July 12th, 2022

Dear Professor Chapman,

Editor-in-Chief *Evolution*:

We are excited to submit our paper entitled “*Jointly modeling the evolution of discrete and continuous traits*” for your consideration as an Original Article.

A common theme in comparative biology is the detection of causal, or least mechanistic, factors that affect the evolution of quantitative characters. One very common phylogenetic comparative approach for these types of questions is to employ an Ornstein-Uhlenbeck (OU) model, which assumes distinct regimes, described by the evolution of a discrete character, are known completely *a priori*. In fact, this is the exact approach by two of us (JMB and BCO) derived in ten years ago in your journal (Beaulieu et al. 2012, vol 66, pages 2369-2383; it has also been cited 500 times according to Google Scholar). However, dependence rarely flows just one way in evolution, and we suspect that as often as a discrete character causes change in the continuous character, continuous characters also influence discrete character evolution, or at the very minimum, can provide information about how they may be evolving in tandem.

Here we develop such a framework to explicitly estimate the joint likelihood for discrete and continuous characters. Specifically, our model combines the probability of observing the continuous character under a generalized OU process with the probability of the discrete character under a hidden Markov model (HMM), linked by a shared underlying regime. We conduct a battery of simulations that demonstrate the reliability of the parameter estimates and, importantly, we demonstrate that joint optimization outperforms the current approach of providing a fixed discrete character history. We also apply our model to a large flowering plant clade to test whether fleshy and dry fruits are correlated with a measure of aridity. Consistent with our expectations, we discover that dry fruits indeed have higher rates of climatic niche evolution, that the climatic niche of fleshy fruits is more conserved and dry fruits have a more humid climatic optimum.

We feel that Drs. Brian Sidlauskas (Oregon State U), Tiana Kohlsdorf (USP, Brazil), or Kjetil Lysne Voje (U. of Oslo, Norway) are good choices to handle our manuscript. We also think Liam Revell (U. of Massachusetts, Boston), Daniel Caetano (Towson U.), Carrie Tribble (U. of Hawaii, Manoa), and perhaps Renske Onstein (iDiv) would be ideal choices as potential reviewers.

Thank you very much for your consideration, and we look forward to hearing from you.

James D. Boyko

Brian C. O’Meara

Jeremy M. Beaulieu