

CLIMATE AND MANAGEMENT EFFECTS ON COMMUNITY DYNAMICS – DEVELOPING MULTISPECIES DEMOGRAPHY

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Summary of the DEMOCOM project:

What are the proximate mechanisms – at the individual level – underlying the assembly and dynamics of ecological communities? Despite its apparent universality, this question is still puzzling scientists – and challenges their methodological limits. **Global changes impact community diversity, structure and, but how these changes are rooted in individual dynamics remain poorly understood. Modeling the dynamics of ecological communities is difficult due to the complex dynamics of interacting species, and the need to integrate information across several biological levels (individuals – populations – communities). Yet, to shed lights on the processes underlying observed community modifications, knowing to what extent each species contribute to the direction and intensity of these modifications is of paramount relevance. For instance, following climate change or human disturbance, conservation and management implications are likely to be different if only two or three interacting species are responsible for an observed change in a community-based index. In the DEMOCOM project, we will develop an integrated statistical framework for estimation and inference about community dynamics via the development of a multispecies demography, bringing together concepts, predictions and tools from both fields of demography and community ecology. Demography aims at capturing variation in size, ages and ontogenic stages within a population. Although well developed for single-species dynamics, demography has received little attention in community ecology. We will develop a statistical framework to fit multispecies stage-structured models to data and partition the contribution of intra-specific and inter-specific demographic variations to changes in community composition (WP1). In particular, i) we will devise community sensitivity analyses to explore how small changes in the demographic rates of species and in the strength of interaction within and between species may affect the structure and resilience of communities, ii) we will extend our deterministic multispecies demographic models to incorporate stochasticity and fully account for environmental variability and iii) we will integrate mathematical structured multispecies models with statistical approaches to properly integrate the complexity of community dynamics and accommodate the various sources of uncertainty at play. Motivated by case studies on wild populations, we will investigate the role of inter-specific interactions in shaping the community-level response to climate change and management interventions in bird, fish and mammal communities (WP2). The data are owned and collected by the partners of the consortium. Besides, these case studies have been carefully selected to start working with relatively simple systems in which we**

have a few species and explicit interactions (seabirds and tunas), then to proceed with more complex systems in which we have more species with many possible interactions (common birds and large carnivores and their ungulate preys). Third, we will develop in concert with end-users an original, generic and user-friendly software (in the R statistical platform) to assist biologists in investigating communities' structure and dynamics through multispecies demography modeling (WP3). Overall, we will adopt a multidisciplinary approach in which important questions in community ecology will be addressed with robust and modern methods from demography, statistics and computing science.

Changes made relative to the previous versions of the pre-project:

1. We have paid a particular attention to make explicit the species interactions we will consider - see Fig. 2 and its application to the case studies in WP2;
2. We have considerably reduced the financial ANR envelope (by almost 10%) by i) cutting the number of internships and ii) requiring less experienced for our post-docs.
3. The dependence between WP1 (models) and WP2 (case studies) is to be expected in projects with original methodological developments. The main risk is some delay in completing the tasks in WP1, which may hamper achieving WP2 objectives; in such a situation, we will consider postponing the recruitment of the post-doc for WP2, and/or have him/her work preferentially on the simplest case studies (objectives 5 and 7 in that order). Note that the PI is used to manage these risks, as he did for a previous ANR-funded project that was successful (<https://goo.gl/EucNli>).
4. We will deal with incomplete data by combining several sources of information in a multispecies demography framework within the integrated community modeling framework that we will specially developed for sparse and heterogeneous data; this will be one of the main methodological outcomes of the project.
5. We now review the existing computer programs to model multispecies demography and demonstrate that a new tool is needed to integrate models and empirical data; we describe in more details the development of this tool, which will be key to this project to make the link between WP1 (statistical developments) and WP2 (case studies) and have the various partners working and experimenting together.

Changes made relative to the 2014 and 2015 projects: The main criticism on the 2014 project, besides the ones listed above, was that our project was too ambitious. We decided to abandon some of the original objectives and to refocus the project on multispecies demography and the link with empirical data (and inherent, associated sparseness and heterogeneity), which, we think, is the originality of our project and rests on the strongest skills of our consortium. Fair concerns were raised about the 2015 project. First, we did not make clear to which degree our approach differs from existing multi-species models. We agree. There is a body of theory and research on stage and size structured populations (in particular in marine communities) that we now appropriately refer to. Based on our assessment of this literature, it transpires that our proposal is original in the sense that it provides a unique statistical framework to fit multispecies models to actual data by combining sparse and heterogeneous sources of information, hence allowing testing the intensity and form of interactions and inferring community dynamics. Second, some reservations were made on data series to infer predictions in the light of global change. We agree that specifically our case study on plants was not as relevant as our bird and fish case studies. We have dropped this case study and replaced it by a mammal case study on the management of large carnivores and their ungulate preys in France for which we have i) > 20 years of data, ii) the involvement of stakeholders in the project via our new partner the French Hunting and Wildlife Agency (ONCFS) and iii) a long collaborative experience.

Qualification and contribution of each partner:

Partner	Name	First name	Position	Implication (man.month)	Role and responsibility
Partner 1: CEFE	Gimenez	Olivier	DR2	40.8	Scientific coordinator. In charge of WP1. Expertise in demographic modeling and capture-recapture analyses. Expertise in capture-recapture data analysis. Expertise in software development and capture-recapture analyses. In charge of WP3.
	Pradel	Roger	DR1	16.8	
	Choquet	Rémi	IR1	16.8	
Partner 2: CEBC	Barbraud	Christophe	CR1	12	Expertise in seabird population dynamics and capture-recapture analyses. Management and updating of databases / Extraction of capture-recapture data.
	Delord	Karine	IE2	4.3	
Partner 3: MARBEC	Chassot	Emmanuel	CR1	12	Expertise in fish population dynamics.
Partner 4: ISEM	Devictor	Vincent	CR1	12	Expertise in community ecology.
Partner 5: CESCO	Robert	Alexandre	MCF1	12	Expertise in demographic modeling.
	Dehorter	Olivier	IR2	8.2	Management and updating of databases / Extraction of capture-recapture data
	Le Viol	Isabelle	MCF1	8.2	
	Jiguet	Frédéric	PR2	8.2	Expertise in species distribution modeling.
Partner 6: MECADEV	Henry	Pierre-Yves	MCF1	12	Expertise in songbird population dynamics and capture-recapture analyses. In charge of WP2.
Partner 7: ONCFS	Marboutin	Eric	IR	12	Expertise in population dynamics.
	Duchamp	Christophe	IE	8	Expertise in large carnivores management
	Guinot-Ghestem	Murielle	IR	4	Expertise in large carnivores management

1. CONTEXT, POSITION AND OBJECTIVES OF THE PROPOSAL

1.1 Context, social and economic issues

Most human activities (e.g., industry, agriculture, fisheries, tourism) and their associated social and economic consequences rely on the use of natural resources and biodiversity through ecosystem services(1–3). However, facing the increasing human demand for natural resources(4, 5), a major stake is to reconcile human development and the conservation of biodiversity within a framework of sustainable use of natural resources (e.g.(6)). Quantifying the dynamics of populations and communities linked to the management of natural resources is an essential step to achieve this.

In spite of the widely recognized role of environmental changes on animal and plant populations, many aspects of species-environment responses remain poorly understood. Consequently, the management and conservation of wild populations rarely, if ever, accounts for the expected changes in environmental conditions. Climate change has become a driver of ecological changes of central importance from social, political and economic perspectives. The last publication from the IPCC suggests that temperature increase will be much higher than previously thought, potentially affecting not only species but also generating major social modifications to cope with those changes(7). Ecological science is at the forefront of this important challenge as it can provide policy makers and societies with concrete tools to describe the causes and consequences of climate change on natural systems and the associated uncertainties. Besides climate change, land use changes and harvesting of natural resources have considerably altered ecosystems and their functioning(8). For example, removal of large predators has potential consequences on food webs and ecosystem functioning, and therefore on human activities directly dependent on a healthy functioning of these ecosystems.

To date, however, the ecological sciences have described potential consequences of climate change and harvest pressures on species and communities through patterns mainly, while if we are to focus on the mechanisms to forecast these consequences, an ambitious integrated framework explicitly incorporating multispecies responses remains to be developed.

In this context, the DEMOCOM project will have several social and economic impacts. First, the developed framework will be relevant for species of commercial interest such as tunas or birds in agro-ecosystems, and will address pressing societal demand like the debate on the conflicts between large carnivores and human activities. Second, we will set up a new platform of data analysis via multispecies demographic models that will be useful for large scale bird and large carnivores monitoring programs running in France but also in other European countries. The bird programs in particular are already used to build biodiversity indicators of climate changes at national and international levels(9). However, the species-specific contributions to the observed changes in the communities' dynamics are ignored and uncertainties associated with these changes not fully acknowledged and dealt with, an issue to which the DEMOCOM consortium will devote a substantial amount of its research effort.

1.2 Position of the project

Our project is in line with the Défi 1 'Gestion sobre des ressources et adaptation au changement climatique' and in particular Axis 1 'Connaissances fondamentales', theme 'Evolution et dynamique des espèces et des populations' of the call for proposal. Indeed, we will investigate the dynamics of communities of birds, fishes and mammals, with an emphasis on the role of interactions in shaping the response of multispecies assemblages to climatic change and management interventions. To do so, we will develop a statistical framework to study the demography of interacting species and to combine heterogeneous and sparse information on stage-structured populations. The adoption of our new, integrative analytical procedure by biologists will be ensured by i) the development of a user-friendly computer package and ii) a close collaboration between model developers, empirical data and people involved in community monitoring in the field.

Our project falls into the category of 'projet de recherche collaborative' since i) we will focus on fundamental research, ii) our consortium is made of community and population ecologists, statisticians and computer scientists from 7 different labs who will collaborate and share their complementary skills and

access to unique, large, long-term multi-specific datasets, to develop a multispecies demography framework. People directly involved in the monitoring of real communities are also involved. The expected results would not be achievable by methodologists in isolation (lack of biological relevance) or by biologists alone (lack of a methodological framework). Overall, we will adopt a multidisciplinary approach in which important questions in community ecology will be addressed with robust and modern methods from the fields of demography, statistics and computing science.

At the national level, this project will nicely fit in the Research Group on Statistical Ecology (GdR EcoStat; <https://sites.google.com/site/gdrecostat/>) recently created by O. Gimenez, which gathers more than 300 statisticians and biologists (including a third of PhD students and post-docs) from 80 teams in 50 labs from all over France. In particular, DEMOCOM will feed the discussions of 4 out of the 10 themes identified by the group: citizen science, community ecology, management of renewable resources and demography. Regarding the later, Hal Caswell (author of the book 'Matrix Population Models', a reference in the field) has recently joined the group with one of his PhD students (Charlotte de Vries) and will obviously be associated to the discussions on multispecies demography.

Besides, at the European level, we will have frequent discussions with the National Center for Statistical Ecology in the UK which develops similar research and with which the consortium has long standing collaborations(10–14).

1.3 State of the art

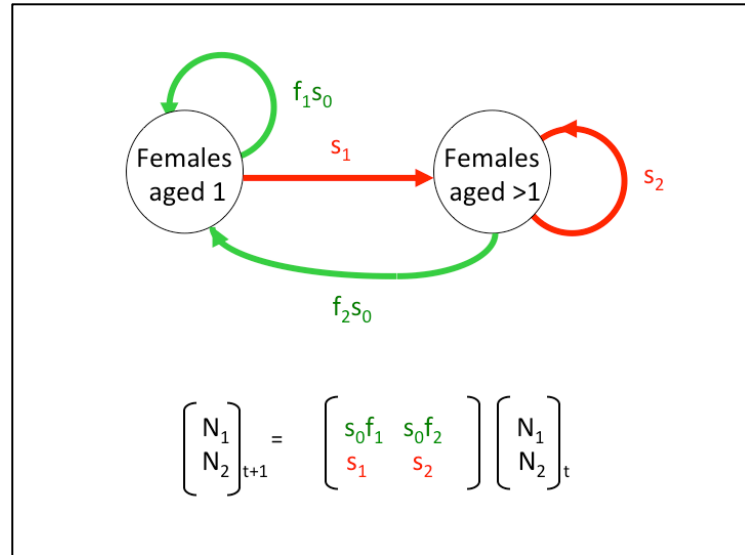
Modeling the dynamics of ecological communities is difficult due to the complex dynamics of interacting species(15). To shed lights on the processes underlying observed community change, knowing how much each individual species contribute to the change and the direction and magnitude of these contributions is of paramount relevance. For instance, following climate change or human disturbance, conservation and management implications would be very different if only two or three focal species are responsible for an observed change in a community-based index. Further, assessing the contributions for meaningful functional groups (e.g. protected vs unprotected, competitive or not, exotic or resident) might be of interest to test ecological predictions or to improve conservation and management plans.

The difficulty to link community changes with individual species dynamics has contributed to divide empirical and conceptual studies in two branches. On the one hand, community-level approaches focus on describing spatial and temporal trends in diversity and composition in space and time. In this case, species richness or diversity indices are often used as integrative descriptors of the community(16). Following environmental changes, community structure and composition are expected to be modified following the relative importance of species interactions and neutral processes(17). But how these processes can be anticipated from the combination of multiple individual population dynamics is not clear. On the other hand, species-level approaches focus on how individual species occurrences or abundances are distributed along environmental gradients. Following disturbance, species' abundances and distributions are expected to be modified according to the position and breadth of the species' niche. For instance, climate change is expected to trigger range shifts of individual species according to their temperature preference(18). But studying species-by-species responses to environmental changes may miss the role played by species interactions on those responses, and do not provide emerging patterns of interest for community ecology.

Overall, while these two levels of study (populations and communities) have independently contributed to better describe biodiversity responses to environmental changes, it remains difficult to link population and community-level dynamics(19). To fully apprehend the community-level consequences of inter-specific interactions, we need to think inside the species box(20). This is actually the core of demography which aims at capturing the variation in size, ages and ontogenic stages ('stages' hereafter) within a population(21). Although well developed for single-species dynamics, demography has received little attention in community ecology despite its large potential to elucidate the role of population stage structure in shaping biodiversity and driving its dynamics. Classical multi-species models based on differential equations have been proposed(22) and extended(23). However these approaches most often ignore the contribution of individual species to community dynamics and focus on the conditions for species' coexistence, or the specific role of competition and dispersal. Moreover, these theoretical models have hardly been supported by real empirical data.

Building demographic models - A variety of models have been proposed to assess single-species population dynamics through available information on demography(21). For birds and mammals, age-structured models are often used (Leslie matrix; Fig. 1). For plants and fishes, stage-structured models are commonly used (Lefkovich matrix). Integral projection models extend age- and stage-structured matrix models to continuous size variables to define a population model, know as integral projection models(24).

Figure 1: Demographic model for a short-lived (bird) population. Two representations are given, the life cycle (top) and the matrix formulation (below). We assume that the dynamics of this bird population (say a barn swallow *Hirundo rustica*) can be adequately represented by a model using two age classes (1st Year and After 1st Year) with respective abundances denoted as N_1 and N_2 , and the following vital parameters: f_1 - number of females fledged per female aged 1, f_2 - number of females fledged per female aged 2 or more, s_0 - survival from fledging until the following spring, s_1 - annual probability of survival from age 1 to 2 and s_2 - annual probability of survival for older birds. This model can be extended to several species (see text for details).



From these models, several precious indicators of the population viability can be derived. For example, the population growth rate generally denoted λ , corresponds to the dominant eigenvalue of the matrix and provides an assessment of the demographic regime of the population, with $\lambda = 1$ when the population is stable, $\lambda < 1$ when the population is decreasing, and $\lambda > 1$ when the population is increasing. To identify which demographic parameters drive population dynamics, perturbation analyses(21) are often used. Among them, elasticity analyses are often performed to measure the proportional changes of population growth resulting from small proportional changes in the demographic parameters. Demographic analyses can be performed either in a deterministic or in a stochastic context. In deterministic models, demographic parameters (i.e. reproductive and survival rates) are assumed to be constant through time. The matrix population model thus brings together mean demographic parameters. In variable environments, demographic parameters are allowed to fluctuate from year to year and year-dependent matrices are thus built. Demographic models have important applications in population conservation and management, and to assess the impact of climate forcing on vertebrate demography.

The DEMOCOM consortium has had a large contribution in demography, with among other examples, the use of elasticity analyses(25), the study of the sustainability of harvest management(26–28) and the evaluation of the impact of climate change on population dynamics(29, 30).

Single-species models have been extended to several species, both in unstructured(31, 32) or structured communities(33), but their integration in combination with field remains very constrained, therefore limiting our understanding of the structure and dynamics of communities. To our knowledge, the only attempt to do so is in marine ecology under the influence of De Roos and his co-workers(33, 34). However, their approach is based on complex mathematical tools and does not benefit from any software implementation, which might explain why it has little percolated into the community of ecologists. In DEMOCOM, our main objective is to develop a statistical framework to combine mathematical multispecies demographic models and time series of data for inference about communities.

Estimating demographic parameters - To calibrate demographic models, one needs to estimate demographic parameters. While the time to event is known in medical, social or engineering sciences (death, marriage and failure respectively), models for estimating wild animal and plant demography must incorporate nuisance parameters to account for incomplete detectability in monitoring individuals(35, 36). Because they circumvent the practical impossibility of an exhaustive monitoring inherent to studies in natural conditions, capture-recapture models have had an important impact on research in population biology by allowing the estimation of most of the demographic parameters (survival, reproduction, dispersal). Besides, capture-

recapture models allow the estimation of environmental effects like temperature or rainfall as well as individual effects such as gender, age, social status with potential interactions among them.

Recently, members of the DEMOCOM consortium have proposed a new formulation of capture-recapture models that distinguishes the underlying demographic process, e.g. survival, from its observation, i.e. detectability (state-space models(37) and hidden-Markov models(38)). This distinction allows modeling data while accounting for possible uncertainty in the assignation of a state to an individual (e.g., a breeding or an epidemiological state; review in(39)). These models have been implemented in a software application called E-SURGE(40)). Without pretending to be exhaustive, the DEMOCOM consortium has been in the front line of capture-recapture models applications, in particular for the evaluation of the impact of climate on demography(29, 41–44) the contribution to the conservation of endangered species(45–48), and the production of guidelines for better management of exploited animal species(49–51). Members of the DEMOCOM consortium have contributed much to the extension of single-species capture-recapture models to multispecies models, either by making the (strong) assumption of exchangeability (i.e. any species in the community could have taken the place of any other species in the observed sample)(52) or by accounting for phylogenetic relationships(53). However, explicitly integrating parameters for the strength of interactions between species in capture-recapture models remains to be done (cf. Fig. 2).

An integrated demographic framework - Until recently, the two steps above were accomplished in sequence, most often by ignoring uncertainty associated with the estimation of demographic parameters. Integrated population models have been recently developed to infer population demography by making an optimal use of all available sources of information (review in(54)). In their simplest form, these models combine population counts and demographic data into a single analysis, which allows the estimation of demographic parameters while simultaneously accounting for various sources of uncertainty in each data source (e.g., measurement error or parameter estimation). Because population count data also contain information about all demographic parameters of the population under study, incorporating both kinds of data into a single analysis can result in higher precision of parameter estimates and enable estimation of parameters that could not be estimated otherwise, like fertility(55).

The DEMOCOM consortium has been involved in theoretical developments on integrated models(11, 13, 56, 57) as well as applications of it(58, 59). This approach has not yet been applied in a multispecies context (but see(60)), but appears to have great potential.

1.4 Objectives (with expected results), originality and novelty of the project

Our main objective is to propose an integrated statistical framework for estimation and inference about community dynamics via the development of multispecies demography – DEMOCOM – bringing together concepts, predictions and tools from both fields of demography and community ecology. The DEMOCOM project will develop an original methodological approach allowing explicit connections between community-based metrics and individual species dynamics. The project is structured in three work packages (WPs).

In WP1, we will develop the methodological framework of DEMOCOM to combine potentially heterogeneous and sparse information on age/stage-structured multispecies populations into dynamic community models (Fig. 2). This will provide the foundations upon which the case studies in WP2 will be developed.

In WP2, we will investigate the dynamics of communities of birds, fish and mammals, with the aim of quantifying the role of interactions in the community-level response to climatic change and management interventions on multispecies assemblages. For all these ‘case study’ communities, we benefit from capture-recapture monitoring datasets collected on natural communities made of 2 to 60 species that have changed under the influence of global environmental disturbances that characterize the last decades. These data are owned and collected by the partners of the present consortium.

In WP3, we will develop a user-friendly computer package to ensure the transfer of knowledge towards biologists. We will adopt a co-construction approach where the end-users (for which we have a good sample with ecologists from CEBC, ISEM, CESCO and MARBEC partners and stake-holders from ONCFS and

MECADEV partners who implement management policies for the former and develop community indicators through the French bird ringing lab [CRBPO] for the latter) will be involved throughout the whole process of the development of the software.

Overall, we will adopt a multidisciplinary approach in which important questions in community ecology will be addressed with robust and modern methods from the fields of demography, statistics and computing science.

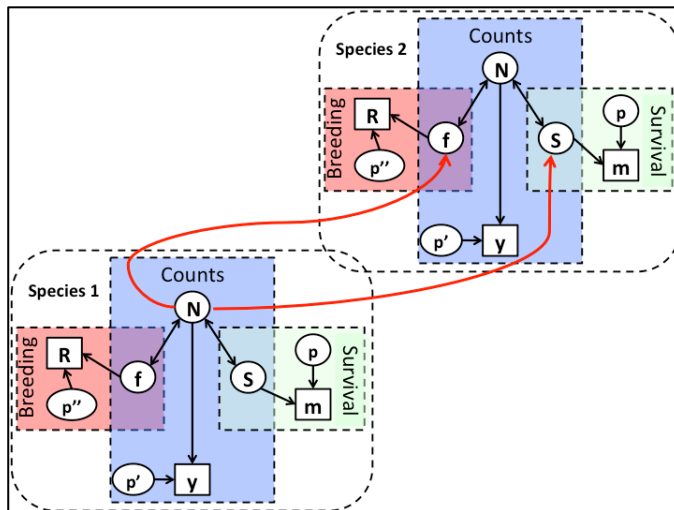


Figure 2: An integrated two-species demographic model. For each of the two species, parameters are in circles, data in rectangles, and arrows are for inter-species dependencies between parameters. The notations are: m capture–recapture data; y species count data; R number of offspring; S survival; p , p' and p'' detection for survival, counts and reproductive data respectively; N abundance. In the ideal situation, three sources of data are available for each species (population counts, breeding and mortality data) that are integrated in a single analytical framework. Some parameters are shared by different sources of information, e.g. survival (green and blue data), which, by increasing the sample size, improves precision and makes some parameters easily estimable otherwise difficult to assess in separate analyses. For each species, arrows between N and f or S go both ways to capture the obvious effect of fecundity and survival of abundance, but also to allow for density-dependence on these demographic parameters. An example of interactions is given between species 1 and 2 that can explicitly be formulated and estimated as

functional/numerical responses by combining all sources of information: the red connectors stand for parameters of a density-dependence effect of species 1 (N) on demography of species 2 (f and S). Within this framework, one can disentangle the effect of variation in climate or habitat on species from inter-specific interactions. For simplicity, we illustrate the framework with two species, but the model can obviously be extended to $K \geq 2$ possibly interacting species (see application of this framework to case studies of WP2).

Task 1 – DEMOCOM with pain and tears: modeling framework

In this WP1, mathematical models and statistical methods will be developed to produce reliable answers to the biological questions raised in WP2. We will also develop the numerical algorithms that will be required for the reliable implementation of these methods.

Originality

- We will provide a formal framework to model and predict community dynamics in response to climate change and management interventions in presence of intra-specific variability of the response;
- The first comprehensive approach to evaluate response of communities to disturbance through dynamics of individuals;
- A formal procedure to assess the sensitivity of community metrics to species interactions and demographic parameters;
- A stochastic realistic framework to analyze communities' structure and dynamics;
- Efficient and reliable procedures to calibrate multispecies dynamics models.

Expected outcome

Regarding its methodological component, our proposal is at the forefront of research in diagnosing and predicting the impact of global change on biodiversity by explicitly incorporating the response of species by their own and in interaction with others. Whereas most biodiversity projection tools have been developed at the population level (PVA(61)) and standardized conservation status (e.g., IUCN) are assessed at the scales of species(62) or ecosystems(63), a mechanistic modeling framework is surprisingly lacking at the community scale(64). Our methodology has the potential to serve as a baseline for next-generation models for biodiversity forecasting.

Task 2 – DEMOCOM in practice: motivating case studies

Our proposal is motivated by several case studies raising questions of particular importance in the management of exploited species and the assessment of the impact of climate change on communities. These case studies will feed in pluri-disciplinary discussions among the members of this project (biologists, statisticians and computer scientists), which will take place preferably in the workshops we will organize at the beginning of each year of the project.

Human activities have modified the dynamics of many natural populations either directly by exploitation, or indirectly by, e.g., modifying climate, to an unprecedented extent over the last decades(2, 65, 66). As a consequence, the natural rate of species extinction has accelerated considerably. These anthropogenic changes to the biosphere have thus raised strong concerns about the loss of biodiversity. Conservation and sustainable use of biodiversity and ecosystem services now largely depend on successful management of ecological communities, which in turn depend on our knowledge and our ability to predict their structure and dynamics.

In this work package, we will use multispecies demographic models to assess the impact of climate on bird communities and that of management strategies on fish and mammal communities. These case studies have been carefully selected to start working with relatively simple systems in which we have a few species and explicit interactions (seabirds and tunas), then to proceed with more complex systems in which we have more species with many interactions (common birds and carnivores-ungulates). Lastly, while the definition of a community is being debated, we have adopted the view of P. Morin and define a community as at least two interacting species(67).

Originality

- First assessment of the relative contribution of climate change relative to predation in a bird predator-prey system;
- First assessment of the impact of climate change on bird communities via their demography (mechanisms)
- One of first examples of multispecies management strategies on a highly valuable commercial fish species;
- The first community management models for large carnivores – ungulates preys (including demography).

Expected outcome

Birds - Our work on seabird communities will provide a unique opportunity for studying the effects of climate change on ecosystems as these top predators are seen as ecological indicators of the marine environment. We will also bring elements for the understanding of individual *versus* species contributions to communities' responses to climate change, using common bird communities as model. Our framework to predict species distribution while accounting for interactions will provide a canvas for future analyses at the large European scale (two-third of the European countries has set up similar bird monitoring observatories for biodiversity assessment).

Fishes - The multispecies fisheries model will be the first of its own and will fulfill important recommendations to work at the level of communities to manage fish stocks.

Mammals - The multispecies model for wolf management will provide the ingredients for predicting changes in the carnivores-ungulates community and for promoting coexistence between these species and human activities, a pressing demand of the civil society.

Task 3 – DEMOCOM for dummies: software development

Eventually, the popularization of new methods in population and community ecology necessarily passes through the development of user-friendly software to allow biologists to use them in a reliable and easy way. This explains the success of single-species computer software(68, 69). Therefore, we will develop a companion program, which will implement DEMOCOM in a freely available computer package. The originality of our approach will be to have the end-users (ecologists and stake-holders from the partners) involved in the development throughout the whole software development process. This approach will be implemented smoothly through several workshops during which these end-users will be invited to test and criticize the current versions of the software to improve its biological relevance and user-friendliness.

Originality

- A user-friendly computer program to investigate communities' structure and dynamics (in the popular language R).

Expected outcome

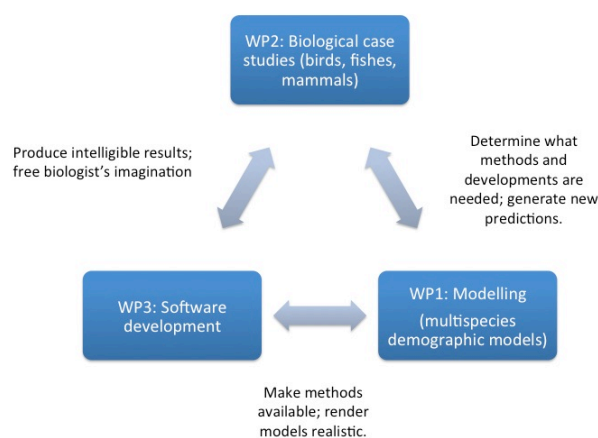
In the context of single population dynamics, user-friendly programs (e.g., VORTEX or RAMAS for demographic models or MARK for capture-recapture analyses) have been extensively used for two decades in the context of biodiversity conservation, not only by researchers, but also by biodiversity managers and world conservation agencies (such as the IUCN) to set conservation priorities(70). This pieces of software, however, are not developed for studying communities and do not allow integrating field data to infer parameters of species interactions. The development of flexible, reliable and user-friendly software in collaboration with end-users of the consortium (ecologists and stake-holders) will contribute to the dissemination of the multispecies demography framework we propose here.

2. SCIENTIFIC AND TECHNICAL PROJECT PROGRAM, PROJECT ORGANISATION

2.1 Scientific program, project structure

Our project is organized in 3 tasks and several objectives. In Task 1, we will focus on developing a multispecies demography framework while Task 3 will implement these tools in a computer program. Task 2 will involve case studies thanks to the tools developed in Tasks 1 and 3. The links between the tasks are indicated on Fig. 3 below, which also shows the intrinsic interdisciplinary nature of the project. Full description of the tasks follows in section 2.4.

Figure 3: Virtuous (hopefully) circle of collaborations between modelers, ecologists and computer scientists in the DEMOCOM project. The biological case studies will motivate new methodological developments thanks to constant discussions between modelers and ecologists (several of them have both skills). In turn, models, when applied to the data, will help generating new predictions that will be tested. If we want the methods to be used by biologists, we need to implement them in a computer package. The discussion between computer scientists and modelers will ensure that the models are realistic. The implementation of a multispecies demographic models in a computer package will provide a reliable and flexible framework to test the predictions generated in the case studies and formally expressed with modelers, but not only, as we expect that the availability of the tool will allow biologists to formulate their own models. In passing, these constant back and forth between ecology and mathematics / statistics will be made easier by all participants engaging in fieldwork, as we have recently argued(71).



2.2 Project management

Olivier Gimenez is the coordinator of this project and will be in charge of the management of its scientific animation. He has the experience required with a previous ANR-funded project that was successful (<https://goo.gl/EucNli>) and will be helped by the administrative team from CEFE.

Realization of the proposed objectives implies close collaborations between the different teams and disciplines required to perform the different tasks (population and community ecologies, demography, statistics, computer science). Hence, the project will start with a kick-off meeting, essentially aiming at clarifying the respective roles within tasks (workshop 1, see section 2.6).

During the course of the project, a scientific animation is required to ensure the consistency and achievements of tasks of the project. Every year the partners will meet to report their latest advances in the project and find solutions to issues encountered during this time. External experts will be invited to these meetings (see section 2.6) to i) discuss the outcome of the project, ii) present work tightly connected to the tasks developed in this project, and iii) help evaluating alternative solutions to faced difficulties. These yearly meetings will be under the format of international workshops. In addition to the first kick-off meeting, three such workshops have been scheduled over the entire period of the project (see section 2.6).

A particular attention will be given to the timing of the recruitment of two 2-year post-docs and a research engineer (2-year contract). To ensure the exchange and transfer of ecological and methodological knowledge between these three key persons and the rest of the consortium, we will hire them in a way that maximizes the overlap between their respective contracts: more specifically, the post-doc on methods will be hired over the period year 1 semester 2 to year 3 semester 1, the post-doc on applications will be hired from year 2 semester 2 to year 4 semester 1 and the research engineer will be hired from year 2 semester 2 to year 4 semester 1 (see also section 2.6).

2.3 Qualification of the project coordinator and partners

Olivier Gimenez (HDR, age 41, CNRS senior researcher, CEFÉ), PI, <https://oliviergimenez.wordpress.com/>, specialist in demography and statistics. Develops research at the interplay between ecology and statistics (so-called statistical ecology) via the setting up of a network of skilled collaborators to address key questions, including the impact of human activities on animal demography and the management of wild animal populations (<https://sites.google.com/site/gdrecostat/>; see also section 1.2).

Leader of the 'Biostatistics and Population Biology' team 2008-2014, now head of the Department of Biodiversity and Conservation (5 teams of researchers with > 35 permanent staff).

Strong experience in leading research projects funded on contracts. From 2008-2011, he has been the PI of a Young Investigator ANR-funded project (ANR JCJC 'CR2M', <https://goo.gl/Bmj6Z4>), three PEPS programs funded by CNRS, several contracts with the French Hunting and Wildlife Agency and co-PI on a NSF grant.

Mentoring: > 30 undergrads, 9 PhD students, 7 postdocs

Publications: > 130 papers (plus 4 book chapters and 2 books), most of which coauthored with French and/or foreign collaborators (from the USA and the UK mainly), 3425 citations, h-index 30.

Vincent Devictor (HDR, age 37, CNRS researcher, ISEM), <http://vincent.devictor.free.fr/>; specialist in macro-ecology and global change impacts on species and communities. Develops key community metrics now used as official indicators.

Publications: 52 papers (Nature Climate Change, Ecology Letters, Journal of Applied Ecology, Conservation Biology...), 2955 citations, h-index 26.

Mentoring: 2 PhDs, 1 post-doc.

Emmanuel Chassot (PhD, age 37, IRD researcher), <http://www.umn-marbec.fr/chassot-emmanuel.html>, specialist in fish demography and stock assessment modeling.

Publications: 27 papers, 4 book chapters, 58 articles in ICCAT/IOTC proceedings

Mentoring: 1 PhD

Christophe Barbraud (HDR, age 46, CNRS researcher, CEBC),

<http://www.cebc.cnrs.fr/Fidentite/barbraud/barbraud.htm/>; specialist of seabird demography and the impact of climate change

Publications: 126 papers (Science, PNAS, ...), 11 book chapters, 2476 citations, h-index 29

Mentoring: 20 undergraduate students, 9 PhD students, 1 post-doc

Pierre-Yves Henry (PhD, age 40, MNHN associate professor, MECADEV),

<http://mecadev.cnrs.fr/index.php?post/Henry-Pierre-Yves>; common bird demography at national scale; proximate responses to climate change. Scientific director of the French bird ringing lab (CRBPO) since 2012 (400 volunteer bird ringers).

Publications: 51 papers, 780 citations, h-index 17

Mentoring: 6 PhD students, 1 post-doc

Alexandre Robert (lecturer at MNHN, age 40, CESCO). Works on population dynamics modeling, small (meta)populations, demo-genetics, evolutionary demography and reintroduction ecology.
Publications: 53 papers, h-index 14

Eric Marboutin (PhD, age 50, Research engineer, ONCFS). Works in population ecology and monitoring of wolves and lynx, habitat and demographic modeling. Specialist of predator-prey relationships, interactions between carnivores and domestic/wild preys. Expertise for several Ministries (Agriculture, Ecology) and for the European Commission.
Publications: 24 papers (Biological Conservation, Science, Animal Cons., ...), 344 citations, h-index 9.
Mentoring: 3 PhDs

2.4 Description by task

2.4.1 Task 1 – DEMOCOM without pain and tears: modeling framework

PEOPLE INVOLVED and CONTRIBUTION

O Gimenez: In charge; development of multispecies demographic models; estimation of demographic parameters for multispecies systems using capture-recapture data; development of integrated community models

Post-doc working on methodological developments (to be hired on ANR funds): ideally someone with a math/stat background; willing to work closely with ecologists

R Pradel: estimation of demographic parameters for multispecies systems using capture-recapture data

R Choquet: estimation of demographic parameters for multispecies systems using capture-recapture data

E Marboutin: application of sensitivity analyses to communities

C Barbraud: feedback on the relevance of multispecies demographic models

PY Henry: feedback on the relevance of multispecies demographic models

A Robert: development of multispecies demographic models;

E Chassot: feedback on the relevance of multispecies demographic models; input in population ecology

V Devictor: feedback on the relevance of multispecies demographic models; input in community ecology

F Jiguet: feedback on the relevance of multispecies demographic models; input in community ecology

C Duchamp: feedback on the relevance of multispecies demographic models; input in community ecology

OBJECTIVES AND DETAILED PROGRAM

Objective 1 – Multispecies demographic models and data

Model building. The study of population abundance and structure in space and time provides the basis to dynamics in single-species population dynamics. Structured population models(21) allow a detailed description of populations changes over time by accounting for observed differences among individuals through discrete classes (according to age, stage or state). These models are widely used in plant and animal demographic studies to carry out the projection of future population size, the estimation of asymptotic population growth rate, age structure, net reproductive rate, generation time and life expectancy (among others). Matrix models have been used to carry out population viability analyzes(72), assess management strategies on life history strategies(27, 28) and investigate the feedback between demography and evolution(49, 73, 74). However, little has been done to extend these models to the dynamics of community as stated by Caswell at the end of his influential book: **‘Models of multiple interacting species, especially where the interactions are strongly age or stage specific, deserve more attention’**. An alternative to matrix models is integral projection models(24, 75). In contrast with matrix models that require discretizing individuals’ states into classes, demographic parameters are modeled as continuous functions of individuals’ states in integral projection models, e.g., size in fishes or body mass in animals(76). Integral projection models retain matrix models analytical advantages like the calculation of sensitivities and growth rate. **We will extend matrix and integral projection models to multiple interacting species (see Fig. 2). By doing so, we will make the multispecies demography framework available which will be adopted to investigate the intensity and impact of intraspecific variation in communities’ structure and dynamics.**

Model fitting. Traditionally, structured population models are calibrated or parameterized using longitudinal data collected at the individual level(21, 24). These data are statistically analyzed to estimate demographic parameters like survival, growth, dispersal and fecundity that are plugged into projection models. However, several sources of uncertainty are associated to parameter estimation, which need to be properly accounted for. First, individuals are difficult to monitor in the wild and may be observed / captured or not at a given sampling occasion. This raises the issue of imperfect detectability, which, if ignored, may lead to biased estimates and flawed inference about demographic parameters(35). Second, there may be uncertainty related to measurement error and non-exhaustive sampling. **To fully integrate the complexity of community dynamics and accommodate the various sources of uncertainty associated with nature, we will integrate mathematical structured population models (Objective 1) with statistical approaches (Fig. 2).** We will resort to hidden process models that have recently received much attention in the literature(37, 39, 77–79) and enable bringing theoretical models (mechanisms) and the analysis of empirical data (patterns) together. We will also extend hidden process models to the simultaneous analysis of data at both the individual and population levels(54). This will allow fully exploiting the data information to increase precision and enabling estimation of parameters that would not be estimable otherwise (fecundity in particular(55)). This approach has never been used with multispecies systems. We will provide the tools to check the goodness-of-fit of the models to the data and parameter estimability. Overall, we will provide a unifying framework to combine the analysis of individual and population data, the construction of matrix and integral projection models and the projection of species, which in turn will allow a great flexibility in handling various biological situations as those described in WP2.

Objective 2: Sensitivity of community structure and dynamics to species interactions

Changes in the growth rate of some species or in the strength of some interaction links can substantially affect the structure and resilience of communities. **We will develop community sensitivity analyses to explore how small changes in the demographic rates of species and in the strength of interaction within and between species may affect the structure and resilience of communities.** Sensibility analysis is a standard tool for single-species populations and enables investigating how small changes in vital rates affect the long run growth rate and extinction risk(21). Sensitivity analyses allow identifying critical life stages and vital rates of species which is of particular importance in the conservation and management of populations(27, 28, 80, 81) and can also be used to evaluate evolution pressure(49, 73, 74). To date, these tools have not been fully developed and seldom used in community ecology(82). By developing community sensitivity analyses, we will be able to identify keystone species and links in a community (keystone means whose removal has particularly strong effect on the community). To quantify the community structure and dynamics, we will use standard community metrics like overall abundance, number of species, or standard diversity indices like the Shannon index. **Besides, we will resort to more recent metrics that will provide precious insights in the community responses to perturbations.** First, we will use community-based indices accounting for differences among species(83). The general idea in this approach is to characterize the functional structure of a community defined as the distribution of species and their abundances in the functional space determined by multiple functional traits(84). Interestingly, this multidimensional approach allows the quantification of inter-species variability in the traits considered. Therefore, two communities with similar functional richness but uneven distribution of individuals among functional traits and/or very original traits can be differentiated. The connection between population dynamics and community composition will be established by investigating whether, and to what extent, these functional metrics are influenced by individual species dynamics through sensitivity analyses. For example, in time, e.g., following climate change, are species with positive dynamics more responsible for the observed change in functional composition of communities than those with negative dynamics? Second, an even more explicit link between community and population dynamics will be established using community-weighted means (hereafter, CWM) to describe community composition with respect to a given species-specific trait. CWMs have successfully been used in global change studies to address the question of community reshuffling in response to environmental perturbations. They have been applied to a variety of traits such as the mean of the realized thermal niche (Community Thermal Index or CTI; (85)), and applied to birds, butterflies, plants and fish communities. A sensitivity analysis can be performed to assess how the inclusion of each species modifies the overall trend in the CWM dynamics(86), hence allowing the explicit testing of predictions on the role played by population dynamics on community changes. For instance, we expect those species most responsible for an increase in CTI to have higher body masses and lower reproductive outputs.

Objective 2 – Moving towards stochastic community dynamics

Deterministic models may miss important aspects of the dynamics of natural communities because they will not include stochastic variability in the species-specific demographic rates. At the single-species level, several studies have shown that the calculation of growth rate and sensitivities could be flawed when populations are exposed to temporally varying environments(87, 88). Besides, environmental variability may increase in response to anthropogenic pressures(89). **We will develop multispecies stochastic demographic models to fully account for environmental variability.** This will be accomplished for both matrix and integral projection models. Deterministic community sensitivities and population growth rate will be extended to their stochastic counterpart(90–92).

DATA COLLECTION AND METHODS

Objective 1:

Model building. The main conceptual change to single-species models will be with regards to the state vector of abundances where, previously, the state vector was divided into the age or stage classes for an individual species, whereas now the state vector will include the various states for all species in the model. In addition, the state process will be modularized(79, 93), broken into sub-processes characterized by simpler matrices each representing only one process, such as birth or survival. Modularizing the sub-processes will provide a flexible and straightforward approach to model building, allowing complex community dynamics to be more easily communicated and manipulated. We will extend the Lotka-Volterra multispecies model(31, 67) for competition (objectives 6-7) and predation (objective 5) to explicitly incorporate intra-specific variability via demographic structure. Noteworthy, we will develop indicators of community dynamics by generalizing single species population growth and extinction probability. In short, these quantities will be calculated in the multispecies demographic model and averaged at the community level (this step will be the object of discussions); we expect that these calculations, by explicitly incorporating species interactions, will be different from the same calculations that a population ecologist would do on each species in isolation, by considering them independent of each other. Overall, our approach explicitly accounting for stage structure will contrast with the approaches currently undertaken in community ecology which focus only on abundance(94–96) and will bring new insight on the effects of intra-specific variability on ecological communities.

Model fitting: In hidden process models, two time series are run in parallel, one captures the dynamic of the true states (latent) and the other consists of observations that are made from these underlying but possibly unknown states. This clear distinction makes it more convenient to model the ecological processes: a) Nonlinear relationships between environmental factors and demographic rates are expected in biology(97). For example, for endothermic animals, cold temperatures may increase energetic costs if resources are limited, whereas hot temperatures may affect cell metabolism, and both processes may negatively affect survival. Therefore, there is a range of temperatures that optimizes survival. However, few studies have shown nonlinear relationships between environmental variables and demographic rates mainly because long-term series are needed and because appropriate modeling tools are lacking. However, since climate variability is stochastic, scenarios of the impact of future climate change on populations that do not explicitly take into account nonlinear relationships may be misleading. We will develop nonparametric approaches to detect nonlinearities and thresholds in the demographic rates(12); b) To capture species interactions, we will explicitly model inter-specific temporal correlations in demographic parameters. The hidden-process modeling approach will enable separating out sampling variation from real interactions(98). To quantify the common fraction between species in the spatial variation of demographic rates, we will implement a decomposition of the variance approach(99–101). Random effects will be included in the models, and variance ratio will capture synchrony.

To fit these models to data, we will resort to simulation techniques that have largely invaded the field of ecology(102). However, despite these algorithms being powerful, they cannot efficiently be applied to arbitrarily complex problems, and developing efficient computation algorithms remains an active area of research(103). The analysis of hidden-process models requires evaluating high-dimensional integrals in the likelihood, which is a difficult task. We will circumvent this issue by implementing, evaluating and comparing up-to-date algorithms. Three general families of algorithms will be implemented. The Kalman

filter(104) provides the best estimates if we assume normality and additivity. To deal with nonlinear phenomenon, other methods will be explored like the extended Kalman filter(105). For small populations, the Gaussian assumption is no longer valid for demographic stochasticity and we will resort to Monte Carlo simulations. First, we will explore Markov chain Monte Carlo algorithms(MCMC(102, 106)). For highly nonlinear or non-Gaussian systems, MCMC are difficult to use(107) and particle filtering will be explored(108, 109). This avenue of research has received little attention in ecology. Algorithms will be compared using simulated values and case studies based on a) numerical convergence b) bias and precision of the estimators and c) speed of computation. We will also study redundancy or model identifiability which occurs when not all parameters are separately estimable(110, 111). This diagnostic will have crucial importance in terms of interpretation of the parameters governing the community dynamics. In addition, we will provide methods to pick the best model among a set of candidate models, each of them standing for a biological prediction about the dynamics and structure of the community. To avoid relying on a single best model and incorporate uncertainty about the choice of this best model, we will develop multimodel inference for community modeling(112, 113). We will also provide additional guidelines for the validation (goodness-of-fit tests) of the selected models as estimation and inference are based on these models. We will rely on existing procedures developed by partner 1 ((114, 115)) and omnibus tests developed in the Bayesian framework(116).

Objective 2: We will extend community sensitivity analyses in three directions: a) A key step will be to develop tools to calculate sensitivities with respect to simultaneous changes in several parameters as the impact of environmental or human disturbance is likely to affect several species of a community; b) We will account for transient dynamics following ecological disturbances or perturbations due to changing climate or management interventions. These disruptions to population structure may lead to realized ratios of life stages in the population that are different from the population's stable demographic distribution. Any such discrepancy will cause short-term variation in species densities that are very different to those that might be expected in a homogeneous environment. We will rely on population inertia(117) which is amenable to sensitivity analyses and captures adequately(118) the discrepancy in the stable stage structures between a population following any disturbance or perturbation and a similar population growing at asymptotic rate; c) We will adapt methods to decompose the variation in species population growth rates into contributions from the multiple demographic rates(119). Regarding community metrics, we will resort to i) community-based indices that are obtained by building a multidimensional functional space with axes corresponding to raw functional traits or to synthetic traits summarizing several raw traits (following a principal component analysis for example), then by summarizing this space with a synthetic index like the quadratic entropy index that captures important features of functional diversity(83), ii) community weighted means of a given assemblage which is calculated as the average value of a trait considered weighted by species abundances in this assemblage.

Objective 3: In temporally varying environments, single-species sensitivities are often calculated from simulations that assume a probability distribution for the environmental states. Based on a recently developed method to estimate elasticities directly from demographic data(90), we will construct a consistent statistical estimator of community sensitivities that will enable us to construct confidence intervals and testing hypotheses about the structure of the communities and the strength of species interactions.

RISKS

Objective 1: Expected risk of model building is moderate to high. Important methodological developments to be produced, but achievable thanks to skills present in the DEMOCOM consortium (in particular, Lebreton at CEFÉ who has an emeritus position, and Robert at CESCO). Although novel, the model fitting has low expected risk because based on powerful methods and experience in the consortium (Gimenez, Pradel, Choquet).

Objective 2: Expected risk is moderate to high due to the complexity of multispecies dynamics models, but achievable in view of existing results on single-species models.

Objective 3: Expected risk is moderate due to the existence of results for single-species models. In case formal results cannot be produced, we will resort to simulations.

2.4.2 Task 2 – DEMOCOM in practice: motivating case studies

PEOPLE INVOLVED and CONTRIBUTION

PY Henry: In charge – analysis of songbird community dynamics, fieldwork on birds

Post-doc working on case studies (to be hired on ANR funds): ideally an ecologist with experience on demography or community ecology of several different systems; willing to spend time working on a computer building models.

O Gimenez: integration of demography and data, fieldwork on carnivores

C Barbraud: analysis of the impact of climate forcing on seabird community dynamics, fieldwork on birds

K Delord: seabird database management, data extraction and organization, fieldwork on birds

O Dehorter: songbird database management, data extraction and organization

A Robert: seabird demographic modeling

I Le Viol: analysis of the impact of climate forcing on songbird community dynamics, fieldwork on birds

E Chassot: analysis of fish population dynamics, fieldwork on fishes

V Devictor: analysis of the impact of climate forcing on songbird community dynamics, fieldwork on birds

F Jiguet: community ecology, fieldwork on birds

E Marboutin: analysis wolf and ungulates interactions, fieldwork on carnivores

C Duchamp: analysis of wolf population dynamics, fieldwork on carnivores

OBJECTIVES AND DETAILED PROGRAM

Most studies on the impact of climate on communities have used occurrence or count data to analyze response patterns. However, if we are to predict the impact of environmental change on community persistence, mechanisms that operate at the population level per species need to be integrated explicitly. Although several studies have made explicit links between environmental variables and demographic rates(43, 120, 121), and others have integrated these into population models(29, 122, 123), there has been no attempt to develop community models to investigate the impact of projected changes in environmental variables through community scenarios.

In this context, our objective is to use DEMOCOM to provide mechanistic models predicting the fate of animal communities exposed to pressures (climatic change, management actions) while accounting for underlying demographic mechanisms, i.e. interacting populations of individuals from locally co-occurring species. .

Objective 4 – Effects of climate on predator-prey systems

Climate change jeopardizes the persistence and distribution of many species, yet our ability to forecast changes in communities' composition and species interactions is hindered by a lack of understanding of the extent to which higher trophic-level interactions may buffer(124, 125) or exacerbate(126) the adverse effects of warming. The Southern Ocean and Antarctica have experienced a substantial increase in temperature(127), making it a unique and critical location for studying the effects of climate change on ecosystems. Variability in sea surface temperature and sea ice environment directly impacts biological processes, which cascade through food webs and are integrated by top predators such as seabirds(128). Previous reports of trophic cascades and ecosystem dynamics induced by predators have focused only on changes in their abundance(129, 130), whereas we will develop mechanistic models to understand more fully how density dependence, climate and predation interact to affect fluctuations in prey and predator populations in the natural world. **Using 30 years of data from a two-level food chain on Kerguelen Island, Southern Indian Ocean, we will use DEMOCOM to integrate predator-prey models with individual stage data and predator and prey abundance to decipher and predict mechanistically the respective roles of climate and predation-climate interactions on population fluctuations.** The predator species, the brown skua (*Catharacta skua lönnbergi*) is the main predator of the blue petrel (*Halobaena caerulea*) and of the thin-billed prion (*Pachyptila belcheri*) during the breeding season at Kerguelen Island. All these are relatively long-lived seabird species, breed throughout their adult lives and reproduce during the austral summer from September to January. Yet they display rather different life histories and we predict contrasted response to climate change(30). DEMOCOM will help accommodating intra-specific variability

in our predictions. In particular, for most of seabird species, individuals recruit at the colony at several years of age and spend their pre-breeding years at sea where they remain unobservable. DEMOCOM will allow estimating juvenile/immature survival via the combination of observed breeding numbers on colonies in the French Austral Territories with individual data (adult survival/reproductive success/dispersal). In turn, we will estimate the potentially nonlinear(12) impact of global changes on juvenile/immature survival and the relative strength of this impact compared to adults for preys, and for the predator. Related to Fig. 2, we will assess the effect of brown skua abundance on the abundance and demographic parameters of its preys and vice-versa.

Objective 5 – Impact of climate on ecological communities

At the scale of a country, bird populations of common species exhibit strikingly similar variations of their survival and reproduction in response to environmental variation. This common component in the variation in population growth rate is likely to be driven by large-scale environmental factors such as climate(131, 132). This common component of variation is likely to be driven by large-scale environmental factors such as climate. This will be the focus of our study. Survival and breeding success are two key components controlling temporal variation in abundance of species, therefore through which we will explain the effect of climate. We will assess the impact of environmental variation through large-scale climatic variables(85, 133) on demographic rates of the 20 commonest songbirds in France. Then, **the weather-demography relationships will be used in DEMOCOM to predict the impact of climate on structure and dynamics of the French community of locally co-occurring bird species.** These changes in bird community structures are documented at the French national level by standardized bird counts and their dependence on global change components are well understood(85, 133), but these count-based analyses have not been able to account for underlying species-specific demographic processes. We will evaluate the relative contribution of demographic traits on population growth rate and community composition for all documented species. Our prediction is that species highly sensitive to climatic disturbances will have the strongest contributions to community changes. From these two unique datasets, the DEMOCOM project will connect, for the first time, how individual species life history traits (juvenile numbers, survival rates measured from CES, see below) have been influenced by climatic fluctuations and how this, in turn, translates into large scale modification of population and community dynamics as described with functional indices or CWM (measured from BBS, see below). Rather than blindly investigating interspecific effects that might suggest competition, as a preliminary step, we will focus on a few species for which we expect competition for food and nesting habitats (namely Blue tit *Cyanistes caeruleus*, Great Tit *Parus major*, Crested Tit *Parus cristatus* and Marsh Tit *Parus palustris*). Then, based on this validation of our approach, we will extend the analysis on the complete datasets with all species. The framework introduced in Fig. 2 will help in disentangling modifications in the community that are due to direct effect of climate from modifications induced by interspecific competition.

Objective 6 – Coexistence in fish pelagic communities

In 2006, fish provided more than 2.9 billion people with at least 20 per cent of their average per capita animal protein intake according to the FAO. Global statistics of capture fisheries and aquaculture indicate that the current supply in fish and seafood products does not meet the global demand, despite the rapid development of aquaculture(134). Meanwhile, the world marine fisheries catches started to show a decreasing trend from the early 1990s(135). This decline is partly due to the global expansion of world fisheries that led to the intense exploitation of the majority of world's major fish stocks and overfishing of a large number of populations(66). There is now a general recognition of the fishing overcapacity in all world oceans and of the necessity to reduce exploitation rates to rebuild marine resources(136). To demonstrate the interest of DEMOCOM in that context, we will use tropical tunas of the Indian Ocean as a case study.

In the recent years, the Indian Ocean represented about 25% of global tuna fisheries production with yellowfin (*Thunnus albacares*; YFT), bigeye (*Thunnus obesus*; BET) and skipjack (*Katsuwonus pelamis*; SKJ). The European purse seine fishing fleet represents 30% of the total tropical tuna catch of the Indian Ocean(137). Stock assessment for tropical tunas remains uncertain due to our limited knowledge of the tunas' communities and a lack of data independent from commercial fisheries. Besides, single-species models have dominated fisheries modeling, although it has been shown that population and community perspectives might lead to very different predictions about fisheries management(138). Tropical tunas are

gregarious fishes that form multispecies free-swimming schools composed of large individuals. Meanwhile, SKJ and juveniles of YFT and BET that are caught associated with floating objects (natural or artificial bamboo rafts generally equipped with satellite-tracked units) are so similar in size and anatomy that fishing skippers cannot identify them and sell them for canning under the same commercial category. Stomach contents and stable isotope analyses indicate that the three tuna species occupy the same niche and compete for food such as small fish and pelagic crustaceans. Some cannibalism and predation of small tunas by large ones could also occur. In addition, their similar size, swimming performances, and habitat suggest common sources of fishing and natural mortality with regards to size-selective fishing and the structuring role of size-based predation in pelagic communities(139). The ontogenetic changes experienced by YFT and BET after the juvenile phase would allow them to extend their spatial and vertical habitat, hence progressively reducing interspecies competition observed for small tunas. However, we currently have a very limited knowledge of tuna mortality, which generates large uncertainties in stock assessments and potentially irrelevant fisheries management. **Using DEMOCOM for tropical tunas, we will investigate coexistence mechanisms at the juvenile stage through a sound combination of information provided by fisheries and scientific tagging data. Using the framework proposed in Fig. 2, we will investigate the covariation between abundance (N) of YFT, BET and SKJ on age-specific survival (S) of all three species. This will greatly improve our knowledge on tuna mortality and growth and eventually contribute to their sustainable exploitation.**

Objective 7 – Wolf-ungulates management using multispecies demography

Large carnivores often focus the attention of various stakeholders. In France, some of them regard wolves as important agents of biodiversity sustainability, whereas others consider them as threats to the sustainability of their economic or recreative activities(140). This emblematic species is a top predator of conservation concern but indeed generates considerable socio-political tension through its impact on sheep farming and possible competition with ungulate hunting. However, the impact of management options (e.g. quotas) on their dynamics remains poorly known, and inappropriate decisions could lead to unexpected population trends in the dynamics of the carnivores and/or its preys (chamois *Rupicapra rupicapra*, mouflons *Ovis ammon*, roe deer *Capreolus capreolus* and red deer *Cervus elaphus*) or worsen the conflicting interactions between carnivores and humans(141). In particular, whether wolves have an opportunistic predation vs. prey selective behavior can have important consequences for managing ungulates damages on forests or wolves depredation to livestock. Also, the question of whether predation by wolves is compensatory or additive to other sources of prey mortalities (hunting and natural mortalities mostly) is of paramount importance for mitigating conflicts. **Using a unique 20 years survey on wolves and their four main preys, DEMOCOM will provide a framework for predator-prey models that will combine all sources of available information about predator and ungulates population dynamics (demographic and behavioral traits), incorporating social wolf structure. We will predict carnivores' population dynamics and its impact on ungulates populations, evaluate cost-effectiveness of current management methods through elasticity analyses to evaluate the importance of interactions and possibly propose new ones in collaboration with stake-holders from ONCFS (who are DEMOCOM partners). By providing a formal framework to predict the response of a predator(s)-prey(s) community to management, this new approach has the potential to contribute to the coexistence between large carnivores and human activities.**

DATA COLLECTION AND METHODS

Objective 4: All three species have been monitored using capture-recapture studies since the mid-1980s on Mayes Island (Kerguelen archipelago) where they are sympatric during the breeding season. For blue petrels, population surveys of the whole island were undertaken in 2002 and 2013, and in the late 1980s/early 1990s and 2014 for the brown skua. Data on the year-round at sea distribution of skuas, blue petrels and thin-billed prions are now available. It will permit to identify the foraging areas used during and outside the breeding season and to extract climate variables relative to these areas from online databases. All the effects of climate are strongly suspected to be indirect, oceanographic fluctuations affecting the food web via physical processes, which in turn affect the prey abundance and distribution and the demographic parameters of petrels and prions. Therefore, we will use models recently developed by the consortium to incorporate direct and indirect effects of external covariates(142). By contrast no study has yet investigated the links between climate fluctuations and the population dynamics of the brown skua. Climate and socio-economic scenarios will be used to obtain the predicted values for climate variables and will be related to demographic

parameters. For each scenario, outputs from several global climate models will be used to account for model uncertainties.

Objective 5: The count-based and capture-recapture-based French breeding bird surveys were started in France in 1989, based on volunteer skilled ornithologists following standardized protocols(143) and provide independent information on individual abundances and demographic processes during the reproduction period. For the count-based French Breeding Bird Survey (BBS), surveyed plots were selected randomly, ensuring that sampled habitats were representative of the whole country (including intensive farmlands, forests, suburbs and cities): each observer provides a locality, and a 2x2 km plot to be prospected is randomly selected within a 10 km radius (i.e. among 80 possible plots). In each plot, a given observer monitors 10 point counts separated by at least 200 m. All visible individuals and singers are counted on these permanent point counts for a fixed period of 5 min, twice a breeding season. For the capture-recapture-based French Constant ringing Effort Site scheme (CES), birds are captured and marked each year during a constant number of sessions, then recaptured over subsequent years, thus providing information on survival, fecundity and recruitment. Over the past 25 years, approx. 2000 sites have been censused (2 200 000 counts) and 218 sites have been monitored by capture-recapture (320 000 captures). Out of the 95 species captured at least once, CES sites document the demography of at least the 20 commonest songbirds in France. On each site high-resolution data on monthly temperature, precipitations are available (combined by MétéoFrance) as well as land-cover characteristics (derived from CORINE land-cover).

Objective 6: We will analyze a unique dataset made of fisheries and tagging data. Using DEMOCOM, we will combine a) conventional tagging data obtained through a large-scale tagging program (2005-2010), the Indian Ocean Tuna Tagging Project funded under the 9th European Development Fund of the European Union (€14 millions), which resulted in 200,000 tagged tunas including 32%, 18%, and 50% of YFT, BET, and SKJ, respectively (fish length at release and recovery and general characteristics of tagging operations and recovery conditions are available), b) otolith data for 215 YFT and 129 BET that will provide age estimation c) length-frequency data for samples of YFT, BET, and SKJ caught by the European purse seiners that have been routinely collected during port sampling operations in a consistent way since 1987, and will provide valuable data to track cohorts.

Objective 7: We will benefit from the monitoring of wolf and its wild preys coordinated by ONCFS. The wolf monitoring is carried out based on a dual sign survey framework(144): (1) An extensive survey is conducted during the year by a network of > 1200 wolf experts who are dispatched to cover the alpine range and report signs of presence. (2) An intensive sign survey is stratified within all previously detected wolf territories using standard snow-tracking and wolf-howling techniques, which allows the collection of scats, hairs, tissues, or urine used in DNA analyses. Individual genotypes are identified using the approach developed by P. Taberlet and colleagues(145, 146), and the costs of genetic analyses are entirely covered by ONCFS. The four ungulate species of wolf preys are being monitored through standard capture-recapture protocols by ONCFS with > 20 years on several hundreds of animals, along with recoveries of dead animals via hunting. Capture-recapture and presence-absence data will be combined in the DEMOCOM framework(147). Stage-structured Leslie matrices will be used for the carnivore explicitly accounting for social structure(148), while standard age-structured models will be used for ungulates; interactions will be explicitly considered (Fig. 2) via the estimation of predations rates that involves abundance of the preys and the carnivores as well as killing rates. Abundance will be treated as state variables and estimated in the integrated community modeling framework DEMOCOM. To estimate killing rates, we will benefit from an ONCFS predator-prey program that will start early 2017 devoted to the monitoring of wolves and its preys using GPS on two individuals per year for 10 years. Elasticity analyses, possibly in stochastic environments, will inform on the most important interactions in the community from a management perspective.

RISKS

Objectives 4: Expected risk is moderate due to our limited knowledge of skua dynamics, but totally achievable thanks to our experience in population dynamics modeling and the experience of Barbraud and Robert with seabird demography.

Objective 5: Expected risk is moderate due to the large dataset to handle with, but achievable thanks to the involvement of Devictor, Dehorter, Le Viol, Henry and Jiguet in the project (Jiguet & Henry are the coordinators of the two national bird monitoring programs, BBS and CES respectively).

Objective 6: Expected risk is moderate due to the large and heterogeneous database to be analyzed, but achievable thanks to the involvement of Chassot in the project and the experience of the team in population dynamics modeling.

Objective 7: Expected risk is low to moderate due the involvement of Marboutin and Duchamp in the project, the invaluable dataset we have at our disposal, the collaboration with the French Hunting and Wildlife Agency (ONCFS) and the long-term collaboration existing between ONCFS and the PI.

2.4.3 Task 3 – DEMOCOM for dummies: software development

PEOPLE INVOLVED and CONTRIBUTION

R Choquet: In charge; strong expertise in the development of computer software

Research engineer (to be hired on ANR funds): ideally someone with previous experience on the development of computer programs; willing to discuss with modelers and ecologists to implement new methods and test them on simulated and real data.

R Pradel: programming of capture-recapture multispecies models

O Gimenez: implementation of multispecies demographic and capture-recapture models; R packages

A Robert: implementation of multispecies demographic models

C Barbraud: beta-tester

PY Henry: beta-tester

E Chassot: beta-tester

E Marboutin: beta-tester

I Le Viol: beta-tester

C Duchamp: beta-tester

OBJECTIVES AND DETAILED PROGRAM

Objective 8 – DEMOCOM computer package development

Eventually, the popularization of new methods in population and community ecology necessarily passes through the development of user-friendly software to allow biologists to use them in a reliable and easy way. This explains the success of single-species computer software(68, 69). Therefore, **we will develop a companion program, which will implement DEMOCOM in a freely available computer package.**

Specifically, the DEMOCOM package will allow:

- Building multispecies deterministic / stochastic matrix projection and integral projection models;
- Evaluate community deterministic / stochastic sensitivities;
- Estimate the parameters of these models using relevant methods and data;
- Carry out model selection and multimodel inference;
- Evaluate the quality of fit of model to the data.

We will rely on the solid experience of the DEMOCOM consortium (in particular R. Choquet) in the development of pieces of software for population dynamics(40, 149) and ecological communities(150).

People doing research in various taxa download our existing pieces of software more than 50 times per month; the DEMOCOM computer program will be devoted towards the large community of scientists working in community ecology and we therefore expect to have at least as many users. We aim at providing a multi-platform software application compatible with Windows, Unix and Mac. To do so, the best option will be to develop packages for the R program(150) which is widely used by ecologists.

An important step before the diffusion of the software application will be to write a user's manual describing the main features and having a list of examples to help new users to become familiar with the syntax. This will be an important deliverable of the project. The end-users of the consortium (ecologists from CEBC, ISEM, CESCO and MARBEC partners and stake-holders from ONCFS and MECADEV partners who implement management policies for the former and develop community indicators through the French bird ringing lab [CRBPO] for the latter) will be 'used' as beta-testers via i) various sojourns of the research engineer in the different partners' labs, ii) live sessions during the workshops that we will have at the beginning of each new year of the project.

DATA COLLECTION AND METHODS

Objective 8: A step of thinking for the implementation will be required to develop a user-friendly and efficient language to specify species demography and community interactions through a carefully designed

user interface. We will extend the language we have already developed for single-species programs to deal with the analysis of data at the individual level(40). To specify the dynamics of communities through population structured models, we will rely on the syntax used by program ULM widely used in forecasting species viability and for which the PI's team has been involved in the development(151). We will implement the modularizing approach proposed by(77) to implement demographic models in several sub-models for survival, reproduction and dispersal. We will pay a particular attention to its computational speed qualities. We will use the potential of graphics cards (GPUs(152)) to implement highly parallel stochastic simulation algorithms(153–155). Beta versions of the program will be tested using simulated data. Real-life case studies described in WP1 will also naturally serve to evaluate the performances of the methods and algorithms we will develop, and also to test realistic and reasonable solutions for building the language for model specification. To do so, the involvement of the consortium end-users will be of paramount importance, as well as the workshops and the hiring of a research engineer (see end of the paragraph above).

RISKS

Objective 8: Expected risk is low due to the strong expertise of the consortium in developing pieces of software (Choquet, Gimenez, Pradel). Note that we have also approached Stéphane Legendre in Paris who has developed and currently maintains the ULM software for demography analyses; even though he's not formally part of the consortium, he's definitely keen to share ideas and we will invite him to the meetings and workshops we will have regarding WP1 and above all WP3.

2.5 Partners description, relevance and complementarity

Our project is highly feasible as members of the project have strong and complementary skills in demography (Gimenez, Barbraud, Henry, Robert), community ecology (Devictor, Jiguet, Le Viol), climate modeling (Barbraud, Devictor, Gimenez, Henry, Jiguet), population management (Gimenez, Chassot, Marboutin), mathematical and statistical modeling and analyses (Pradel, Gimenez, Choquet, Robert) and computer science including software development (Choquet, Pradel, Gimenez). The datasets we will use are the property of members of the consortium (Chassot for fishes, Marboutin and Duchamp for mammals, Henry, Jiguet and Barbraud for birds). It is composed of dynamic junior and senior researchers producing cutting-edge publications. The multispecies dimension we want to inject in our research is a new, important and vital step forward for research in demography as single-species models have generally been favored so far, but are strikingly inappropriate for addressing the societal challenges of biodiversity management. Despite the risk, the feasibility of this shift is high thanks to a) the combination of community and population ecologists with modelers, b) the fertile and stimulating research environment in the labs involved which are key players in the community ecology and population dynamics modeling, c) the fact that the case studies rely on longitudinal data that have been and are still collected over the years; the data are already available, so that we can start working on day 1 of the project, e) the long and solid experience of our consortium in developing computer packages for population dynamics and ecological communities, and f) fruitful former bipartite collaboration between all partners of the present consortium. The fact that the different partners already have a well established habit of working together, embodied by joint publications, is an undeniable asset. It ensures a quick launch of our work, as well as the fluidity of work relations during the project, providing strong support for its good functioning.

For the most technically challenging questions in the project, we have ensured the collaboration of external experts with which we already have strong links: Byron Morgan for integrated population modeling, Dave Koons and Jean-Michel Gaillard for demographic models and sensitivity analyses, Shripad Tuljapurkar for demographic models in stochastic environments, Perry De Valpine and Ruth King for estimation methods.

Partner 1: CEFE Montpellier

The Centre of Evolutionary and Functional Ecology (CEFE, head: R. Joffre) has a large experience in population dynamics, integrated modeling, behavioral and global change ecology. Research activity in the CEFE revolves around central issues in ecology and evolution: adaptation biodiversity, global change, and sustainable development. The CEFE is involved in international collaborations with more than 100 different laboratories from 35 different countries. This includes 19 International programs of scientific cooperation of which 12 are European programs. The Biodiversity and Conservation department (head: O Gimenez), where this research will be carried out, is very strong, with 35 permanent research staff, many of which are internationally renowned scientists. The major areas of research in the department include the demography of animal populations, community ecology and the study and anthropogenic effects on the environment. Projects in the department are based on the combination of modeling approaches and long-term field studies.

Partner 2: CEBC Chizé

The Centre d'Etudes Biologiques de Chizé (CEBC, head: X. Bonnet) develops research programs on the ecology of populations and individuals within the context of global changes, with a strong perspective of conservation of animal populations and ecosystems. The Marine Predators team (head: H. Weimerskirch), with 11 permanent staff and more than 20 PhDs, postdocs and non-permanent staff, is involved in international collaborations with more than 50 laboratories from 12 different countries. The team has a strong experience in seabird ecology (in the French Southern Territories). The major research areas in the team include the population dynamics, foraging ecology, and trophic ecology of seabirds and marine mammals and the study of the effects of global changes on these top predators. Research projects in the team are based on modeling approaches, long-term field studies (some > 55 years) and integrated databases.

Partner 3: MARBEC Sète

The MARine Biodiversity, Exploitation and Conservation lab (MARBEC, head: L. Dagorn) hosts a diverse group of researchers from the CNRS, IRD, IFREMER and the University of Montpellier working in various areas of Marine Science. The laboratory has a long history of expertise in the ecosystem approach to fisheries, ecosystem and population modeling (development of two prominent marine ecosystem models, OSMOSE and APECOSM, and a tool for modeling larval dispersal, ICHTHYOP), marine conservation and management, fisheries database development and marine ecology. The laboratory possesses a sophisticated set of facilities, including a cluster of computers used to develop numerical models and run mid- to large-size simulations, as well as laboratories for the treatment and analyses of biological samples. Furthermore, the lab has recently embarked on a data and metadata storage process known as the Ecoscope that will eventually host existing databases (such as a worldwide tuna fishery catch and effort database).

Partner 4: ISEM Montpellier

The Institute for Evolutionary Science of Montpellier (ISEM, head: A. Mignot) is one of the leading research lab in France on evolutionary science and ecology. It has a long tradition of combining several research fields related to biodiversity sciences at multiple ecological levels (from genes to ecosystems), taxonomic groups, and spatial and temporal scales. ISEM plays a central role in leading French research in ecology and evolution and resonates strongly at international level. ISEM hosts many researchers in close collaborations with their colleagues at the CEFÉ with which they are used to conduct joint projects due to their complementary skills and logistic supports. Within ISEM, the Biodiversity Dynamics Interactions and Conservation (BIODICEE) is very active and composed of 3 permanent researchers sharing interests in several aspects of community ecology either theoretical or more applied. The BIODICEE is particularly familiar with experimental projects, programming and large datasets processing.

Partner 5: CESCO Paris

The Centre for Ecology and Conservation Sciences (CESCO, head: R. Julliard) includes twenty permanent researchers and is specialized in ecology, evolution and conservation biology within the department of Ecology and Biodiversity Management. It has developed national-wide citizen monitoring programs (BBS and others: see <http://vigienature.mnhn.fr>). The CESCO research is focused towards three themes: 1) Modeling and monitoring of biodiversity structure and dynamic, including adaptive dynamics 2) Viability and restoration of populations and communities, and 3) Biodiversity scenarii. This last theme aims to build scenarii of the evolution of both diversity and ecosystem services in relation to the current global environmental change in order to provide scientific advice to decision makers (e.g. CESCO provides the "Farmland Birds Index" to the European commission, and indicators of biodiversity trends to the national observatory of biodiversity of the French environmental ministry).

Partner 6: MECADEV Brunoy

The Adaptive Mechanisms and Evolution lab (MECADEV, head: F. Aujard) is involved as Pierre-Yves Henry is coordinator of the Constant bird ringing Effort Sites (*STOC Capture*), which will provide the capture-mark-recapture data for the long-term analysis of common birds demography in France. He is also the scientific director of the *Centre de Recherches sur la Biologie des Populations d'Oiseaux* (CRBPO, the French Bird Ringing lab, hosted by CESCO), which coordinates bird ringing by 600 professionals and volunteers in France.

Partner 7: ONCFS Gières

ONCFS is a public agency devoted to wildlife and game sustainable management. Its missions include monitoring of patrimonial species, R&D on hunting, management and conservation of wildlife, and environmental police. ONCFS has a leading role in implementing governmental policies and a key position in the management of large carnivores. Within ONCFS, the Unité Prédateurs et Animaux déprédateurs (Head: M. Guinot-Ghestem) has a leading position in wildlife study and monitoring in France, supervising a

network of > 1200 observers covering the French territory allowing the implementation of large databases on large carnivores (including wolves) and their preys.

2.6 Task schedule, deliverables and milestones

Proposed tasks and objectives

Task	Title	Year 1		Year 2		Year 3		Year 4	
		S1	S2	S1	S2	S1	S2	S1	S2
WP1	DEMOCOM with pain and tears: modeling								
Ob 1	Multispecies demographic models								
Ob 2	Sensitivity of community structure and dynamics								
Ob 3	Moving towards stochastic community dynamics								
WP2	DEMOCOM in practice: motivating case studies								
Ob 4	Effects of climate on predator-prey systems								
Ob 5	Impact of climate on ecological communities								
Ob 6	Coexistence in fish pelagic communities								
Ob 7	Wolf management and community ecology								
WP3	DEMOCOM for dummies: software development								
Ob 8	DEMOCOM computer package development								
		☺	☺		☺		☺	☺	

☺ Kick-off meeting and subsequent workshops (including software testing); ☺ International workshop on multispecies demography and community dynamics

Deliverables and milestones: see next page

2.7 Scientific justification of requested resources

Note: Over the course of the project, we plan to hire several 1-year and 2-year master students to develop 6-month project (maximum) as part of the different Tasks (training charges @€546/month = €3276). In agreement with all partners, each of them will receive funding for at least two students for the 4 years. Even though the content of their project is not entirely known at the moment, we see several important reasons to plan these recruitments: from experience with other ANR projects (see section 1.2), the help of master students is invaluable as their contribution allows testing new ideas coming along the way, applying the methods we develop to new datasets (different from those included in the initial project) and most often leads to a publication. Besides, it provides a good opportunity for the post-docs and young researchers of the project to get a substantial experience in supervising students. Master students clearly bring life to a team and cohesion to a consortium like DEMOCOM, in particular via their co-supervision shared by two or more partners. Knowing and having worked with master students make them strong candidates for applying to PhD grants offered by the national doctoral schools (possibly to work on the DEMOCOM project). Last but not least, it has become more and more difficult, if not impossible, to hire master students using the recurrent credits that we receive from the French ministry of Research, and the ANR funding is one of the last way to cover the training charges.

Partner 1: CEFE Montpellier (requested funding: €325111)

Non-permanent staff ('personnels non permanents avec financement ANR demandé')

- A 2-year post-doc will be recruited ('chercheur CDD'; €5145*24); s/he will play an essential role in the lead of the methodological developments planned in WP1. It will ideally be someone with a math/stat background with strong programming skills; s/he will be willing to work closely with ecologists. Obviously, s/he will demonstrate good interpersonal skills needed for working as part of a large team. The post-doc will work under the supervision of O. Gimenez and will be based at CEFE (partner 1).
- A 2-year research engineer ('IR CDD'; €3655*24); s/he will play a leading role in WP3 by being in charge of the software development. S/he will ideally be someone with previous experience in the development of computer programs; willing to discuss with modelers and ecologists to implement new methods and test them on simulated and real data. The post-doc will work under the supervision of R. Choquet and O. Gimenez and will be based at CEFE (partner 1).
- Two 6-month students will be hired to work on WP1 and WP3 (2 x €3276 = €6552)

Deliverables and milestones:

Project management		
Workshop 1 – kick-off meeting	Takes place max 2 months after project starts	O Gimenez
Workshop 2	Takes place max 14 months after project starts	O Gimenez
Workshop 3	Takes place max 26 months after project starts	O Gimenez
Workshop 4	Takes place max 38 months after project starts	O Gimenez
Website of the project (in English; using Google sites [free] templates preferably)	Operational max 6 months after project starts	O Gimenez
Work package 1: models		
Scientific publication: multispecies demographic models; age/stage structured	Submitted max 24 months after project starts	O Gimenez
Scientific publication: multispecies integral projection models	Submitted max 26 months after project starts	O Gimenez
Scientific publication: community sensitivity analyses (birds)	Submitted max 30 months after project starts	R Pradel
Scientific publication: community sensitivity analyses for transient dynamics (wolf)	Submitted max 32 months after project starts	E Marboutin
Scientific publication: relative importance of demographic param. in community dynamics	Submitted max 30 months after project starts	I LeViol
Scientific publication: integrated community models; comparison of estimation methods	Submitted max 42 months after project starts	O Gimenez
Scientific publication: multispecies demographic models in a stochastic framework	Submitted max 24 months after project starts	A Robert
Scientific publication: integral projection models as state-space models	Submitted max 30 months after project starts	O Gimenez
Scientific presentations: At least 10 talks or posters (over the entire project)	Submitted max 42 months after project starts	All
Work package 2: case studies		
Scientific publication: Effect of climate forcing on a simple predator-prey system	Submitted max 24 months after project starts	C Barbraud
Scientific publication: Impact of climate forcing on a community of songbirds	Submitted max 36 months after project starts	PY Henry
Scientific publication: Coexistence of tuna species, with emphasis on the role of age	Submitted max 36 months after project starts	E Chassot
Scientific publication: Community modeling of large carnivores and their preys (meth.)	Submitted max 30 months after project starts	C Duchamp
Scientific publication: Recommendations on managing wolf-ungulate communities (appl.)	Submitted max 30 months after project starts	C Duchamp
Policy report: Recommendations on management of wolf-ungulate communities	Submitted max 30 months after project starts	E Marboutin
Policy report: Recommendations on management of tuna communities	Submitted max 36 months after project starts	E Chassot
Scientific presentations: At least 10 talks or posters (over the entire project)	Max 46 months after project starts	All
Work package 3: software		
Scientific publication: introduction of the software (for Methods in Ecol and Evol)	Submitted max 46 months after project starts	R Choquet
Report: Users' guide	Available max 46 months after project starts	R Choquet
Website: tutorial with case studies on a wiki (e.g., http://occupancyinesurge.wikidot.com/)	Online max 46 months after project starts	All
Broader deliverables		
Two post-doctoral researchers, one research engineer and several master students trained	By the end of the project	All
Scientific publication: Review paper on multispecies demography	Submitted max 44 months after project starts	All
Popular publication: the link between demography and animal communities	Submitted max 46 months after project starts	All
International workshop: multispecies demography, community dynamics and software	Takes place max 46 months after project starts	All

Travel ('missions')

- Attendance of international conferences for dissemination of the project's results and exchange of ideas with the broader scientific community. These are budgeted at 16000€, estimated assuming a total of 8 participations over the 4 years of the project, at 2000€/unit on average.
- Attendance of national conferences. These are budgeted at 8000€, estimated assuming a total of 8 participations over the 4 years of the project, at 1000€/unit on average.
- Internal meetings and other travel: involving just a subset of the partners or with other experts, for working on particular tasks (e.g. data exchange, specific analyses). Estimated at €8000.
- Four 3-day workshops (including the kick-off meeting but excluding the international workshop at the end of the project for which the attendees will have to pay fees): budgeted at a total of 30000€, estimated assuming 1050€ per person for international travel and accommodation in Montpellier for 5 collaborators, plus meals for 25 participants @30€/day for 3 days.

Other expenses ('autres dépenses externes')

- Software and hardware, estimated at €9000, assuming six workstations at €1500 each.
- Publication fees (figures charges, page charges) plus general functioning charges (printing, postage, stationary etc) estimated at €9000 over the four years.

Partner 2: CEBC Chizé (requested funding: €23816)

Non-permanent staff ('personnels non permanents avec financement ANR demandé')

- Two 6-month students will be hired to work on WP2 (2 x €3276 = €6552).

Travel ('missions')

- Attendance of international conferences for dissemination of the project's results and exchange of ideas with the broader scientific community. These are budgeted at 6000€, estimated assuming a total of 3 participations over the 4 years of the project, at 2000€/unit on average.
- Attendance of national conferences. These are budgeted at 2000€, estimated assuming a total of 2 participations over the 4 years of the project, at 1000€/unit on average.
- Internal meetings and other travel: involving just a subset of the partners or with other experts, for working on particular tasks (e.g. data exchange, specific analyses). Estimated at €3000.

Other expenses ('autres dépenses externes')

- Software and hardware, estimated at €3000, assuming two workstations at €1500 each.
- Publication fees (figures charges, page charges) plus general functioning charges (printing, postage, stationary etc) estimated at €1500 over the four years.

Partner 3: MARBEC Sète (requested funding: €20036)

Non-permanent staff ('personnels non permanents avec financement ANR demandé')

- Two 6-month students will be hired to work on WP2 (2 x €3276 = €6552).

Travel ('missions')

- Attendance of international conferences for dissemination of the project's results and exchange of ideas with the broader scientific community. These are budgeted at 4000€, estimated assuming a total of 2 participations over the 4 years of the project, at 2000€/unit on average.
- Attendance of national conferences. These are budgeted at 1000€, estimated assuming a total of 1 participations over the 4 years of the project, at 1000€/unit on average.
- Internal meetings and other travel: involving just a subset of the partners or with other experts, for working on particular tasks (e.g. data exchange, specific analyses). Estimated at €4000 (E Chassot is based in the Seychelles [expatriation] for the 2 first years of the project).

Other expenses ('autres dépenses externes')

- Software and hardware, estimated at €1500, assuming one workstations at €1500 each.
- Publication fees (figures charges, page charges) plus general functioning charges (printing, postage, stationary etc) estimated at €1500 over the four years.

Partner 4: ISEM Montpellier (requested funding: €18956)

Non-permanent staff ('personnels non permanents avec financement ANR demandé')

- Two 6-month students will be hired to work on WP1 and WP2 (2 x €3276 = €6552).

Travel ('missions')

- Attendance of international conferences for dissemination of the project's results and exchange of ideas with the broader scientific community. These are budgeted at 4000€, estimated assuming a total of 2 participations over the 4 years of the project, at 2000€/unit on average.

- Attendance of national conferences. These are budgeted at 2000€, estimated assuming a total of 2 participations over the 4 years of the project, at 1000€/unit on average.
- Internal meetings and other travel: involving just a subset of the partners or with other experts, for working on particular tasks (e.g. data exchange, specific analyses). Estimated at €2000.

Other expenses ('autres dépenses externes')

- Software and hardware, estimated at €1500, assuming one workstation at €1500 each.
- Publication fees (figures charges, page charges) plus general functioning charges (printing, postage, stationary etc) estimated at €1500 over the four years.

Partner 5: CESCO Paris (requested funding: €197433)

Non-permanent staff ('personnels non permanents avec financement ANR demandé')

- A 2-year post-doc will be recruited ('chercheur CDD'; €5145*24); s/he will play an essential role by leading the application of WP1 to the case studies in WP2. S/he will ideally be someone with a strong background in ecology with experience on demography and/or community ecology of several different biological systems; s/he will be willing to spend much time working on a computer building models. Obviously, s/he will demonstrate good interpersonal skills needed for working as part of a large team. The post-doc will work under the supervision of A. Robert, P.-Y. Henry and O. Gimenez and will be based at CESCO (partner 5) with several short sojourns that will be scheduled to work with the different partners involved in WP2.

- Three 6-month students will be hired to work on WP1 and WP2 (3 x €3276 = €9828).

Travel ('missions')

- Attendance of international conferences for dissemination of the project's results and exchange of ideas with the broader scientific community. These are budgeted at 12000€, estimated assuming a total of 6 participations over the 4 years of the project, at 2000€/unit on average.
- Attendance of national conferences. These are budgeted at 4000€, estimated assuming a total of 4 participations over the 4 years of the project, at 1000€/unit on average.
- Internal meetings and other travel: involving just a subset of the partners or with other experts, for working on particular tasks (e.g. data exchange, specific analyses). Estimated at €4000.

Other expenses ('autres dépenses externes')

- Software and hardware, estimated at €7500, assuming five workstations at €1500 each.
- Publication fees (figures charges, page charges) plus general functioning charges (printing, postage, stationary etc) estimated at €6000 over the four years.
- Equipment for captures of birds: 40 euros per mistnet x 10 units per new site x 10 new sites per year = 4000 euros / year x 4 years = 16000 euros. Bird ringers volunteer for the collection of STOC Capture (Constant Effort ringing Site) data. However, as any citizen-based monitoring project, we need to provide volunteers with incentives to maintain their involvement, and their willingness to follow this rather time-consuming, expensive and exhausting protocol. The basic incentive to recruit and maintain bird ringers is to provide them with part of the mist-nets they need. Hence, with the ANR funding, we will fund the creation of 10 new STOC Capture sites per year, what compensates for the number of CES sites where ringing stops per year.

Partner 6: MECADEV Brunoy (requested funding: €0)

Partner 7: ONCFS Gières (requested funding: €15716)

Non-permanent staff ('personnels non permanents avec financement ANR demandé')

- Two 6-month students will be hired to work on WP1 and WP2 (2 x €3276 = €6552).

Travel ('missions')

- Attendance of international conferences for dissemination of the project's results and exchange of ideas with the broader scientific community. These are budgeted at 2000€, estimated assuming a total of 1 participations over the 4 years of the project, at 2000€/unit on average.
- Attendance of national conferences. These are budgeted at 1000€, estimated assuming a total of 1 participations over the 4 years of the project, at 1000€/unit on average.
- Internal meetings and other travel: involving just a subset of the partners or with other experts, for working on particular tasks (e.g. data exchange, specific analyses). Estimated at €2000.

Other expenses ('autres dépenses externes')

- Software and hardware, estimated at €1500, assuming one workstation at €1500 each.
- Publication fees (figures charges, page charges) plus general functioning charges (printing, postage, stationary etc) estimated at €1500 over the four years.

3. DISSEMINATION AND EXPLOITATION OF RESULTS, INTELLECTUAL PROPERTY, GLOBAL IMPACT

3.1 Global impact

The research proposed opens new and important horizons in biodiversity dynamics and forecasting. Regarding the case studies, Objective 4 on seabird communities in Antarctica will provide a unique opportunity for studying the effects of climate change on ecosystems as these top predators are seen as reliable indicators of global changes and of the state of the marine ecosystems and biodiversity. Expected results for Objective 5 are the understanding of individual *versus* species contributions to communities' responses to climate change, using common bird communities as model. Two-third of the European and North-American countries have set up similar biodiversity monitoring observatories (with bird indicators) as the ones that we will use in that project(9). The framework we will develop to predict species distribution while accounting for intra-specific variability and interactions will provide a canvas for future analyses in Europe and North America. The multispecies fisheries model we will develop in Objective 6 will be the first of its own and will fulfill important recommendations made in the field to switch at the level of communities to manage fish stocks(138). The multispecies model for large carnivores management in Objective 7 will provide the ingredients for promoting coexistence between these species and human activities, a pressing demand of the civil society.

Regarding the methodology, our proposal is at the forefront of research in diagnosing and predicting the impact of global change on biodiversity by explicitly incorporating the response of species by their own and in interaction with others, and the models and methods we will develop has the potential to serve as a baseline for next-generation models for biodiversity forecasting (Objectives 1-3). We will develop flexible and generalizable methodologies that could then be used in any other communities than the one considered here and in other regions. In particular, the development of flexible, reliable and user-friendly software will contribute to the national and international visibility of our consortium and young researchers (Objective 8).

Finally, the project will enhance the research capabilities for frontier research in France and Europe by a) reinforcing the links between population and community ecologies by gathering senior scientists and young scientists largely involved in the project and b) hiring 2 (non-necessarily French) researchers and 1 research engineer who will be employed on the DEMOCOM project with long-term contracts (2 years). They will be trained by the members of the DEMOCOM team, will collaborate with researchers associated to the project (national and international), will attend workshops and benefit from specific training in statistics, demography and community ecology provided in the DEMOCOM labs (doctoral schools' lectures), and will benefit from the DEMOCOM members' network (in particular regular exchanges with the UK National Centre for Statistical Ecology <http://www.ncse.org.uk/> in which the PI is a international member) and will thus acquire necessary competencies, abilities to gain their own independence afterwards.

3.2 Dissemination and exploitation of results

Communication to scientific audiences

We will attend international conferences and publish papers in ranked A statistical and biological journals, including papers to publicize the software. In the same vain, we will organize symposia and/or workshops (if proposals accepted) in the meetings of the French and British Ecological Societies, as well as at the International Statistical Ecology Conference in 2018 and 2020 (the PI was in charge of the organization of ISEC2014 at Montpellier).

Related to the methods and software, we will organize an international workshop in the last year gathering people involved in the project and external collaborators (scientists, managers from abroad with interest and expertise in community ecology). The aim will be to operate a transfer of knowledge using the software and make DEMOCOM available. The feasibility, relevance and impact of this workshop will be high thanks to the strong experience that Partners 1 and 6 have accumulated over the years in the dissemination of practical tools for the statistical and mathematical analysis of complex datasets to students, researchers and conservation practitioners (see section 2.3).

The DEMOCOM consortium has discussed the issue of sharing the long-term research data used in this project since several journals have now changed their policies and make this a requirement. Every data used in this project will be shared freely among partners, and also the object of a written ‘contract’ for its use and application, and embargoes will be negotiated with the journals upon publication of results if needed.

Communication to managers and decision makers

Some of the DEMOCOM outputs will be disseminated to managers and decision makers. Importantly, stakeholders involved with ONCFS will provide first hand communication to managers and decision makers.

- C Barbraud (partner 2) has regular contacts and work in collaboration with the Réserve Naturelle Nationale des Terres australes françaises (Natural Reserve of the French Austral Territories). Results on the effects of climate change on the demography of skuas and their main preys at Kerguelen will be transferred to the Naturel Reserve. This organism will integrate some of the findings in its next five-year management plan.
- E Chassot (partner 3) has regular contacts with the regional bodies in charge of tuna fisheries management. Results on the demography of pelagic fish communities will be presented through oral communications at the annual working groups and Scientific Committees of the Indian Ocean Tuna Commission (IOTC) and International Commission for the Conservation of Atlantic Tunas (ICCAT).
- F Jiguet (partner 5) is in charge of the common birds indicators at CESCO and is already communicating these results to ONERC, the French Observatory of the effects of climate warming and the Ministry of Ecology. This organism is eager for more precise indicators of responses to climate change, so our results on the response of common bird communities in the face of climate change will be of special interest to them and should be easily transferred. Besides, the CESCO is based at the Paris Museum where is also hosted the European Topic Center on Biodiversity, with interactions favoring the dissemination of scientific results to the European Environment Agency and therefore to stakeholders.
- E. Marboutin, M. Guinot-Ghestem Murielle (partner 7) have close relationships with managers from departmental hunting federations and other research units at ONCFS (on game bird species in particular). The transfer of the outcomes of the project will obviously benefit from this proximity. Also, they have direct access to decision makers from the ministries of both ecology and agriculture as ONCFS is in charge of implementing the government policies in terms of management.

Communication to a non-specialist audience

- *Public conferences organized at the National Museum of Natural History* (partners 5 and 6): The Natural History Museum organizes each year several events, monthly or weekly, aiming towards a general audience such as public lectures, conferences which can be as many opportunities to share our results to a non specialist audience, but with a strong interest for science. In addition, CESCO takes part in training in Ecology aimed at environmental managers and policy makers. These interventions facilitate the transfer of information (knowledge, methodology) towards policy makers.
- *Regards of The Société Française d'Ecologie*: the French Ecological Society devotes part of its website to opinion papers emanating from researchers and aimed at the general public (<http://www.sfecologie.org/regards/>), with the possibility of interactions when readers react to the articles. V Devictor is largely involved in this action (partner 4). The DEMOCOM consortium plans on writing an opinion paper on why population and community ecologists should join their efforts in the study of animal responses to climate change and management interventions, supported with examples from the literature and / or the DEMOCOM project.
- *Fête de la science* is a yearly exhibition and will represent a great opportunity for us to share our projects with a general audience.

Communication to students

Last but not least, several members of the DEMOCOM consortium have teaching responsibilities and will disseminate through their teaching the knowledge, methods and ecological results to their respective audiences, hence making them aware of the importance of integrating demography in community ecology. As teachers, we will use singular results from the project as ‘text book examples’ in the lectures that we regularly deliver to undergraduate and graduate students.

- R. Pradel and R. Choquet (partner 1): « Population dynamics for conservation biology » for Master students;
- O. Gimenez (partner 1): « Biostatistics for ecologists » for Master students;
- C. Barbraud (partner 2): « Impact of global changes on southern ocean seabirds » for Master students;
- A. Robert (partner 5): « Dynamique des populations et évolution des traits d'histoire de vie - applications de modèles matriciels » for Master students;
- I. Le Viol (partner 5): « La préservation de la biodiversité : méthodologie et concepts », « Méthodologies d'échantillonnages, analyses de données » for Master students;
- P-Y Henry and O Dehorter (partners 5 & 6): « How to analyze data from bird ringing programs » for volunteer bird ringers and biodiversity managers (<http://www2.mnhn.fr/crbpo/spip.php?rubrique94>).

Non-target audience

We will publish the latest news of the consortium, including workshop reports, on a website specifically devoted to the project. We do not envisage anything fancy or expensive, but sufficiently attractive to be read: a Google or a WordPress site will do the job, which will be maintained by the PI (see his personal website <https://oliviergimenez.wordpress.com/> for an example). A social network medium we have found very efficient to communicate about science is Facebook, and we plan to have one for the project that will be regularly updated; the PI has had a fruitful experience with the page that he has been maintaining for his former team for a year now, with almost 1500 followers (<https://goo.gl/xs6bno>).

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