



## A match made in the Anthropocene: human-mediated adaptive introgression across a speciation continuum

**Fernando Racimo** based on reviews by Michael Westbury, Andrew Foote and Erin Calfee

A recommendation of:

Introgression between highly divergent sea squirt genomes: an adaptive breakthrough?

Christelle Fraïsse, Alan Le Moan, Camille Roux, Guillaume Dubois, Claire Daguin-Thiébaud, Pierre-Alexandre Gagnaire, Frédérique Viard, Nicolas Bierne (2022), *bioRxiv*, 2022.03.22.485319, ver. 4 peer-reviewed and recommended by Peer Community in Evolutionary Biology <https://doi.org/10.1101/2022.03.22.485319>

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#### Data used for results

- <https://zenodo.org/record/6992403>

#### Scripts used to obtain or analyze results

- <https://www.biorxiv.org/content/10.1101/2022.03.22.485319v3.supplementary-material>

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### Recommendation

The long-distance transport and introduction of new species by humans is increasingly leading divergent lineages to interact, and sometimes interbreed, even after thousands or millions of years of separation. It is thus of prime importance to understand the consequences of these contemporary admixture events on the evolutionary fitness of interacting organisms, and their ecological implications.

*Ciona robusta* and *Ciona intestinalis* are two species of sea squirts that diverged between 1.5 and 2 million years ago and recently came into contact again. This occurred through human-mediated introduction of *C. robusta* (native to the Northwest Pacific) into the range of *C. intestinalis* (the English channeled Northeast Atlantic). In this study, Fraïsse et al. (2022) follow up on earlier work by Le Moan et al. (2021), who had identified a long

genomic hotspot of introgression of *C. robusta* ancestry segments in chromosome 5 of *C. intestinalis*. The hotspot bears suggestive evidence of positive selection and the authors aimed to investigate this further using fully phased whole-genome sequences.

The authors narrow down on the exact boundaries of the introgressed region, and make a compelling case that it has been the likely target of positive selection after introgression, using various complementary approaches based on patterns of population differentiation, haplotype structure and local levels of diversity in the region. Using extensive demographic modeling, they also show that the introgression event was likely recent (approximately 75 years ago), and distinct from other tracts in the *C. intestinalis* genome that are likely a product of more ancient episodes of interbreeding in the past 30,000 years. Narrowing down on the potential drivers of selection, the authors show that candidate SNPs in the region overlap with the cytochrome family 2 subfamily U gene - involved in the detoxification of exogenous compounds - potentially reflecting adaptation to chemicals encountered in the sea squirt's environment. There also appears to be copy number variation at the candidate SNPs, which provides clues into the adaptation mechanism in the region.

All reviewers agreed that the work carried out by the authors is elegant and the results are robustly supported and well presented. In a round of reviews, various clarifications of the manuscript were suggested by the reviewers, including on the quality of the newly generated sequencing data, and some suggestions for qualifications on the conclusions reached by the authors as well as changes in the figures to increase their clarity. The authors addressed the different concerns of the reviewers, and the new version is much improved.

This study into human-mediated introgression and its consequences for adaptation is, in my view, both well thought-out and executed. I therefore provide an enthusiastic recommendation of this manuscript.

## References

Fraïsse C, Le Moan A, Roux C, Dubois G, Daguin-Thiébaud C, Gagnaire P-A, Viard F and Bierne N (2022) Introgression between highly divergent sea squirt genomes: an adaptive breakthrough? bioRxiv, 2022.03.22.485319, ver. 4 peer-reviewed and recommended by Peer Community in Evolutionary Biology. <https://doi.org/10.1101/2022.03.22.485319>

Le Moan A, Roby C, Fraïsse C, Daguin-Thiébaud C, Bierne N, Viard F (2021) An introgression breakthrough left by an anthropogenic contact between two ascidians. *Molecular Ecology*, 30, 6718–6732. <https://doi.org/10.1111/mec.16189>

## Reviews

Toggle reviews

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### *Evaluation round #1*

DOI or URL of the preprint: <https://doi.org/10.1101/2022.03.22.485319>

Version of the preprint: 2

### *Author's Reply, 25 Aug 2022*

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**Decision by *Fernando Racimo*, 24 Jun 2022**

Thank you for your patience. Your preprint has now been seen by three reviewers, who all generally think this is a very well designed and executed study. They provide a list of comments that should be reasonable to tackle, in large part involving stylistic edits and textual clarifications, but no major criticism, so I believe this can lead to a recommendation after they are addressed. I am looking forward to receiving your revised preprint.

**Reviewed by *Michael Westbury*, 27 May 2022**

Fraïsse et al have submitted a really nice manuscript about adaptive introgression in sea squirts in the English Channel. It shows how invasive species may actually help native species in some respect which is positive considering how many invasive species there are around the world. It confirms previous findings using smaller datasets but at a more robust scale through the inclusion of phased whole genomes. Overall I have very little to criticise, the analyses seem suitable for the purposes and results robust as a result.

I only have a few specific comments listed below:

40: Persist for long what? durations?

126: It would be nice to add a short summary of the sequencing results, coverage etc and then send the reader to Table S1 for more details.

137: We cannot tell apart the intra and interspecific hybrids in the figure. I suggest different colours or shapes in the figure to make it clearer.

164: There is another chromosome in figure S4B that has a higher value than chr5. Is there an explanation for that? Maybe this is chromosome length which you mentioned later but wasn't super clear.

168: How do you know it is weakly correlated? Just visual inspection or a regression line?

344: Where could this natural hybridisation have occurred? Since the species are now found in the Pacific and Atlantic oceans it seems like a long dispersal

389: Italics are missing

457-458: How was species determined a priori? Does this mean they are easy to tell apart morphologically?

483: Supplementary scripts: Was there any adapter trimming/PE read merging? Anything processing prior to mapping

501: I assume this is to test for reference bias? Would be good to mention that

517: Is this mutation value known for sea squirts or estimated?

544: The tools/software used in this section are lacking

588: How was the log-ratio test run?

**Reviewed by *Andrew Foote*, 24 Jun 2022**

Fraïsse et al. present the results of an elegant study which provides strong evidence for recent introgression due to shifts from allopatric to partially sympatric distributions in *Ciona* sea squirts. The work builds upon previous work done using sparse markers, much of it from the same research group. The use of phased whole genomes in this study both confirms the hypotheses of, and provides a significant increase in resolution over, the previous work done using RAD-seq and other markers.

The care and attention to detail throughout is really appreciated. As is the authors embracing of making all aspects of the study open access. A good example being the provision of the scripts via links (I will likely be

using some of these myself in the future, so thank you on behalf of our research community). One thing I lost track of was understanding which of the many datasets were used in which study and why this was. So an additional table in the supplementary materials listing the datasets, the analyses they were included in, key characteristics distinguishing each dataset, and the rationale for the choice of dataset for each analysis would be helpful.

As the authors highlight, local recombination rate is a likely cause of variation along the genome in the introgression rates (outside of the hotspot of Chr5). Given the extensive analyses done by the authors, it was a little surprising to see that recombination rates were not estimated to confirm this. Local recombination estimates could also provide support for the SFS-model based approach in addressing whether short and long introgressed tracts reflect different introgression events (which is alluded to later in the demographic modelling section based on the recombination rate provided by Duret). But this is perhaps this could be included in the next draft, or is in a forthcoming study by Duret?

Regarding the introgression hotspot on chromosome 5, the presence of tandem repeats, and the region of missing data reminded me of the outlier region in the comparison of hooded and carrion crows (Poelstra et al. 2014). From memory, that study found that much of the functional variation associated with the colour polymorphism between the two crow species was in this region, and that low recombination rate due to long flanking repeat regions caused this to segregate between the two species. That study suggested that although functional, it may not be adaptive, rather just a consequence of the local genomic architecture. Could reduced recombination be enough to explain the patterns in the introgression hotspot, without evoking adaptation (I appreciate the authors have run a number of tests for selective sweeps, but I am just trying to play devils advocate).

The discussion is quite lengthy and covers some of the same ground as the introduction. It takes a while to get into the discussion of the new results. For example, lines 327-337 cover the findings of previous studies, which are also summarised in the introduction. Some summary of the work that led to the present study is of course justified, but could this be condensed?

Figure 2A. The shading of allele frequency runs 'low' to 'high'. Can the range be specified as actual frequencies in the figure legend?

My comments are just very minor points, that may not need any revision. The work is extremely thorough. I came away inspired by this study and excited to take some of the findings and apply them to my own work. I feel this would be an exceptional contribution to any journal that published evolutionary biology research. My congratulations to the authors.

*Reviewed by [Erin Calfee](#), 27 May 2022*

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