# SUMMARY

In a rapidly changing world, we need operational tools to predict and manage responses of biodiversity. The unprecedented rapid changes presently observed in natural habitats also represent a unique opportunity to improve our knowledge of evolutionary mechanisms in wild bird populations.

## *Determinants of evolutionary potential in wild populations*

To date, although it is clear from both theoretical and empirical work that adaptation can influence the persistence of populations on short time scales, biodiversity scenarios are conspicuously lacking an evolutionary component. One major limitation to the implementation of scenarios including adaptation dynamics is that our knowledge of evolutionary potential and constraints is still too imperfect. In this project, we propose to improve our understanding of adaptive mechanisms in wild populations by integrating theoretical and empirical approaches in wild bird populations at different spatial and taxonomic scales.

## *A quantitative and molecular genetics approach*

Using state of the art molecular and quantitative genetics tools in combination with demographic analysis, we used several populations / species of birds studied in the long-term to identify i) forces of selection acting on natural populations, and especially forces driven by climate change, ii) environmental factors affecting dispersal rates, with a special interest for habitat structure and fragmentation, iii) ecological and phylogenetic factors shaping genetic architecture and affecting its stability, and iv) regions of the genome showing signatures of selection and therefore likely to be partially responsible for local adaptation. Using a comparative approach among populations and species allowed investigations of evolutionary processes at different time and space scales to link micro and macroevolutionary patterns.

## *Results*

First, we show that the force of natural selection is influenced by climate warming. In particular, a long-term study of blue tits reveals that extreme climatic events such as very warm springs can strongly increase the force of natural selection on timing of breeding. Second, we show a strong conservatism of genetic architecture for morphology and life history traits in blue tits at a small temporal scale (~ 20 years) and at a spatial scale of up to 400 km despite large habitat differences. Responses to selection could therefore be predicted at the temporal and geographic scales at which management decisions are made. However, the evolutionary potential varies among populations across Europe or between species depending on ecological conditions and the phylogenetic proximity of species.

## *Scientific production*

This project has resulted in 27 publications, and 16 are still in preparation or submitted. These publications are organized around five major themes: the patterns of variation of the evolutionary potential, the local adaptation, the study of the selection pressures, the conservation implications (adaptation to climate change and population dynamics) and finally promoting the study of evolution in wild populations.

# INTRODUCTION

In a rapidly changing world, we need operational tools to predict and manage responses of biodiversity. To date, although it is clear from both theoretical and empirical work that adaptation can influence the persistence of populations on short time scales, biodiversity scenarios are conspicuously lacking an evolutionary component.

One major limitation to the implementation of scenarios including adaptation dynamics is that so far, attempts to predict adaptive responses in wild populations have yielded equivocal results [1,2], suggesting that **our understanding of evolutionary potential, and hence of evolutionary constraints is still rather limited. In order to integrate evolutionary biology into conservation action, we thus need to improve our understanding of evolutionary potential in the wild, as well as the extent of its variation within and across populations, between species and among taxa.**

Predicting evolutionary responses requires knowledge of trait inheritance and selection pressures acting on this trait. Most often, the simple univariate case is investigated. However, phenotypes result from the interaction of several characters that are potentially linked functionally, developmentally and genetically, and approaching phenotypes as a set of independent traits may give a very misleading picture of expected phenotypic responses to selection [3]. The importance of G matrices (the matrix of additive genetic (co) variances) in imposing constraints has thus been increasingly acknowledged in the past couple of years. In many cases, genetic variance is not present in all directions so that some combinations of traits cannot be achieved [4,5]. Such genetic architecture leads to reduced rate of adaptation compared to expectations in the absence of genetic correlations.

Five major questions on genetic architecture emerge:

(1) What is the pace of change of genetic architecture e.g. how many generations or which geographical distances are needed before a change in G is observable?

(2) Does the rate of change in the G matrix depend on the type of trait studied, *i.e.* life history traits, behavioural traits, and morphological traits?

(3) Which species are more likely to maintain constant genetic architecture? We believe this question has simply never been investigated. In the same way that species can display different sensitivities to global [6] and climate change [7] based on their ecological niche, our aim here is to understand how the evolutionary potential of a set of species is distributed. For example, do species that are more phylogenetically similar also harbour similar constraints/ evolutionary potential?

(4) Can existing quantitative genetic methods estimating G matrices quantitatively capture the evolutionary dynamics of constraints imposed by climate change? Since G matrices most likely reflect past selection patterns, are they in line with the selection signatures measured at the genomic level?

(5) What are the factors influencing the genetic architecture? Theory predicts that G matrices should be influenced by mutation, **selection**, genetic drift and **migration**[1] [8–10], but there is very scarce information about which of these forces play a key role in wild populations [10].

The aim of this project was to improve our understanding of adaptive mechanisms in wild populations by integrating theoretical and empirical approaches in wild bird populations at different spatial and taxonomic scales. Originally, the project was organized around four tasks:

Task 1- **Temporal stability of the matrix G**: Evaluate the stability of the matrix G from datasets but also identify the selection patterns affecting the G matrices. Comparison of empirical results with theoretical predictions.

Task 2- **Signature of selection at the genomic level**, approach between habitats. Characterization of genetic variability and genomic selection signatures to better understand gene flow and population differentiation

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[1] Note that from here migration refers to dispersal between populations and not seasonal migration

Task 3- **Spatial scales of the stability of G**: Analysis of the stability of G in relation to the selection and gene flow. Multivariate analysis of local adaptation.

Task 4- **Macroevolutionary approach**: Estimation of genetic variance-covariance matrices on more than 20 species. Characterize their variation and relate to phylogenetic covariance of species. Identification of ecological and phylogenetic factors affecting the G structure and determining the evolutionary potential. Application to conservation.

However, further gaps in our knowledge and missing stepping stones were identified during the project. Task 2 was broaden to the study of local adaptation to get a deeper understanding of evolutionary mechanisms at play on small geographic scales. Task 4 was divided into 1) Investigating changes of G at the macroevolutionary scale and 2) the deepening our understanding of the effect of environmental change on populations by investigating phenotypic and population dynamics effects of environmental change. Finally, two other aspects were emphasized. First, because evolutionary potential is the interplay between G matrices and selection, we also focused on characterizing natural selection in wild populations. Second, we aimed at promoting quantitative genetic studies. Notably, publishing collaborative papers revealed the challenge and difficulties arising from the use of public data archiving, which we addressed.

# METHODS

Using state of the art molecular and quantitative genetics tools in combination with demographic analysis, we used several populations / species of birds studied in the long-term to identify i) forces of selection acting on natural populations, and especially forces driven by climate change, ii) environmental factors affecting dispersal rates, with a special interest for habitat structure and fragmentation, iii) ecological and phylogenetic factors shaping genetic architecture and affecting its stability, and iv) regions of the genome showing signatures of selection and therefore likely responsible for adaptation to different environments. Using a comparative approach among populations and species will allow investigating evolutionary processes at different time and space scales and hence link micro and macroevolutionary patterns.

# MAIN RESULTS

## *Patterns of genetic architecture (Tasks 1, 3, 4)*

We show a strong conservatism of genetic architecture for morphology and life history traits at small temporal scale (~20 years) and on a spatial scale up to 400km in spite of large habitat differences [11]. These results are at odds with several studies suggesting strong variability of the G matrix [12,13]. Our results suggest that responses to selection can be predicted over time and geographic scales over which management decisions are made. This work was done in collaboration between Partners 1 &2. Interestingly, we also found some variation of G matrices at larger spatial scale (e.g. across Europe [14]) and across species.

A major result is that we can detect a signal of phylogenetic conservatism for G matrices across species: constraints exist regarding the variation of the G matrix but matrices are not similar across all species [15]. Such changes were found for life history traits but not for morphology, confirming the prediction of Arnold et al [16]. A strong prediction was also that specialist species are likely to have lower evolutionary potential than generalist species because they are submitted to more constant selection pressures. However, this prediction received only slight support, so that we probably do not expect a much higher extinction risk of specialists only based on these estimates of their evolutionary potential [15,17]. This work was done in collaboration between Partners 1, 2 & 3.

### Natural selection (New Task)

Predicting responses to selection requires accurate estimation of selection, a complex task in the wild e.g. because of spatial heterogeneity and the difficulty to estimate fitness [18,19]. We also showed how skewness in the distribution of phenotypic traits may lead to detect directional selection even at equilibrium, resulting in erroneous expectations of evolutionary response [20].

Predictions of evolutionary responses also require to understand how environmental changes affect selection pressures. In the face of climate change, a further complexity is the increase rate of extreme events. For the first time, a thorough investigation of extreme climatic events reveals that they can substantially increase the strength of selection during the birds' breeding period [21].

### Local adaptation and gene flow (Task 2)

First, we applied next generation DNA sequencing (RAD-Seq) to test whether phenotypically differentiated populations of wild blue tits breeding in a highly heterogeneous environments exhibit genetic structure, in particular in relation to habitat type. We found multiple evidence that genetic variation is influenced by geographical distance but also habitat type [22] (deciduous vs. evergreen oaks) ref. Second, we combined these results with available phenotypic data and show that the very strong divergences in phenotypes across the two habitats for a wide range of traits (including personality traits [23], and colour ornaments[24]), reveal a fascinating case of adaptation to environmental heterogeneity at a very fine geographical scale compared to the species dispersal abilities [25]. Overall, the combination of approaches converges to the conclusion that the strong phenotypic differentiation observed in Mediterranean blue tits is a fascinating case of local adaptation.

### Responses to climate change and Applications to conservation (Task 4)

Predictions for conservation require to understand

(1) How does demographic heterogeneity affect population dynamics via variation in survival? We first assessed the link between demographic heterogeneity and environmental conditions by focusing on a well-known component of heterogeneity: the positive covariation of survival and breeding success within population. We showed that the positive variation increases when conditions are favorable [26]. We also investigated the effects of actuarial senescence on population dynamics and showed that senescence can affect population dynamics and viability [27] including in managed populations [28].

(2) Which traits are of importance for population persistence? Changes in phenology and body size are often mentioned as two of the most important responses to climate change. To understand and predict extinction risks based on these phenotypic characteristics it is crucial to understand the nature of these responses. We investigated the role of (mal)adaptive plasticity and evolution in phenology and body size changes. While changes in body size seem in general maladaptive [29], changes in phenology are often adaptive [30,31]. Most often these changes are due to plasticity but consistent directional selection pressure for earlier breeding suggest that focusing on evolutionary potential and constraints for these traits is of major importance. This work was done by Partners 1 &2.

### Long term data archiving (New Task)

Public data archiving is the archiving of primary data used in publications so that they can be preserved and made accessible to all online. Public data archiving is increasingly required by journals. However, the costs of public data archiving might be underestimated, in particular with respect to long-term studies. We showed why such policy might decrease the incentive to maintain or start new long term monitoring programs. The article was published in TREE [32] and got a reply from editors from the major journals in ecology and evolution [33].

## DISCUSSION

In term of the defined tasks, the work is almost complete. Although some manuscripts are not published yet, they will be in the near future. We have now a clearer picture of the rate of change of the G matrix, which is more stable on the short term than previous studies led to believe (but see [10]). In contrast with this, our results also show that the G matrix is not stable over long time scales, challenging a fundamental hypothesis of macroevolutionary studies which consider the genetic architecture to be stable. Future studies should integrate this finding and evaluate the extent to which estimations of evolutionary rates are invalidated by the violation of this assumption. In terms of macroevolution, this work has also led to the development of a project with Michael Morrissey (St Andrews University) to investigate how genetic architecture explains evolutionary allometry and thus long term evolutionary trajectories, focusing on in birds.

Our objectives also included the prediction of extinction risk based on evolutionary potential and to communicate these results to stake holders. However, building eco-evolutionary models is still a great challenge, as can be seen from recent controversy around IPMs [34,35], even for univariate models. It should thus be a full project on its own to develop models including a multivariate perspective. It is part of our plans to apply for funding for a two years post doc to tackle these issues.

Because of this, the integration of evolutionary potential into predictive models is not done and for obvious reasons communication to stake holders did not occur on these specific issues. However limits to adaptation and evolutionary constraints are of interest and Anne Charmantier contributed to the redaction of the report of the French Academy of Science on the mechanisms of adaptation of biodiversity to climate change and their limits[2]. Discussions are ongoing with UICN to evaluate how even just using our conceptual advances could be fruitfully used.

## CONCLUSIONS

Predictability of evolution is possible but it is still a great challenge, both applied and theoretical. Many progresses have been made and we believe this project has significantly contributed to clarify how genetic architecture, natural selection and thus evolutionary responses are shaped in wild populations. However, while evolution can be predicted in relatively simple and well characterized systems such as human flu or cow milk production, further integration of ecological and evolutionary dynamics are still needed before predictions can be safely applied to predictive models for wild animal populations.

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[2] http://www.academie-sciences.fr/pdf/rapport/rads_270617.pdf
[3] In bold, publications from the project

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