

ParrotNet WG 4 – Evolutionary Change and Prediction of Invasion

All available evidence will be reviewed including current research and datasets, to establish extent and nature of evolutionary change by invasive parakeets in response to novel environments. Utility of different data types will be evaluated and prioritised for predicting future invasion pathways. WG4 will comprise Action participants with expertise in molecular genetics and all aspects of evolutionary ecology and invasion biology, together with other scientific and academic expert contributors.

Task 1: Review available evidence for adaptation by parakeets, set in context of climate change, environmental disturbance, urbanisation and agricultural land-use change across Europe (linking to WG3).

Task 2: Evaluate and compare utility of different data types for detecting signals of adaptation. Identify important gaps in knowledge and datasets and allocate STSMs accordingly (linking to WG3).

Task 3: Harmonise priority datasets across national boundaries, summarise and set results in context of environmental and anthropological change.

Milestone 1: Report on evidence for adaptation

Milestone 2: Protocols developed for harmonisation of national data sets and STSMs aligned.

Milestone 3: Publish findings on evidence for evolutionary change by invasive parakeets.

In order to evaluate the extent to which invasive parakeets are likely to undergo evolutionary changes, and the ramifications this may have, WG4 first discussed which general mechanisms that were most likely to act on parakeet invasions. During these discussions, the following topics emerged: (1) behavioural flexibility, (2) intraspecific variation, (3) enemy release, (4) introduction effort ('propagule pressure') and (5) adaptive, micro evolutionary changes.

(1) Behavioural flexibility.

Luna et al (2017) hypothesized that indeed, climate similarity favors biological invasion, but a match between seasonality in the novel range and the timing of life cycle events of the invader also influences the outcome of species introduction. Yet, such phenology effects on invasion success have generally been neglected. Whether a phenological mismatch limits the non-native range of the ring-necked parakeet in Europe, was the focus of this WG4 study. Given the latitudes at which parakeets have

established across Europe, they breed earlier than expected based on breeding dates from their native Asian range. Moreover, comparing the breeding dates of European populations to those of parakeets in Asia, to five native breeding bird species in Europe and to the start of the growing season of four native European trees, the discrepancy between expected and actual breeding phenology is greater in northern Europe. In these northern populations, this temporal mismatch appears to have negative effects on hatching success, and on population growth rates in years that are colder than average. Phenological mismatch also can explain why parakeets from African populations (that are more likely to breed in autumn) have been poor invaders compared to parakeets from Asia. These lines of evidence support the hypothesis that the reproductive phenology of the ring-necked parakeet can be a limiting factor for establishment and range expansion in colder climates. Results provide growing support for the hypothesis that the match between climate seasonality and timing of reproduction (or other important life cycle events) can affect the establishment success, invasive potential and distribution range of introduced non-native species, beyond the mere effect of climate similarity.

(2) Intraspecific niche variation

A second main hypothesis identified was that intraspecific niche variation at least partly underlies the invasion success of parakeets. Indeed, Jackson et al. (2015) argue that understanding genetic patterns and evolutionary processes that reinforce successful establishment is paramount for elucidating mechanisms underlying biological invasions. However, little is known about the evolutionary genetic origins of invasive parakeets, and about what population genetic signatures tell us about patterns of invasion. Jackson et al. (2015) set out to reveal the ancestral origins of invasive ring-necked parakeet populations across the invasive range, and explore the potential influence of climate and propagule pressure from the pet trade on observed genetic patterns. Ring-necked parakeet samples representing the ancestral native range were collected from museum specimens, and modern samples from the invasive range were gathered from across Europe, Mauritius and Seychelles, and sequenced for two mitochondrial DNA markers comprising 868 bp of cytochrome b and control region, and genotyped at 10 microsatellite loci. Invasive populations comprise birds that originate predominantly from Pakistan and northern areas of India. Haplotypes associated with more northerly distribution limits in the ancestral native range were more prevalent in invasive populations in Europe, and the predominance of Asian haplotypes in Europe is consistent with the higher number of Asian birds transported by the pet trade outside the native range. The authors conclude that successful establishment of invasive species is likely to be underpinned by a combination of environmental and anthropogenic influences.

Based on the findings of Jackson et al. (2015), Strubbe et al. (2015) reasoned that intraspecific genetic variation may be indicative of intraspecific variation in environmental niche requirements. Strubbe et al. (2015) subsequently assessed whether the ring-necked parakeets' association with human-modified habitats in the native range and its within-taxon niche structure shape the distribution of invasive populations at biogeographical scales and influence the reliability of predictions of invasion risk. They found that ring-necked parakeets show considerable niche expansion into climates colder than their native range. Only when incorporating a measure of human modification of habitats within the native range do bioclimatic envelope models yield credible predictions of invasion risk for parakeets across Europe. Invasion risk derived from models that account for differing niche requirements of phylogeographic lineages and those that do not achieve similar statistical accuracy, but there are pronounced differences in areas predicted to be susceptible for invasion. Strubbe et al. (2015) concluded that information on within-taxon niche structure and especially association with humans in the native range can substantially improve predictive models of invasion risk. To provide policymakers with robust predictions of parakeet invasion risk, including these factors into bioclimatic envelope models is recommended.

Intrigued by the fact that ring-necked parakeets have so successfully invaded parts of Europe, despite being introduced in small numbers, at least according to ornithological literature, Jackson et al. (in prep) investigated the genetic variation present in European parakeet populations. These authors attempt at estimating the true severity of population bottleneck and associated loss of heterozygosity using microsatellite genotype data. They applied our novel approach to calculate bottleneck effects across 10 populations of invasive ring-necked parakeets in Europe, against a backdrop of population genetic architecture. Their findings demonstrate that observed genetic bottlenecks are substantially milder than would be expected from demographic records of population growth, and were supported by higher than expected numbers of founders based on allelic frequency data. High levels of within-population genetic diversity were observed across all invasive populations. The discrepancies between the severe population bottlenecks indicated by historical demographic data on invasive parakeet populations, mild genetic bottlenecks inferred from the genetic data and high contemporary levels of genetic diversity, suggest that the invasive populations of ring-necked parakeet in Europe have been 'topped-up' by continuing escapes from captive populations. For policy-makers tasked with managing the spread of invasive species, an important role of genetic contributions from additional individuals in successful invasions would suggest that policies to prevent such releases by way of minimising trade and breeding for pets, can ameliorate the invasive alien species problem.

Along similar lines, Edelaar et al (2015) noted that while genetic diversity is hypothesized to be an important factor explaining invasion success, there is no consensus yet on how variation in source populations or demographic processes affects invasiveness. Edelaar and colleagues (2015) used mitochondrial DNA haplotypic and microsatellite genotypic data to investigate levels of genetic variation and reconstruct the history of replicate invasions on three continents in the monk parakeet (*Myiopsitta monachus*). They evaluated whether genetic diversity at invasive sites could be explained by (i) the native source populations from which they were derived and (ii) demographic bottlenecks during introduction. Genetic data indicated a localized source area for most sampled invasive populations, with limited evidence for admixing of native source populations. This pattern largely coincides with historical data on pet trade exports. However, the invasive populations are genetically more similar than predicted from the export data alone. The extent of bottleneck effects varied among invasive populations. The observed low genetic diversity, evidence of demographic contraction and restricted source area do not support the hypothesis that invasion is favoured by the mixing and recombining of genetic variation from multiple source populations. Instead, they suggest that reduced genetic variation through random processes may not inhibit successful establishment and invasion in this species. However, convergent selection across invasive sites could also explain the observed patterns of reduction and similarity in genetic variation and/or the restricted source area. In general, the alternative explanation of intraspecific variation in invasive potential among genotypes or geographic areas is neglected, but warrants more attention as it could inform comparative studies and management of biological invaders.

Meanwhile, Ancillotto et al (2016) noted that most studies have been carried out on ring-necked and monk parakeets, as they are the most successful invasive parrots globally. Recently, however, reports of invasive Alexandrine parakeet *Psittacula eupatria* have increased. The authors first summarized the current knowledge on the occurrence of Alexandrine parakeets outside their natural range and then assessed the degree of niche conservatism during the invasion process. Their results show that Alexandrine parakeets have established invasive populations predominantly in Europe, parts of the Middle east and Far Eastern countries such as Japan and Singapore. During the ongoing invasion of Europe, the Alexandrine parakeet considerably expanded its niche into colder climates with respect to those occupied in the native range. The Ancillotto et al (2016) study offers some support to the hypothesis that interspecific facilitation with previously established ring-necked parakeets *Psittacula krameri* may contribute to niche expansion and invasion success of congeneric Alexandrine parakeets. Species Distribution Models including both native and invaded range occurrence data predict a high invasion risk across multiple parts of the globe where the species is currently not yet present, thus

indicating a high potential for the Alexandrine parakeet for further invasion success and range expansion.

(3) Enemy release

Mori et al. (2015) were the first to focus on an important but often overlooked form of competition with native species, namely the parasite-mediated one. Introduced species may bring their own parasites from their native ranges (spillover) or get native parasites from native species, thus increasing the parasites' spread and transmission risk (spillback). Thus, a complete knowledge of parasites hosted by introduced species is important to assess and to possibly prevent impacts. Ring-necked and monk parakeets have been introduced in many European countries, where they established a number of alien reproductive populations. Mori and colleagues (2015) sampled 21 ring-necked parakeets and 7 monk parakeets from Italy and identified 35 arthropod ectoparasites belonging to five species. Amongst those, one species was native to India (*Neopsittaconirmus lybartota*), where alien populations of ring-necked parakeet may have been originated, and one species from South America (*Paragoniocotes fulvofasciatus*), which is typically found of the monk parakeet in its native range. The other three species of arthropod parasites were native to Italy and commonly found on native species, suggesting the possibility of spillback processes.

(4) introduction effort ('propagule pressure')

Cardador et al. (2015) realized that although propagule pressure and environmental constraints are among the most important factors determining invasion success, studies considering both factors simultaneously are scarce. Moreover, while recent evidence suggests that the environmental requirements of individuals from different geographical ranges may be different, the role of propagule origin in invasions has been largely overlooked. Their aim was to disentangle the relative role of niche requirements, propagule origin and propagule pressure on the distribution of an invasive bird species. Indeed, differences between niches of native Asian and African parakeets were found, with the Asian niche matching the European niche more closely. In the invasive European range, distribution of parakeets was mainly explained by the pure effect of year of first importation (as a proxy of time since first introduction), the pure effect of geographical origin of propagules and the joint effect of environmental suitability and year of first importation, but not by overall propagule pressure. Only when taking into account the fraction of individuals whose native niche fitted better the European conditions – Asian parakeets – was the role of propagule pressure highlighted by models. Thus, while environmental-based predictions calibrated on native ranges can constitute a useful first-screening tool, incorporating information about propagule pressure and especially about the variability in its

geographical origin may result in a much more thorough assessment of invasion risk. Trade data reveal as a valuable proxy of propagule origin and pressure that can be combined with niche modelling for predicting the fate of trade-mediated invasions in a variety of organisms.

Building on the above results, Cardador et al. (2016) focussed on the role of wildlife trade as a driver of parakeet invasions more generally. Wildlife trade is currently the most important and increasing source of vertebrate invasive species. However, exhaustive analyses of potential side effects of trade regulations on this pathway of introduction are lacking. They addressed this by combining environmental niche models and global trade data on parrots (Psittaciformes), one of the most widely traded and worldwide invasive taxa. We used the wild bird trade bans of United States (1992) and Europe (2005) as case-studies. Results showed that regional bans can generate geographic redirections in trade, with important consequences on worldwide invasion risk. While the amount of parrots traded internationally remained largely constant, changes in trade destination occurred. Consequently, the world surface predicted at risk of parrot invasions increased with successive bans. Of concern, a redirection of trade toward developing countries was observed. Attention should be paid on the mismatch between the global requirements of invasion management and the regional scales governing trade regulations.

(5) Adaptive, micro evolutionary changes.

Based on above-mentioned findings that European invasive populations occupy a colder climatic niche than in their native range, L Gros and colleagues (2016) argued that two main hypotheses may explain the success of Ring-necked parakeets in Europe: admixture between individuals from different origins and/or rapid adaptation to new environmental conditions. They applied molecular data to the origin of European populations of ring-necked parakeets, in order to assess whether these populations result from admixture between individuals from different source populations. They also investigated the morphology of individuals from European populations and from the native range to assess whether the invasive populations have morphologically diverged from their source and could have become adapted to European conditions. Le Gros et al. (2016) found evidence of admixture in some of the European populations but not all of them. Admixture between individuals from different origins within European populations thus cannot explain alone their invasive success. Conversely, they found that the morphology of the individuals from European populations has diverged from the morphology of native individuals, in a similar direction. Rapid adaptation to European environmental conditions via phenotypic plasticity or natural selection could thus be a factor explaining the invasive success of ring-necked parakeets in Europe.

Sells et al. (in prep) took this line of reasoning a step further, and applied a genomic approach to investigate whether adaptation within novel environments in response to fluctuating selective pressures can improve our understanding of how parakeet populations are able to invade areas much colder than their native range. They applied ddRAD-Seq and SNP genotyping to the ring-necked parakeet to identify signatures of microevolution through natural selection, that may help explain the species' remarkable establishment success and global distribution. Hierarchical analysis allowed identification of population structure at progressively finer spatial scales, progressively removing confounding processes that can mask signatures of selection. Globally introduced populations were of predominantly Asian ancestry, with differentiation of African native populations occurring through historical evolutionary processes. Levels of genetic diversity were maintained between Asian ancestral and all introduced populations, with genetic impoverishment found in African native populations. Reduced standing variation (and adaptive potential) in the African ancestral genome, could explain the near absence of African haplotypes in introduced populations. More recent island colonisations showed distinct structure likely reflecting strong founder effects. At the finest geographic scale, within Europe, weak neutral population structure reflected the origin of source populations within Asia. However, under a Bayesian approach to isolate signatures of rapid selection in response to climatic change, we identified linear correlations between allele frequencies and environmental variables across a climate spectrum. These correlations are proposed as evidence for rapid selection in response to climatic change within introduced ring-necked parakeet populations.

WG4 linked publications

Published

- Ancillotto, L., Strubbe, D., Menchetti, M. & Mori, E. (2016) An overlooked invader? Ecological niche, invasion success and range dynamics of the Alexandrine parakeet in the invaded range. *Biological Invasions*, **18**, 583-595.
- Cardador, L., Carrete, M., Gallardo, B. & Tella, J.L. (2016) Combining trade data and niche modelling improves predictions of the origin and distribution of non-native European populations of a globally invasive species. *Journal of Biogeography*, **43**, 967–978.
- Cardador, L., Lattuada, M., Strubbe, D., Tella, J.L., Reino, L., Figueira, R. & Carrete, M. (2017) Regional Bans on Wild-Bird Trade Modify Invasion Risks at a Global Scale. *Conservation Letters*, *in press*.
- Edelaar, P., Roques, S., Hobson, E.A., Gonçalves da Silva, A., Avery, M.L., Russello, M.A., Senar, J.C., Wright, T.F., Carrete, M. & Tella, J.L. (2015) Shared genetic diversity across the global invasive range of the monk parakeet suggests a common restricted geographic origin and the possibility of convergent selection. *Molecular Ecology*, **24**, 2164-2176.

Gros, A., Samadi, S., Zuccon, D., Cornette, R., Braun, M.P., Senar, J.C. & Clergeau, P. (2016) Rapid morphological changes, admixture and invasive success in populations of Ring-necked parakeets (*Psittacula krameri*) established in Europe. *Biological Invasions*, 1-18.

Jackson, H., Strubbe, D., Tollington, S., Prys-Jones, R., Matthysen, E. & Groombridge, J.J. (2015) Ancestral origins and invasion pathways in a globally invasive bird correlate with climate and influences from bird trade. *Molecular Ecology*, **24**, 4269-4285.

Luna, A., Franz, D., Strubbe, D., Shwartz, A., Braun, M.P., Hernández-Brito, D., Malihi, Y., Kaplan, A., Mori, E., Menchetti, M., van Turnhout, C.A.M., Parrott, D., Chmielewski, F.-M. & Edelaar, P. (2017) Reproductive timing as a constraint on invasion success in the Ring-necked parakeet (*Psittacula krameri*). *Biological Invasions*, 1-13.

Mori, E., Ancillotto, L., Groombridge, J., Howard, T., Smith, V.S. & Menchetti, M. (2015) Macroparasites of introduced parakeets in Italy: a possible role for parasite-mediated competition. *Parasitology Research*, **114**, 3277-3281.

Postigo, J.-L. (2016) New records of invasive Parakeet hybrids in Spain. A great opportunity to apply the rapid response mechanism. In: *European Journal of Ecology*, p. 19

Strubbe, D., Jackson, H., Groombridge, J. & Matthysen, E. (2015) Invasion success of a global avian invader is explained by within-taxon niche structure and association with humans in the native range. *Diversity and Distributions*, **21**, 675-685.

In prep

Jackson, H., Strubbe, D., Nichols, R., Edelaar, P., Matthysen, E. & Groombridge, J.J. (*in prep.*) Do invasive populations experience expected severe bottlenecks from founder effects? A novel method to estimate genetic bottleneck effects using a globally invasive bird as a model system.

Edelaar, P., Groombridge, J.J., Matthysen, E., Ogden, R., Sells, J., Strubbe, D., Warren, B. (*in prep*) Signatures of rapid natural selection under climatic change in the globally introduced ring-necked parakeet *Psittacula krameri*.

Sell, J., Groombridge, J.J., Tsagkogeorga, G., Ogden, R., Matthysen, E. & Strubbe, D. (*in prep*). Draft genome assembly for the globally introduced ringneck parakeet *Psittacula krameri*.

Sells, J. Groombridge, J.J., Strubbe, D. & Ogden, R. (*in prep*). The efficacy of non-invasive feather-extracted DNA for ddRAD-Seq