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Are all the roads leading to Rome?

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A recommendation of

Charbonnel N, Galan M, Tatard C, Loiseau A, Diagne CA, Dalecky A, Parrinello H, Rialle S, Severac D, and Brouat C. Differential immune gene expression associated with contemporary range expansion of two invasive rodents in Senegal. *bioRxiv* 442160, ver 5 peer-reviewed and recommended by *PCI Ecology* (2019). DOI: 10.1101/442160

Identifying the factors which favour the establishment and spread of non-native species in novel environments is one of the keys to predict -and hence prevent or control- biological invasions. This includes biological factors (i.e. factors associated with the invasive species themselves), and one of the prevailing hypotheses is that some species traits may explain their impressive success to establish and spread in novel environments [3]. In animals, most research studies have focused on traits associated with fecundity, age at maturity, level of affiliation to humans or dispersal ability for instance. The "composite picture" of the perfect (i.e. successful) invader that has gradually emerged is a small-bodied animal strongly affiliated to human activities with high fecundity, high dispersal ability and a super high level of plasticity. Of course, the story is not that simple, and actually a perfect invader sometimes –if not oftentakes another form... Carrying on to identify what makes a species a successful invader or not is hence still an important research axis with major implications.

In this manuscript, Charbonnel and collaborators [2] provide an interesting opportunity to gain novel insights into our understanding of (the) traits underlying invasion success. They nicely combine the power of Next-Generation Sequencing (NGS) with a clever comparative approach of two closely-related invasive rodents (the house mouse *Mus musculus* and the black rat *Rattus rattus*) in a common environment. They use this experimental design to test the appealing hypothesis that pathogens may be actors of the story, and may indirectly explain why some non-native species are so successful in invading novel habitats.

It is generally assumed that the community of pathogens encountered by non-native species in novel environments is different from that of their native area. On the one hand (the enemyrelease hypothesis), it can be hypothesized that non-native species, when they arrive into



a novel environment, will be relaxed from the pressure imposed by their native pathogens because local pathogens are not adapted (and hence do not infect) to this novel host. Because immune defence against pathogens is highly costly, non-native species establishing into a novel environment could hence reallocate these costs to other functions such as fecundity or dispersal apparatus. This scenario has been termed the "evolution of increased competitive ability" (EICA) hypothesis [1]. On the other hand (the EICA-refined hypothesis [4]), one can assume that invaders will encounter new pathogens in newly established areas, and will allocate energy toward cost-effective immune pathways to permit allocating a non-negligible amount of energy toward other functions. Finally, a last hypothesis (the "immune protection" hypothesis) assumes major changes in pathogen composition between native and invaded areas, which should lead to an overall increase in immune investment by the native species to successfully invade novel environments [4]. This last hypothesis suggests that only non-native species being able to take up the associated costs of immunity will be successful invaders.

The role of immunity in invasion success has yet been poorly investigated, mainly because of the difficulty to simultaneously analyse multiple immune pathways [4]. Charbonnel and collaborators [2] overpass this difficulty by screening all genes expressed (using a whole RNA sequencing approach) in an immune tissue: the spleen. They do so along the invasion routes of two sympatric invasive rodents in Africa and compare anciently and newly invaded areas (respectively). For one of the two species (the house mouse), they found a high number of immune-related genes to be up-regulated in newly invaded areas compared to anciently invaded areas. All categories of immune pathways (costly and cost-effective) were up-regulated, suggesting an overall increase in immune investment in the mouse, which corroborates the "immune protection" hypothesis. For the black rat, patterns of gene expression were somewhat different, with much less pronounced differentiation in gene expression between newly and anciently invaded areas. Among the few differentiated genes, a few were associated to immune responses and some of theses genes were even down-regulated in the newly invaded areas. This pattern may actually corroborate the EICA hypothesis, although it could alternatively suggest that stochastic processes (drift) associated to recent decrease in population size (which is expected during a colonisation event) are more important than selection imposed by pathogens in shaping patterns of immune gene expression.

Overall, this study [2] suggests (i) that immune-related traits are important in predicting invasion success and (ii) that two successful species with a similar invasion history and living in similar environments can use different life-history strategies to reach the same success. This later finding is particularly relevant and intriguing as it suggests that the traits and strategies deployed by species to colonise new habitats might actually be idiosyncratic, and that, if general trends actually emerge in regards of traits predicting the success of invaders, the devil might actually be into the details. Comparative studies are extremely important to identify the general rules and the specificities sustaining actual patterns, but these approaches are yet poorly used in biological invasions (at least empirically). The work presented by Charbonnel and colleagues [2] calls for future comparative studies performed at multiple spatial scales (native vs. non-native areas, anciently vs. recently invaded areas), multiple taxonomic res-



olutions and across multiple traits (to search for trade-offs), so that the success of invasive species can be properly understood and predicted.

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Appendix

Reviews by Nadia Aubin-Horth and one anonymous reviewer, DOI: 10.24072/pci.ecology.100011