

Reply to comments by Gurvich et al. (2016) on “Fruiting phenology as a “triggering attribute” of invasion process: Do invasive species take advantage of seed dispersal service provided by native birds?”

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In 2005, Gurvich et al. proposed that “once a non-indigenous species has arrived to a new ecosystem and become established, the likelihood that it spreads, and thus becomes invasive, may depend on just one or very few characteristics, called ‘triggering attributes’ (TA). We propose that a TA is a vegetative or regenerative attribute discontinuously distributed in comparison to the resident community. This attribute allows the species to benefit from a resource that is permanently or temporarily unused by the resident community.” “The winter fruit phenology of two fleshy fruited invaders (*P. angustifolia* and *Ligustrum lucidum*) was proposed as an example of TA that would allow these two species to take advantage of a resource (bird dispersal) that resident fleshy-fruited species—whose fruits are ripe in summer and autumn—cannot tap during the winter” (Gurvich et al. 2016). We believe that the model they proposed is a very valuable one, and useful to identify special traits involved in plant invasion processes. In a recent response to an article

that evaluates if a vegetative attribute behaves as a TA (Vergara-Tabares et al. 2015), Gurvich et al. (2016) expressed disagreement regarding the logic used to develop the experimental design and the main conclusions of the study. The arguments of Gurvich et al. (2016) demonstrate some misinterpretation of the study and its results, and we believe it deserves clarification.

We feel that the authors fail to interpret correctly the aim of our study, when they claimed that it “aimed at testing our triggering attribute model (TA, Gurvich et al. 2005).” In our study we did not test the model per se, but we empirically tested if a particular attribute, plant fruiting uncoupled from the fruiting of the majority of plant species in the system, indeed operated as a triggering attribute allowing the plant species to take advantage of the seed dispersal service. We used a comparison of two congeneric and invasive *Pyracantha* species that differ in their fruit maturation period to make such test. The logic behind our experimental design can be summarized as follows: two congeneric invasive plant species that share most of their attributes important to seed dispersal by birds and differ in the timing of their fruiting maturation allowed us to control for the effect of other fruiting attributes (*P. coccinea* coupled with native plants and *P. angustifolia* uncoupled; Figure 2 in Vergara-Tabares et al. 2015). We expected that the invasive plant with uncoupled fruiting would use the seed dispersal service disproportionately more than the

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species with fruiting coupled with that of the natives. On the other hand, the lack of difference between the invasive species regarding the seed dispersal service would serve as evidence that the uncoupled fruiting does not provide an advantage over the use of such a resource and is not indeed the attribute that triggers the plant invasion. In the last scenario, other attributes shared by the invasives would be responsible for the expansion and invasion of the species (e.g., fruit display, fruit color and aggregation per branch, number of seeds per fruit).

Based on the TA model, Gurvich et al. (2016) claimed that the empirical prediction under their model is that “*P. angustifolia* should show dispersal rates similar to those of the dominant fleshy-fruited resident of the invaded system,” and then they suggested that data of Vergara-Tabares et al. (2015) supported this idea: “*P. angustifolia* has the same assemblage of bird dispersers as *C. ehrenbergiana*, but operating during a different seasonal period.” However, this is a different prediction from the one we tested. Although valid, such prediction focuses on the species, trying to explain differences in the use of the resource (i.e., seed dispersal service), but not the attribute that is involved in such response. On the other hand, the prediction we tested in the study focuses on the attribute per se, discontinuity of fruiting in the community. We could test the prediction that uncoupled fruiting phenology is the trait that provides an advantage to the invasive plants regarding seed dispersal, by means of using congeneric plant species that share most attributes involved in seed dispersal effectiveness, and contrast only in fruiting phenology. In this way our results are valid only to test our own prediction but not the one proposed by Gurvich et al. (2016), as they asserted. Our data cannot support their prediction mainly for two reasons. First, the dominant fleshy-fruited resident plant in the study system is *L. molleoides* not *C. ehrenbergiana* (see Table 1, Appendix in Vergara-Tabares et al. 2015). Second, similarity in the assemblage of bird dispersers does not

determine the dispersal rate. In fact, the proxies most used to infer dispersal rate are rates of visitation by disperser birds and fruit consumption by those birds.

Finally, we need to clarify an assertion by Gurvich et al. (2016) that clearly we did not claim throughout our study. The phrase “dispersal would probably not be the TA that underlies the success of *P. coccinea* in the invaded system” implies that dispersal is a triggering attribute. According to Gurvich et al. (2005) dispersal would not be an attribute of the plant species, but a resource or service provided by the resident community. What we stated in regards to *P. coccinea* is that “other characteristics of the plants may be more important to make a better use of the dispersal service in the system to be a successful invader, (e.g. fruit display, fruit color and aggregation per branch).”

In summary, we agree with Gurvich et al. (2016) in that we have not rejected the TA model. The aim of our study was not to test the model as such but only to test the quality of a particular trait as a triggering attribute. We insist that the results of our study show that, as opposed to the fruiting phenology, other attributes shared by both *Pyracantha* species may be responsible for the success of their invasion.

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