatively little is known about the inflorescence traits and their link with the plant traits described previously for example. Indeed, we could easily conceive that the size or color of inflorescence would play a role in plant selection (Gomez et al. 2003) in summer as we observed a lot of headless plants on the field. As the concentration of nutrients vary among the plant organs and influence the herbivore nutrient intake (Bailey et al. 1996), information about the preferred plant parts by herbivores could also improve the investigation of resource partitioning among species, but it would require to additionally perform microhistology on faeces (Pompanon et al. 2012), direct observations or recorded movies from movie camera head or neck placed on animals.

In addition, even if the importance of biomechanical trait, relatively to the chemical defences such as secondary compounds, has been already underlined by some researchers working on herbivorous insects (Coley 1983, Lowman & Box 1983, Ohmart & Edwards 1991, Steinbauer et al. 1998) and mammals (Wright & Vincent 1996), including data on plant secondary compounds and the species-specific ability of ungulates to cope with it could help to improve our understanding of the selection of some plant species.

b) Thoughts about rules of ungulate community assembly

In our study area, competition did not drive habitat selection of chamois and mouflon at the plant community-level (Darmon et al. 2012). Even though there was no negative effect of the mouflon on the spatial axis of the ecological niche of the chamois, the large spatial overlap observed at a broader scale led us to wonder about the competition for food resources. Our work demonstrated no negative impact of mouflon on chamois population on the taxonomic and functional feeding axis of the ecological niche (paper II). Chamois and mouflon were able to partly partition resources during the main part of the year, and even in autumn when the quality of the vegetation began to decrease. The partial taxonomic and functional niche partitioning seemed to be partly allowed by different diet selection criteria between chamois and mouflon over the year (paper III), which could be itself partly explained by morphological features of herbivores (paper III). It supports the idea that grazing ungulates with differing morphology occupy separate feeding niches (Murray & Illius 2000). Therefore, an introduced species with similar body size and similar ecological needs as native species of the same trophic level does not necessarily influence the relationships between the native species and its resources negatively, which contradicts the “usual” observed competition (Forsyth 2000, Lovari et al. 2014, Ferretti et al. 2015). Even though the coexistence has been observed on the spatial, temporal, and food axis of the ecological niche, the question of competition between both ungulates should be further considered in the context of increasing ungulate densities, of density-dependence (Garel et al. 2011), and with regard to the contrasted conclusions regarding chamois and mouflon co-occurrence (Bertolino et al. 2009, Chirichella et al. 2013).

The consistency of a coexistence pattern in chamois and mouflon interactions could be investigated through the study of other pairs of sympatric/allopatric sites for instance. Additionally, downscaling the analysis of food partitioning at the individual-level could allow determining whether competition may act a finer scale and impact only a subset of individuals.

Whereas the competition between species is usually seen as a major structuring force of communities, facilitation could also be involved in the species coexistence (Gordon 1988, Arsenault & Owen-Smith 2002, Waldram et al. 2008). In our study (paper II), we observed that chamois population in sympatry had an equal or higher diet quality than in allopatry. We suggested different hypotheses for this observation (see discussion of the paper II), and one of it was a facilitation effect of mouflon populations. Indeed, mouflon could allow a better access to suboptimal resources of high quality for chamois in sympatry, by reducing grass height or removing stems (Arsenault and Owen-Smith 2002). This effect could be predominant during the growing season (Arsenault and Owen-Smith 2002). However, competition should dominate facilitation during period of low biomass availability (Arsenault and Owen-Smith 2002). Because of a too low sample size and because mouflon shift to forest habitat in winter, we have not been able to assess the interactions between chamois and mouflon during a period of very low resource availability (in autumn, the resource availability decreases but not enough to result in competition, paper II). However, in winter, mouflon are subject to overlap with forest ungulates (roe deer and red deer, Redjadj 2010), and as individuals should be restricted to small refuge areas where vegetation is still available, the population density within food areas should increase and in turn, enhance inter- and intra-specific competition. However, this remain to be tested, as done in paper II, by comparing situations of sympatry and allopatry.

c) Why do species differ in their among-individual variability? An unsolved question

One of the questions that remained unsolved at the end of the paper I was the determination of the causes of the intra-specific variability and why the degree varied among species. Our results demonstrated that the niche variation hypothesis (NVH, Van Valen 1965) was supported at the intra- and inter-specific level: the wider the niche, the larger among-individual variation. Our hypothesis that sociality (SH) could drive inter-individual variability has been rejected. On the contrary, the most social species had the highest degree of among-individual variation and the largest population niche width. Sociality could actually be seen, not as favoring diet similarity due to the spatial overlap of individuals within a group, but as a driver of dissimilarity because of a stronger intra-specific competition within a social group (aggressiveness activity in large moose groups noticed in Molvar & Bowyer 1994) leading to stronger diet differentiation. Those results were in agreement with some experimental studies performed with fishes (Svanbäck and Bolnick 2007) for which inter-individual variation increased with population density. In contrast, solitary species such as roe deer should be less prone to intra-specific competition at the fine spatial scale, as each individuals should be able to feed on their preferred resources without pressure from congeners in their close vicinity. In addition, as roe deer are supposed to have a lower digestive plasticity than mouflon, we hypothesized that morpho-physiological characteristics could constrain the degree of among-individual variability.

Further analysis should be performed to go deeper in the understanding of the causes of individual specialization and why it varies among species. This would require a higher diversity of large herbivores, such as found in Africa, that would encounter no confounding effects between sociality, body size and feeding type (for example, different sociality levels for a single feeding type, Jarman 1974, Fritz and Loison 2006).

At the intra-specific level within a season, different factors such as sex, age, experience, social status, physiological requirements or preferences (Araùjo et al. 2011) can promote inter-individual variability. For example, status of individuals within a group could favor diet differences: subordinate individuals might be forced to feed on suboptimal resources (Araùjo et al. 2009). In addition, sex could partly explain among-individual variation, and the degree of among-individual variation could also vary between sexes (Nifong et al. 2015, Smith et al. 2015). Additional analysis with our data would be required to estimate the effect of sex on among-individual variation. Environmental factors could also be at play in the individual specialization. Indeed, fine-scale differences in the spatial distribution (patchiness) of resources (Durell 2000) could enhance among-individual variability.

Finally, in this work, a faeces was not associated to an individual and we were therefore not aware of its diet variation over several days or months. Even though a faeces is an approximation of an individual’s diet over several days (Castle 1956, Rayé et al. 2011), an individual diet is likely to be more diversified than the diet assessed from one of its faeces. Therefore, the other ideal exploration would be to set longitudinal study in order to follow individuals over long period of time, through the genetic identification of faeces, and study the intra-individual diet variation.

d) Linking taxonomic and functional β-diversity

Within a species, it has been demonstrated that domestic and wild individuals (sheep, goats, fallow deer) display different preferences for protein to energy ratio to meet their needs (Atwood et al. 2001), but also that they can respond differently to plant secondary compounds (Provenza et al. 2003, Bergvall 2009). Hence, individual differences in diet selection criteria could also be observed for chamois and mouflon as we noticed a relatively high among-individual variation at the taxonomic level. Our analysis on diet selection criteria (paper III) took into account all the individuals and not the mean diet of the population. However, the among-individual variability was not quantitatively measured. Even if our results showed significant effects of some plant traits on diet selection (leaf toughness and nitrogen content, paper III), we hypothesize that the absence of significant relationships for other traits could be related to (1) the absence of effect for all the individuals, or (2) a strong inter-individual variation hiding a general pattern at the species level. Additional analysis on functional β-diversity (Swenson et al. 2010, Meynard et al. 2011, Villéger et al. 2013) could give insights about the among-individual variation in diet functional niches. This could help to determine whether some individuals benefit from a higher resource quality intake over others. For example, a population can show a strong among-individual variation at the taxonomic level but a low among-individual variability at the functional level, suggesting that individuals avoid intra-specific competition by feeding on different plant species, but also avoid a differential nutrient intake among individuals by all feeding on high quality plants. On the contrary, a higher functional beta-diversity would suggest an imbalance in the nutrient access among individuals, and so, differences in development, growth and reproduction. This taxonomic and functional approach of the inter-individual diet variability should be helpful to understand the variation in fitness among individuals, and in turn the consequences on population dynamic.

e) Thoughts about the effects of increasing populations densities on among-individual variation, and how it could affect population dynamic

In addition to the emergence of functional ecology, the integration of intraspecific variability is a promising approach to understand the dynamic of communities (see the thesis introduction). Our results on ungulates (paper I) also confirmed that among-individual variability is the rule rather than the exception and that morpho-physiological constraints may not be as strong a previously thought as the three species (and even the roe deer sometimes classified as “obligate non-grazer” and expected to rely on few key resources, Abbas et al. 2011, 2013, Redjadj et al. 2014) exhibited digestive plasticity. Indeed, among-individual variability is a ubiquitous phenomenon in both vertebrate and invertebrate populations such as gasteropods, fish, amphibians or reptiles (Bolnick et al. 2007) which occurs within the food axis of the ecological niche.

As we are in a context of increasing population sizes in Europe (Milner et al. 2006, Maillard et al. 2010, IUCN red list: increasing trend for roe deer, red deer, isard and ibex/unknown trend for chamois and wild boar), we are particularly interested in how individuals would respond to increasing conspecific and allospecific densities. If population density increases, will individuals tend to be more specialized in order to reduce competition? Or will they tend to increase their niche breadth to include suboptimal resources as the preferred ones will decrease, and then enhance the homogenization of the population?

In the fig.39, we suggest different possible evolution of among-individual variation as a consequence of an increase in population density (due to a higher abundance of populations or aggregation of individuals in specific areas), through intra-specific competition (fig.39a,b) and inter-specific competition (fig.39c,d). These predictions are not exhaustive and we saw in the introduction that, in addition to the type of rank-preference variation in the focal species, many other factors can influence the direction of individual specialization, such as individual plasticity or resource availability (see section *2.2.d*, Araùjo et al. 2011). For these predictions (fig.39), we focused on cases where the preferred resources were decreasing. However, inter-specific competition could also decrease the abundance of suboptimal resources of the focal species. We hypothesized that it would slightly impact the position or niche width of focal individuals and species, and we did not explore it.

Because of the increase in ungulate population densities in Europe (Milner et al. 2006, Maillard et al. 2010, IUCN red list: increasing trend for roe deer, red deer, isard and ibex/unknown trend for chamois and wild boar), the availability of preferred resources may decrease. Hence intra- and inter-specific competition could be strengthened and in turn influence among-individual variation within competing species.

Even though the multiple outcomes of among-individual variation, we saw in the introduction that different studies on different organisms came to similar conclusions, i.e. the increase of (1) intra-specific competition induces among-individual variation through individuals using different subset of resources (Araùjo et al. 2008, Svanbäck et al. 2004, 2007, fig.40), (2) inter-specific competition reduces niche width though decrease variation in resource use (the inverse of ecological release) (Van Valen 1965, Knudsen et al. 2007, Costa et al. 2008, Bolnick et al. 2010, fig.40). In turn, changes in among-individual variation caused by the shift of some individuals on suboptimal resources would lead to decrease their diet quality. As the diet quality affects body condition (Prins 1996, WallisDeVries 1998, Stewart et al. 2005), it would in turn impact the survival, growth and reproduction of individuals (fitness) (Kie 2003, Cook et al. 2004, fig.40). Consequently, a feedback loop would decrease the density of populations (fig.40). This pattern would be in agreement with the phenomenon of density-dependence (Saether 1997, Coulson et al. 2000, Stewart et al. 2005, Bonenfant et al. 2009 and references therein) and inter-specific competition (Forsyth & Hickling 1998, Latham 1999, Richard et al. 2010, Lovari et al. 2014, Ferretti et al. 2015) regulating population densities in a predator-free environment.

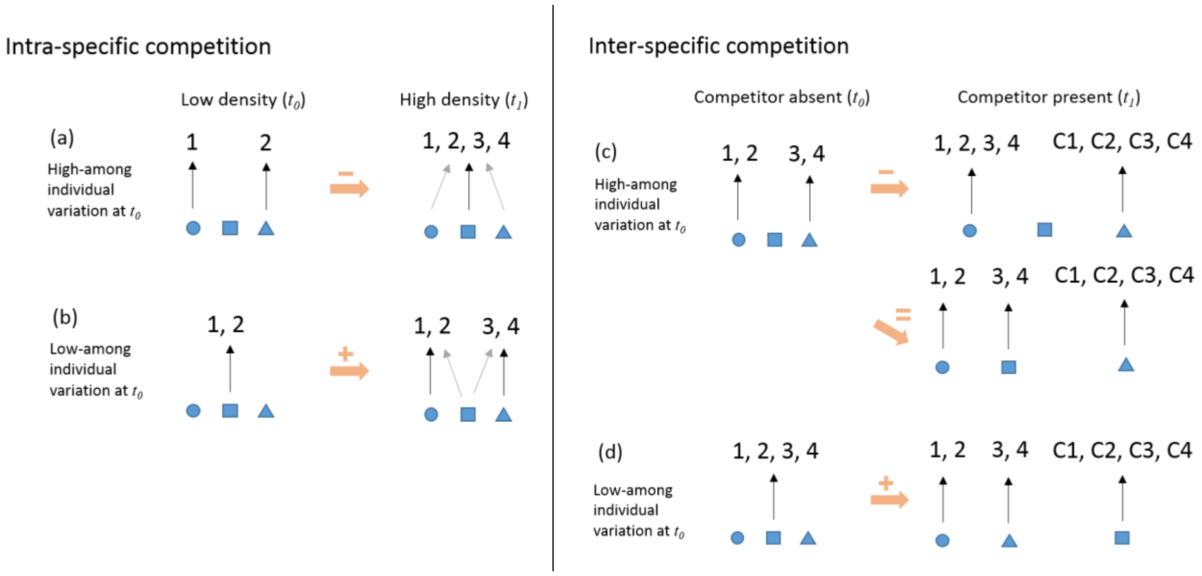


Figure 39. Inspired from Araùjo et al. 2011. Illustration of how intra- and inter-specific competition caused by an increase in population density can affect the among-individual variability of a focal species (represented by the individuals 1, 2, 3, 4). Arrows represent direct consumption of a resource by a consumer (arrows in grey represent consumption of suboptimal resources in low quantity). “Plus” or “Minus” indicate the sign of the effect on the degree of among-individual variation. (a) At low density, individuals differ in their rank-preference resources and therefore have different diets. At higher density reducing the preferred resources, all individuals converge to the same alternative resource and the degree of among-individual variability decreases. (b) At low density, individuals have the same preferred resources. At higher density, the preferred resource becomes scarce and individuals specialize on alternative resources, increasing the diet variation. (c) Competitor does not overlap with the focal species and individuals of the focal species have distinct preferred resources. Because of the increase in population density of the competitor, its niche width increases and overlaps with some individuals of the focal species, which enhances inter-specific competition. Individuals of the focal species are forced either (1) to converge to the same resources (circle) because the alternative resource (square) is of low quality or difficult to find, decreasing the degree of among-individual variability, or (2) individuals of the focal species impacted by competition shift on the alternative resource to avoid intra-specific competition. (d) Competitor does not overlap with the focal species and individuals of the focal species have the same preferred resources (low among-individual variation). Because of the increase in population density of the competitor, its niche width increases and overlaps with some individuals of the focal species, which enhances inter-specific competition. In order to avoid intra-specific competition, individuals of the focal species specialize on different alternative resources.

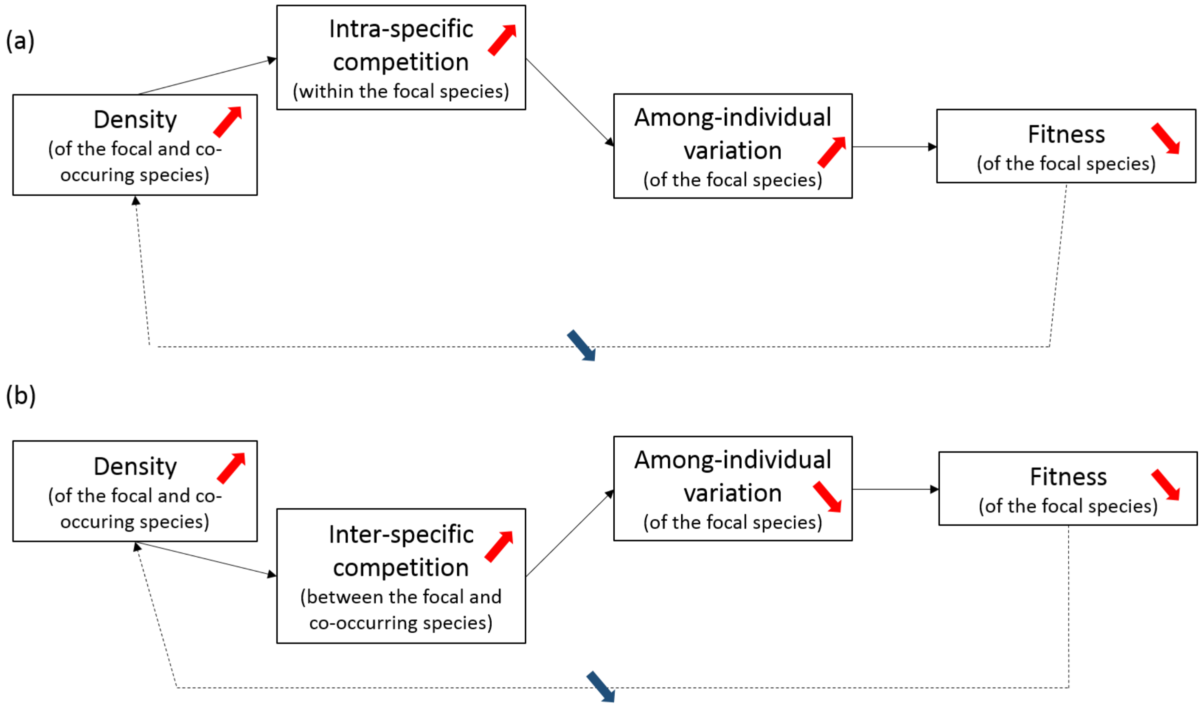


Figure 40. Hypothetical causal models about how density could influence among-individual variation and fitness of the focal species through intra- (a) and inter-specific competition (b).

How density affects among-individual variation is not well understood. Indeed, tracking the evolution of among-individual variation as a function of population density requires that long-term extensive and intensive faeces samplings, in addition to population censuses, be done for co-occurring species within a community (Nicholson et al. 2006). In addition, as habitat characteristics (vegetation composition and structure) can fluctuate in response to herbivory pressure or abiotic environmental changes (temperature, precipitation), it can lead to variable response of animals not only dependent on density (Kie et al. 2003).

Otherwise, we could investigate the effect of density on among-individual variation by comparing sites differing in their population densities. However, it would require that sites have the same carrying capacities in order that habitat quality would not confound the effect of density-dependence (Kie et al. 2003).

Studies trying to determine or predict how population density affects population dynamic, through density-dependence (Stewart et al. 2005, Bonenfant et al. 2009 and references therein) or inter-specific competition (Forsyth & Hickling 1998, Richard et al. 2010, Lovari et al. 2014, Ferretti et al. 2015), usually focus on a single impacted species. In order to predict how multiple populations would regulate by considering both intra- and inter-specific interactions, it would require to use a network-based approach of food webs including multiple species from a community (Montoya et al. 2006, Ings et al. 2009, Blüthgen et al. 2010). Indeed, the ecological network approach would be useful to better understand how large herbivores are structured according to food resources, but also how the diversity and density of ungulates and resources would affect the stability of the system (Thebault et al. 2005, 2010, Narwani & Mazumder

2012). We saw in this thesis that an individual-based approach could improve our understanding of community structuration. Therefore, downscaling the trophic interactions networks to the individual-level (Ings et al. 2009, Dupont et al. 2011, Tur et al. 2014, Dupont et al. 2014) would be necessary to explore the evolution of network stability in time in response to changes in ungulates population densities or in plant community composition and abundance.

7.3 Integrating functional interactions between large herbivores and plant communities into species distribution models

In the face of global change, species distributions models seek to develop quantitative models able to predict to which extent a species can adapt in the future (Thuiller et al. 2013, Wisz et al. 2013). However, these models lack the incorporation of biotic interactions between species (such as competition, predation or facilitation) that vary in time and space (Poisot et al. 2012) and that influence species distribution patterns (Guisan & Thuiller 2005, Van der Putten et al. 2010, Thuiller et al. 2013, Wisz et al. 2013). Hence, combining trophic network and species distribution models could be particularly relevant to predict spatial and temporal variation in community composition (Pellissier et al. 2013).

In the following paragraphs, we intend to show how our results on functional interactions between large herbivores and plant communities could be used in species distribution models.

Given our results, species distribution models could concern large herbivores or plant communities. However, as they are linked through trophic interactions, they can mutually affect themselves through feedback loops, which make models complicated. In the first case where plant species limit the herbivores distribution, we will assume that the fluctuations of the vegetation composition and relative abundance depends on other factors than herbivore selection, such as climate and land use change. In the second case where herbivores limit plant species, we will assume that the herbivory pressure is constant on the same functional traits and is not influenced by the vegetation changes.

a) Plant species can limit the herbivores distribution

As large herbivores have to cope with changing environment where available food resources fluctuate in terms of composition and relative abundance, predicting if an ungulate population could persist in such a fluctuating environment could be useful for conservation program or population management.

In this thesis, we showed that ungulate diet selection is partly dependent on plant functional trait such as leaf toughness and leaf nitrogen content, suggesting that functional traits of food plants can determine the distribution of herbivores. Indeed, if the diet selection criteria of herbivores are known in terms of plant functional traits, it should then be possible to ignore local species composition and predict the diet of large herbivores in new environment from the knowledge of plant functional traits and herbivore preferences. Even though we are aware that ungulate population dynamics are not only driven by bottom-up controls (food resources) but also by top-down or transversal effects, the knowledge of their diet quality within a changing environment could partly help to predict their persistence.

However, this approach would require information on both the traits and the relative proportion and distribution of plant species in the studied landscape and their evolution in time, in order to determine precise functional vegetation maps. Moreover, knowledge about the physiological limits of ungulates, such as the lower boundary of energetic needs required to survive and reproduce or how they respond to temperature increase (Marchand et al. 2015), should be assessed to model their spatial distribution response to environmental changes (Thuiller et al. 2013).

Finally, in order to be confident with our results on diet selection criteria and determine if they can be generalized and used for other field of studies such as species distribution modelling, additional studies in other areas differing in their plant species composition should be first conducted.

b) Herbivores can limit plant species distribution

Climate and land use change (intensification or abandonment of domestic grazing) are two drivers expected to strongly influence the vegetation in temperate ecosystems (Boulangeat et al. 2014). Their simultaneous impacts on biodiversity at regional scales in the Ecrins National Park have been tested (Boulangeat et al. 2014). We could hypothesize that large wild herbivores could also mitigate or emphasize the previous effects. Indeed, as densities of wild large herbivores are increasing in different regions of the world over recent decades (Côté et al. 2004, Milner et al. 2006, Maillard et al. 2010, IUCN red list), they can have significant impact on vegetation and on above- and below-ground communities, leading to conservation issues (Rooney 2001, Mysterud 2006). Hence, a new approach taking into account the triple-effect of climate, land use and wild herbivores could be investigated to predict more specifically the dynamic of vegetal communities. The model could take into account the functional and taxonomic preferences of herbivores, their habitat selection and their intensity of resource use.

In 1983, in the end of the first chapter of his book “Wildlife feeding and nutrition”, Robbins said that “the application of much of the wildlife nutrition data to field management is both an art and a science because of the lack of adequate knowledge of many control mechanisms determining the outcome of any manipulation”. Finally, he concluded that many challenges need to be met, especially the questions about competition, winter feeding of wildlife, diet formulation, effects of habitat manipulation, predator-prey interactions, etc. Forty-two years later, I feel more optimistic, about the reliability of data we are now obtaining about wildlife feeding ecology that can be useful for managers. The literature cited and the work realized here show that progress has been made when it comes to understand how species and individuals interact, how animals feed during periods of low resource availability, what are the factors implied in the diet choices but also to improve the methodology and have access of more precise diet data (DNA-metabarcoding). A large part of the amazing databases used in this thesis remain to be explored (e.g. diets from forest environment, inflorescence trait measurements, food selection ratios) and should bring additional cues for the understanding of ecosystem functioning.

I finally hope that I convinced you that both taxonomic and functional approaches, and among-individual and interspecific interactions studies, can bring complementary visions highly valuable for our understanding of ecological processes, and that some of our results can be relevant for conservation and management practices.

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ABBREVIATIONS

ANPP. Aboveground net primary productivity
BIC. Between individual component
BSC. Biological species concept
C. Carbon
CP. Crude protein
CWM. Community weighted mean
DM. Dry matter
DN. Dietary nitrogen
DNA. Desoxyribonucleic acid
FD. Functional diversity
FM. Fresh matter
FN. Fecal nitrogen
GPS. Global positioning system
LDMC. Leaf dry matter content
LNC. Leaf nitrogen content
LPT. Leaf punch toughness
LCC. Leaf carbon content
LT. Leaf thickness
MCP. Minimum convex polygon
N. Nitrogen
NIRS. Near-infrared spectroscopy
NSCA. Non-symmetric correspondence analysis
NVH. Niche variation hypothesis
OFT. Optimal foraging theory
P. Phosphorus
PCA. Principal component analysis
PCR. Polymerase chain reaction
PDMC. Petiole dry matter content
PSC. Phylogenetic species concept
RMSEC. Root mean standard error of calibration
RMSEP. Root mean standard error of the prediction
SH. Sociality hypothesis
SLA. Specific leaf area
TDMC. Twig dry matter content
TNW. Total niche width
WIC. Within individual component

LIST OF APPENDICES

Appendix 1 – Table A1. Mean frequency of sequences (FS, %) and mean frequency of occurrence (FO, %) over the year of plants found in the faeces of chamois, mouflon and roe deer in the Bauges Game and Wildlife Reserve. Numbers in bold have a frequency higher than 5%.

Appendix 2 – Table A2. List of plant species used for functional trait measurements. The associated frequences correspond to the relative proportion of the plant in the Armenaz and Charbonnet pastures. The total line gives the number of plant species sampled per season and the sum of the frequencies for each pasture.

Appendix 3 – Figure A1. Rarefaction curves* for the three species (chamois, roe deer and mouflon) and the four seasons (spring, summer, autumn and winter).

Appendix 4 – Figure A2. Map of vegetal communities in the Armene pasture.

Appendix 1 – Table A1. Mean frequency of sequences (FS, %) and mean frequency of occurrence (FO, %) over the year of plants found in the faeces of chamois, mouflon and roe deer in the Bauges Game and Wildlife Reserve. Numbers in bold have a frequency higher than 5%.

	Chamois (FS, %)	Chamois (FO, %)	Mouflon (FS, %)	Mouflon (FO, %)	Roe deer (FS, %)	Roe deer (FO, %)
Abies alba	0,29	1,97	**6,74**	**14,63**	2,89	**10,38**
Acer	0,35	3,64	0,90	**11,71**	0,42	3,77
Alchemilla alpina	0,99	**12,90**	0,54	**7,32**	0,50	**6,60**
Alnus viridis	1,15	**9,56**	1,44	**11,22**	1,37	**7,55**
Alopecurinae	0,01	0,30	0,00	0,00	0,00	0,00
Anthriscus cerefolium	0,01	0,30	0,00	0,00	0,00	0,00
Anthyllis vulneraria	0,57	**8,65**	0,25	3,90	0,01	0,47
Apiaceae	1,30	**12,14**	3,78	**24,88**	0,58	**6,13**
Arabis alpina	0,00	0,15	0,00	0,00	0,00	0,00
Arctostaphylos uva-ursi	0,28	3,79	0,00	0,00	0,00	0,00
Aruncus dioicus	1,31	**6,22**	0,00	0,00	0,96	**12,74**
Asteraceae	2,57	**27,77**	0,40	**6,83**	1,69	**17,45**
Asterales	0,02	0,46	0,00	0,00	0,00	0,00
Astrantia	0,14	2,58	0,05	0,98	0,00	0,00
Athyrium vidalii	0,14	0,30	0,00	0,00	0,00	0,00
Avenella flexuosa	0,02	0,46	0,00	0,00	0,00	0,00
Betula pendula	0,02	0,46	0,22	2,93	0,00	0,00
Betulaceae	0,28	3,03	4,06	**19,02**	1,80	**12,26**
Bistorta vivipara	0,53	**7,59**	0,06	1,95	0,00	0,00
Brassicaceae	0,00	0,00	0,04	0,49	0,00	0,00
Calamagrostis varia	0,00	0,00	0,02	0,49	0,00	0,00
Campanula	0,01	0,15	0,04	0,98	0,10	0,94
Campanulaceae	0,06	1,37	0,00	0,00	0,00	0,00
Cardamine pentaphyllos	0,00	0,00	0,03	0,49	0,00	0,00
Carduinae	0,03	0,46	0,03	0,49	0,24	1,42

Chaerophyllum hirsutum	0,12	0,91	0,03	0,98	0,03	0,47
Chamerion angustifolium	1,91	**9,26**	0,81	**9,27**	0,96	**9,43**
Clinopodium vulgare	0,01	0,15	0,00	0,00	0,00	0,00
Cornus sanguinea	0,00	0,00	0,07	0,49	0,39	3,77
Coronilla vaginalis	0,00	0,00	0,02	0,49	0,00	0,00
Dactylis glomerata	0,05	0,76	0,90	**13,66**	0,00	0,00
Deschampsia cespitosa	0,00	0,00	0,01	0,49	0,00	0,00
Dryas octopetala	0,04	0,76	0,00	0,00	0,00	0,00
Dryopteridaceae	0,00	0,00	0,40	4,39	0,00	0,00
Epilobium montanum	0,06	0,91	0,00	0,00	0,19	3,77
Equisetum	0,14	0,91	0,02	0,49	0,49	2,36
Euphorbia	0,07	0,91	0,61	3,90	0,02	0,47
Fagus sylvatica	0,04	0,76	0,09	0,98	0,03	0,47
Festuca	0,08	1,67	0,11	1,46	0,08	0,47
Filipendula ulmaria	0,87	3,79	0,26	1,46	4,04	**14,15**
Fraxinus excelsior	0,14	0,76	0,28	2,44	1,40	**10,38**
Galium	0,10	1,97	0,23	2,93	0,22	4,25
Gentiana	0,01	0,15	2,08	**12,68**	0,01	0,47
Geranium robertianum	0,06	1,06	0,05	0,98	0,10	1,89
Geranium sylvaticum	**5,34**	**33,84**	0,73	**8,78**	1,42	**12,26**
Geum	0,16	3,19	0,04	0,49	0,93	4,72
Globularia nudicaulis	2,45	**21,24**	0,44	**5,85**	0,20	1,89
Hedera helix	0,00	0,00	0,02	0,49	0,00	0,00
Hedysarum hedysaroides	0,93	**5,01**	0,00	0,00	0,00	0,00
Helianthemum nummularium	**27,34**	**63,58**	4,88	**27,32**	5,83	**11,32**
Hippocrepis emerus	0,00	0,00	0,00	0,00	0,11	0,47
Hordelymus europaeus	0,24	2,28	0,30	2,44	0,00	0,00
Hypericum	0,94	**11,68**	0,09	1,95	0,00	0,00
Juniperus	1,78	**9,41**	0,04	0,49	0,10	0,47

Knautia	0,09	1,37	0,08	1,46	0,00	0,00
Larix decidua	0,07	0,91	0,04	0,98	0,10	1,89
Lathyrus	0,03	0,61	0,00	0,00	0,51	4,72
Lathyrus pratensis	0,80	**7,74**	2,57	**17,56**	0,08	2,36
Leontodon hispidus	0,62	**9,71**	0,12	1,95	0,00	0,00
Linaria alpina	0,00	0,00	0,02	0,49	0,00	0,00
Lonicera	0,01	0,30	0,12	1,95	0,15	1,42
Lotus corniculatus	**7,62**	**54,02**	2,49	**28,29**	1,00	**10,38**
Luzula sylvatica	0,04	0,46	0,00	0,00	0,01	0,47
Lysimachia	0,17	2,58	0,02	0,49	0,09	2,36
Melica uniflora	0,05	0,30	0,00	0,00	0,00	0,00
Mentheae	0,13	2,73	0,04	0,98	0,00	0,00
Monolepis asiatica	0,00	0,00	1,95	**12,68**	0,00	0,00
Onagraceae	0,05	0,91	0,04	0,49	0,03	0,47
Onobrychis montana	**8,78**	**36,72**	**24,02**	**53,17**	3,71	**8,96**
Ononis natrix	0,01	0,15	0,00	0,00	0,00	0,00
Oxalis	0,00	0,00	0,00	0,00	0,04	0,94
Phyteuma spicatum	0,05	0,91	0,00	0,00	0,39	**6,60**
Picea abies	0,44	3,95	1,25	**10,73**	0,00	0,00
Pinus sylvestris	0,07	0,46	0,15	1,95	0,00	0,00
Plantago	0,04	0,91	0,00	0,00	0,00	0,00
Plantago alpina	0,10	1,52	0,00	0,00	0,00	0,00
Polygonatum verticillatum	0,00	0,15	0,00	0,00	0,01	0,47
Potentilla	0,03	0,76	0,00	0,00	0,00	0,00
Primula	0,00	0,00	0,05	1,46	0,00	0,00
Primulaceae	0,00	0,00	0,04	0,98	0,00	0,00
Prunella	0,01	0,30	0,00	0,00	0,00	0,00
Prunus	0,00	0,00	0,00	0,00	0,08	1,42
Pulsatilla alpina	0,06	1,06	0,17	2,44	0,00	0,00

Pyreae	1,29	**12,14**	0,61	**7,80**	1,15	**14,62**
Ranunculus	0,04	0,76	0,00	0,00	0,40	4,72
Ranunculus tuberosus	0,21	3,64	0,14	2,93	0,23	2,83
Rhamnus alaternus	0,00	0,00	0,02	0,49	0,00	0,00
Rhinanthus alectorolophus	0,04	0,76	0,00	0,00	0,53	3,77
Rhododendron ferrugineum	0,06	1,37	1,08	**8,29**	0,03	0,47
Rosodae	**16,97**	**47,80**	**24,18**	**63,41**	**53,46**	**92,45**
Rosularia alpestris	0,04	0,61	0,03	0,49	0,00	0,00
Rubiaceae	0,01	0,15	0,00	0,00	0,01	0,47
Rumex	3,40	**23,37**	3,64	**20,49**	5,78	**27,36**
Salix	0,77	**7,13**	0,84	**8,29**	0,46	**6,60**
Sambucus	0,19	0,46	0,16	2,44	0,82	**10,85**
Sanguisorba minor	0,13	2,12	0,43	4,88	0,73	**6,60**
Saxifraga aizoides	0,00	0,00	0,16	0,49	0,00	0,00
Saxifraga oppositifolia	0,06	1,21	0,14	0,49	0,00	0,00
Saxifraga paniculata	0,00	0,15	0,00	0,00	0,00	0,00
Saxifraga rotundifolia	0,20	2,43	0,03	0,49	0,43	4,25
Sedum	0,02	0,30	0,09	0,98	0,00	0,00
Sempervivum tectorum	0,01	0,30	0,12	1,95	0,00	0,00
Silene latifolia	0,03	0,46	0,00	0,00	0,09	0,47
Silene vulgaris	0,39	3,79	0,67	4,39	0,49	2,36
Solanoideae	0,00	0,00	0,00	0,00	0,11	0,47
Succisa pratensis	0,00	0,00	0,00	0,00	0,02	0,47
Tilia	0,00	0,00	0,00	0,00	0,10	1,42
Trifolium	0,08	1,82	0,00	0,00	0,09	1,42
Trifolium badium	0,01	0,30	0,00	0,00	0,02	0,47
Trollius europaeus	0,00	0,00	0,02	0,49	0,00	0,00
Ulmus glabra	0,00	0,00	2,16	**9,27**	0,34	2,83
Urtica dioica	0,01	0,30	0,79	**5,37**	0,02	0,47

Vaccinium myrtillus	1,65	**11,23**	0,16	2,44	1,01	**6,13**
Vaccinium uliginosum	1,98	**7,89**	0,06	0,98	0,00	0,00
Valeriana	0,15	1,97	0,00	0,00	0,00	0,00
Veronica	0,00	0,00	0,00	0,00	0,10	2,36
Veronica beccabunga	0,00	0,15	0,00	0,00	0,00	0,00
Veronica montana	0,00	0,00	0,00	0,00	0,01	0,47
Viburnum lantana	0,01	0,15	0,20	3,90	0,02	0,47
Vicia cracca	0,00	0,00	0,00	0,00	0,04	0,94
Viola	0,00	0,15	0,00	0,00	0,19	2,83

Appendix 2 – Table A2. List of plant species used for functional trait measurements. The associated frequences correspond to the relative proportion of the plant in the Armenaz and Charbonnet pastures. The total line gives the number of plant species sampled per season and the sum of the frequencies for each pasture.

	June	July	September	Armenaz	Charbonnet
Abies alba	x	x	x	0,00	0,01
Acer pseudoplatanus	x		x	0,00	0,28
Alchemilla alpina	x	x	x	0,50	0,15
Alchemilla vulgaris	x	x	x	0,68	0,24
Alnus viridis	x	x	x	1,87	0,11
Anthyllis vulneraria		x	x	0,03	0,09
Arctostaphylos uva-ursi	x	x	x	0,02	0,00
Arnica montana	x	x	x	0,00	0,00
Aruncus dioicus	x	x		0,00	0,00
Astrantia major		x	x	0,58	0,00
Bistorta vivipara (Polygonum viviparum)		x		0,00	0,00
Campanula rotundifolia	x			0,01	0,57
Cardamine pentaphyllos	x			0,00	0,00
Carduus defloratus	x	x	x	1,56	1,09
Carex sempervirens	x	x	x	32,32	27,53
Centaurea uniflora			x	0,06	0,00
Chaerophyllum hirsutum	x	x	x	1,11	0,13
Crocus vernus	x			0,00	0,00
Dactylis glomerata	x	x	x	1,78	8,31
Deschampsia cespitosa	x	x	x	4,14	3,00
Epilobium angustifolium	x	x	x	0,00	0,00
Fagus sylvatica	x		x	0,00	0,00
Festuca ovina	x	x	x	0,59	2,40
Festuca rubra	x	x	x	8,14	5,41
Filipendula ulmaria	x	x		0,00	0,00
Fragaria vesca	x	x		0,00	0,00
Fraxinus excelsior			x	0,00	0,00
Galium odoratum	x	x	x	0,19	0,19
Gentiana purpurea	x	x	x	3,58	1,72
Geranium sylvaticum	x	x	x	1,10	1,02
Geum montanum			x	0,01	0,00
Globularia nudicaulis	x	x	x	0,30	0,27
Hedera helix	x			0,00	0,00
Helianthemum nummularium	x	x	x	0,71	0,87
Heracleum sphondylium	x	x	x	1,56	5,62
Hieracium murorum		x	x	0,02	0,33
Hordelymus europaeus	x	x	x	0,00	0,00
Hypericum richerii	x	x	x	0,19	0,11
Juniperus communis	x		x	1,01	0,11
Knautia arvense	x	x		0,10	0,32

Laserpitium latifolium	x	x	x	1,56	5,62
Lathyrus pratensis		x	x	0,02	0,02
Leontodon hispidus			x	0,08	0,00
Lonicera xylosteum	x	x	x	0,00	0,00
Lotus corniculatus	x	x	x	0,02	0,02
Luzula sylvatica	x			0,14	0,16
Melica uniflora	x			0,00	0,00
Mercurialis perennis	x		x	0,00	0,04
Nardus stricta	x	x	x	6,82	0,29
Onobrychis montana	x	x	x	0,00	0,08
Origanum vulgare			x	0,00	0,00
Phyteuma spicatum	x	x		0,00	0,00
Picea abies	x	x		0,00	0,00
Plantago atrata		x	x	0,02	0,03
Polygala chamaebuxus	x			0,00	0,00
Potentilla erecta			x	0,11	0,03
Pulsatilla alpina	x	x	x	1,51	1,24
Ranunculus tuberosus	x	x	x	0,21	0,20
Rhinanthus alectorolaphus		x		0,00	0,06
Rhododendron ferrugineum	x	x	x	1,03	0,38
Rosa montana	x	x	x	0,04	0,00
Rubus fruticosus	x	x	x	0,04	0,02
Rumex alpinus	x	x	x	0,37	0,08
Rumex arifolius	x	x		0,37	0,08
Salix		x		0,03	0,00
Salvia pratensis			x	0,00	0,33
Sambucus nigra			x	0,00	0,00
Sanguisorba minor	x			0,00	0,00
Saxifraga rotundifolia	x	x		0,06	0,00
Sempervivum tectorum	x	x		0,00	0,00
Serratula tinctoria		x	x	0,00	0,00
Sesleria caerulea	x	x	x	9,43	14,21
Silene dioica	x			0,38	0,32
Sorbus chamaemespilus	x			0,00	0,07
Taraxacum officinale	x			0,00	0,00
Thymus serpyllum	x	x	x	0,34	0,08
Trifolium badium		x		0,17	0,00
Trifolium pratense		x	x	0,17	0,00
Urtica dioica			x	0,17	0,35
Vaccinium myrtillus	x	x	x	1,23	0,25
Vaccinium uliginosum	x	x	x	2,66	0,02
Vaccinium vitis-idaea	x		x	0,82	0,02
Valeriana montana	x	x	x	1,82	1,03
Veratrum album	x	x		0,28	0,61
Total	64	59	59	92,11	85,56

Appendix 3

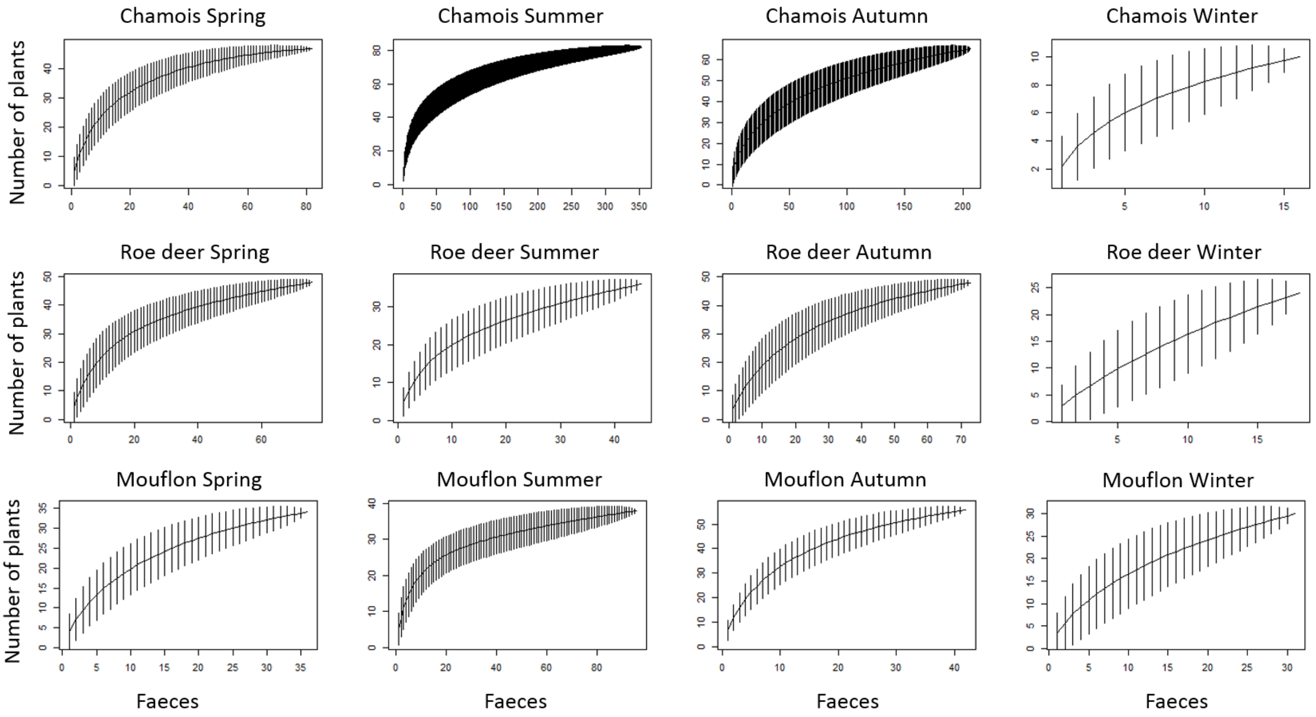

Figure A1. Rarefaction curves* for the three species (chamois, roe deer and mouflon) and the four seasons (spring, summer, autumn and winter).

*For each species and season, rarefaction curves are obtained by sub-sampling different subset of faeces samples with different sizes and by calculating the mean number of species found for each of the subset.

Appendix 4

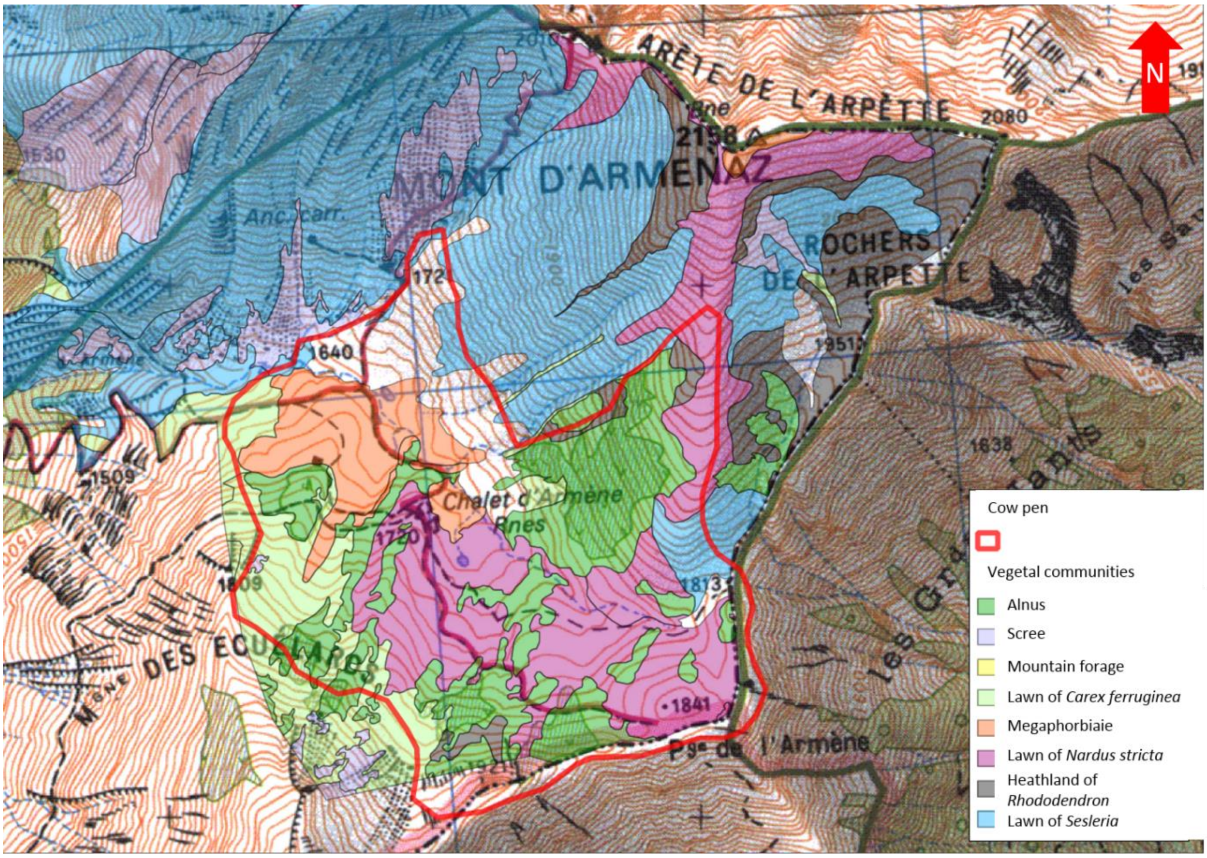

Figure A2. Map of vegetal communities in the Armene pasture.

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