Debate over the importance and meaning of *native range* in invasion biology: reply to Courchamp et al.

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In their response to Pereyra (2019), Courchamp et al. (2020) considered problems with the concept of native range in invasion biology. They start by agreeing with Pereyra that the concept of native range has limitations, but then proceed to criticize the work for what they perceive as "flawed logical reasoning," "a misleading selection of examples", "cherry picking," and a failure to appreciate the usefulness of this admittedly poorly defined concept. Here, we respond to the criticisms of Courchamp et al., while addressing the important problems that remain with the application of the native range concept.

Problematic Concept of Native Range

The concept of native range is central to invasion biology, despite the suggestion by Courchamp et al. that "invasion biology is less concerned with the precise identity of a species' range than the certainty that the species is non-native in a region." Without knowing the limits and history of the native range of a species, one cannot determine exactly where a species may be native. This is particularly obvious in cases where species are considered non-native and are therefore discriminated against by invasion biologists (Davis et al. 2011) because they are found just outside their perceived native range. Several examples illustrating the difficulties of determining the native or non-native status for a variety of species are discussed by Guiaşu (2016) and Pereyra, among others, and cannot be reconsidered here due to space limitations.

Courchamp et al. assert that a native range exists and is real, even if its history or limits, and therefore its past and current extent, may be unknown. Obviously, every species originated in a particular geographic location; then, its range may have changed over time for many reasons. However, if the extent and history of a native range are unknown, the fact that it may exist remains a vague and theoretical notion with limited or no practical applicability in many cases. In the absence of that knowledge for some species, one cannot be certain of

their native or non-native status in many regions. Courchamp et al.'s suggestion that lack of knowledge about the native ranges of species is a "human fallacy" that does not negate the validity of the concept itself seems beside the point. If a presumably biogeographic concept is not applicable to a variety of species at diverse locations and in many ecosystems, then that concept will not be useful in those cases and therefore cannot be considered universal.

Courchamp et al. also equate the evolution of the boundaries of a species' range with the evolution of other traits of the species. The problem with this contention is that invasion biologists often rely on a static view of native range, which ignores the dynamic nature of the distributions of species in the real world (Guiaşu 2016).

Courchamp et al. agree with Pereyra that no theoretical definition of *native range* is provided in the invasion biology literature, but then state that invasion biologists do not need to define the term because they rely on "centuries of research of another discipline, biogeography." However, the concept of native range was not a central focus of biogeography— certainly not for centuries. Native range is important in the much younger field of invasion biology, so invasion biologists should properly define this concept.

On the subject of the universal nature of the native range concept, Courchamp et al. offer a confusing argument. On the one hand, they present a rather strained comparison between native range and gravity, but, on the other hand, say that "biology is not a science like physics, and there are few universal laws that are true in all cases." To be a universal concept, native range has to apply to all species. For example, is it possible to differentiate naturally dispersing plankton from plankton that dispersed through human action? Is it possible in today's human-dominated world to take into account all the ways, direct and indirect, in which people may affect the distributions of other species? What is the native range of a hybrid resulting from interbreeding between a native and a non-native species?

Such hybridization processes can be regarded unfavorably by invasion biologists (Guiaşu 2016). Several of the legitimate questions Pereyra raises regarding the concept of native range are not addressed at all by Courchamp et al. For example, how does one determine the native range of a species without having a clearly defined non-native range in which human influence is demonstrated?

How do Courchamp et al. address examples and questions such as these? Short answer: they do not. They simply reaffirm what we never denied: there are cases where the difference between native and non-native species seems obvious (e.g., the introduction of cats on remote islands). Those examples by themselves are not sufficient to make native range a universal concept. Even for some notorious invasive species, such as the yellow crazy ant (*Anoplolepis gracilipes*), native range is unknown (Cooling & Hoffman 2015), and therefore this species is likely considered non-native even in the region it evolved in.

Clearly, in some cases, such as the golden jackal (*Canis aureus*) discussed by Pereyra, the lack of knowledge of the precise limits of a native range has a direct impact on the determination of the status of the species in particular regions, where the species may be (perhaps erroneously) considered non-native and therefore becomes a target of control programs. One would think that invasion biologists should be more concerned about such examples, rather than simply dismissing valid criticisms as "cherry picking" and asserting yet again the importance and value of invasion biology without acknowledging the persistent and fundamental problems in this field.

Native Range, Native or Non-native Status, and Overgeneralizations

In their attempt to diminish and dismiss points made by Pereyra, Courchamp et al. sometimes offer overly general comments without supporting references. For example, they state that

native ranges "are known in most cases." Ironically, they accuse Pereyra of "overgeneralizing" "by cherry picking examples that are marginal and failing to consider the typical state for the majority of species." It is well known that invasion biology has a taxonomic and geographical bias (Pyšek et al. 2008). Therefore, some groups of organisms, such as the aforementioned plankton, are poorly studied by invasion biologists. It is very unlikely that the native ranges of most of the approximately 1.8 million species currently recognized are known. In fact, very little is known about many of these species and their dynamic distributions. It is rather self-serving of invasion biologists to dismiss examples that do not fit neatly into the favored invasion biology narrative as marginal. On what basis was such a label attached to these examples? Was it because they are inconvenient? And, what is the "typical state for the majority of species" in this context? Because there is not a clear understanding of the native or non-native status of numerous species in many parts of the world, dismissing all this growing evidence, as other invasion biologists have done (e.g., Frank et al. [2019]), is repetitive and increasingly unconvincing.

Because Courchamp et al. mention ant species, we respond with some information on ants as well. Ellison et al. (2012) acknowledge that it is unknown how many ant species found in New England (U.S.A.) are native and how many are non-native because systematic surveys of ants in this region only started in the early 20th century. This is likely true for many other species in many other parts of the world. Shapiro (2002) stated that the butterfly fauna in a region of California was not studied before the mid-20th century and added that in this case "there are neither old records nor old specimens" and therefore "the composition of the pre-European fauna is thus unknowable." The same applies to crayfish species in Ontario. The oldest museum records available are from the early 1900s and are incomplete. As a result, nothing is known about the distributions of crayfish species in Ontario before the early

20th century (Guiaşu 2016). So, how do the centuries of research in biogeography mentioned by Courchamp et al. help determine native range in such cases?

Conclusions

The debate about the concept of native range is intensified by the fact that determining native or non-native status for various species may have important implications for the ways in which one perceives and treats these species. Although Courchamp et al. state that only a minority of non-native species are considered problematic, this assertion is at odds with the guilty-until-proven-innocent approach often taken by invasion biologists toward all such species (Guiaşu 2016; Yanco et al. 2019). Thus, while invasion biologists may claim they are not against all non-native species, in reality non-native species are regarded with suspicion in general by many in this field (Guiaşu 2016; Guiaşu & Tindale 2018; Pereyra & Ocampo Reinaldo 2018).

On a conceptual level, native range relies on the idea that human impacts on the dispersal of other species have to be considered unnatural and therefore undesirable.

Therefore, this concept further isolates humans from the rest of the natural world they are an influential part of.

Overall, the response by Courchamp et al. to Pereyra's analysis of the native range concept is unpersuasive. Courchamp et al. hint at a possible link between Pereyra's essay and what they perceive as "the increase in denial of invasion biology." Recent articles (Russell & Blackburn 2017; Ricciardi & Ryan 2018, cited by Courchamp et al. 2020) containing accusations of science denialism aimed at critics of certain aspects of invasion biology have been criticized by a variety of researchers and are considered unfounded attempts to shut down legitimate debate (e.g., Boltovskoy et al., 2018; Guiaşu & Tindale 2018; Munro et al.

2019). Instead of invoking science denialism, invasion biologists would be better served if they developed a reliable, nonarbitrary definition of *native range* that applies well to all taxa and regions.

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