



Another call for the end of invasion biology

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The restriction of invasion biology to non-native species has been laid down as one founding principle of the discipline by many researchers. However, this split between native and non-native species is highly controversial. Using a phenomenological approach and a more pragmatic examination of biological invasions, the present paper discusses how this dichotomy has restricted the relevance of the field, both from theoretical and practical viewpoints. We advocate the emergence of a broader disciplinary field.

In his book ‘The ecology of invasions by animals and plants’, Elton (1958) indicates from the very first pages that there are “two rather different kinds of outbreaks in populations: those that occur because a foreign species successfully invades another country, and those that happen in native or long-established populations. This book is chiefly about the first kind – the invaders”.

Whatever the influence this monograph may have had in the development of the discipline (see Simberloff 2011a for a very detailed historical analysis), the restriction of the field that it introduces is considered by many researchers today as one founding principle of the discipline (Richardson et al. 2000, Colautti and MacIsaac 2004, Richardson and Pysek 2004, 2006, Wilson et al. 2009a). Native species have de facto been ignored in the bulk of the literature devoted to invasions (Davis et al. 2001). This split between native and non-native species has fuelled a controversy that has given rise even quite recently to lively exchanges (Valéry et al. 2008, 2009, Wilson et al. 2009b, Davis et al. 2011, Hulme et al. 2011, Thompson and Davis 2011a, b, Van Kleunen et al. 2011). We believe that the distinction between native and non-native species has limited value, both theoretically and practically.

Native versus non-native species: an inappropriate dichotomy from a theoretical viewpoint

A phenomenon (from Greek, *phainen*, ‘to appear’) can be defined as an “object appearing as such” (Husserl 1913). In other words, it corresponds to what is perceived by the senses. In this particular case, a biological invasion manifests itself by the appearance of a state of dominance of a species

and the rapidity of change observed. Therefore, we consider these two traits as necessary and sufficient to characterise a biological invasion; in other words and more precisely, we exclude the impact criterion that is retained by some researchers (further details in Valéry et al. 2008).

There is nothing in this characterisation that precludes native species; however, the field has generally not been willing to consider native species under the umbrella of invasive species (but see Davis and Thompson 2000, Davis et al. 2001, 2011, Valéry et al. 2008, 2009, Thompson and Davis 2011a, Carey et al. 2012 for exceptions). In reality, examples of native species (be it plants or animals) that become rapidly dominant, and are thus considered invasive, are numerous (Simberloff 2011b, Carey et al. 2012). Only two of them will be mentioned here:

1) The western juniper *Juniperus occidentalis* has spread throughout many types of grasslands since the late 19th century (i.e. sagebrush shrub steppe, riparian and aspen communities) in the USA and now covers 9 million hectares (Burkhardt and Tisdale 1976, Miller and Tausch 2001, Wall et al. 2001, Miller et al. 2005). Its rate of spread and area have reached unprecedented levels since the Holocene (Miller and Tausch 2001, Miller et al. 2005): the forests of eastern Oregon increased from 456 000 ha in 1936 to 2.2 million ha in 1988, which is an average increase of about 33 500 ha year⁻¹ (Miller et al. 2005). The dominance, which has been acquired in a few decades, and varies between habitats, is unequivocal and has inevitably led to a decrease in the density and cover of formerly dominant species (e.g. big sagebrush *Artemisia tridentata*, Idaho fescue *Festuca idahoensis*, aspen *Populus tremuloides*). The density of western juniper can be between

50 and 350 trees per hectare in xeric sites; it is generally between 500 and 900 trees per hectare in mesic sites, and can sometimes reach a record density (i.e. 1500 trees per hectare) in aspen communities (Miller et al. 2000, 2005, Wall et al. 2001, Johnson and Miller 2006). The main driver behind the competitive advantage of western juniper is closely linked to European settlement whose activities have resulted in a very strong decrease in fire frequency: livestock grazing (reduced combustible biomass), road infrastructures (fire barriers), and preventive and active fire control (Burkhardt and Tisdale 1976, West 1999, Wall et al. 2001, Miller and Tausch 2001, Miller et al. 2005, Johnson and Miller 2006).

2) Another example is that of the black vulture *Coragyps atratus*, whose population is thriving and is currently estimated at 20 million individuals (Rich et al. 2004, Blackwell et al. 2007, Carrete et al. 2009); it now constitutes the most abundant of the seven species of New World vultures (i.e. Cathartidae). Its natural range, bounded to the south by Uruguay, central Chile and northern Argentina, extends northwards to southeastern USA (del Hoyo et al. 1994, Buckley 1997, Birdlife International 2012). The black vulture's demographic increase is rapid: according to long-term data of the Breeding Bird Survey (BBS) and the Christmas Bird Count (CBC), the annual growth rate in North America was about 6% over the last two decades (Avery 2004, Sauer et al. 2011). The dominance of this medium-sized species (1.1–1.9 kg) over other scavengers is due to its extreme sociability and to agonistic relationships towards heterospecifics: the intraspecific aggregation of black vultures when foraging and their high aggressiveness towards other species around a food resource (e.g. carcasses) allow them to 'win' in interference competition, even taking advantage over much larger species than themselves, such as the Andean condor *Vultur gryphus* (8–15 kg) (Carrete et al. 2010). These behavioural traits thus provide an advantage over other less gregarious/social species (e.g. the Turkey vulture *Cathartes aura*), and/or less abundant or even endangered species (e.g. Andean condor and Californian condor *Gymnogyps californianus*) (Carrete et al. 2010). Because of their very low sensitivity to human presence – e.g. the black vulture is known as an 'urban scavenger' in some cities in South America, and even nests on window sills and the roofs of skyscrapers (Hill 1991) –, the increase in feeding opportunities related to human development (e.g. rubbish dumps, cattle and wildlife road kills) constitutes the key factor that has made this demographic explosion possible. The black vulture is now considered an example of a 'successful' species that responds positively to anthropogenic environmental changes (Carrete et al. 2009, 2010).

These two examples, amongst others, clearly show that some native species benefiting from a change in their environment can meet both characteristic traits of a biological invasion. The restriction of the biological invasion phenomenon to only non-native species is thus, unnecessarily restrictive. This is a fortiori also true for the additional restriction, introduced by some researchers (Wilson et al. 2009b, Richardson et al. 2011), who consider that among non-natives, only species transported by humans can become invasive.

Native versus non-native species: an inoperative dichotomy from a practical viewpoint

The examination of concrete situations sheds even more light on the lack of relevance of the split between native and non-native species, which may even lead to nonsensical results in some cases:

1) The attribution of different qualifying terms to refer to the rapid increase of a population, depending on whether or not it occurs in the original range of the species, is not justified in view of actual cases, such as the European starling, *Sturnus vulgaris* (Feare 1984, Pascal et al. 2006), the Colorado potato beetle, *Leptinotarsa decemlineata* (Forister et al. 2007) or the little fire ant, *Wasmannia auropunctata* (Foucaud et al. 2009a, Orivel et al. 2009) for which the demographic parameters correspond to the two characteristic traits of the invasion phenomenon very well (cf. above), both in their native range and in areas of introduction.

The in-depth genetic analyses to which the latter species has been subjected recently (Foucaud et al. 2009a, Orivel et al. 2009), clearly show that populations invading human-altered habitats outside their natural range (i.e. Caribbean, Florida, several west African countries, many Pacific islands and recently, Israel) come from populations which are already invasive in this type of habitat within their native range (i.e. Central and South America) (Foucaud et al. 2009b). The acquisition of this prior adaptation to invade human-altered habitats outside the native range, owing to human pressures similar to those encountered in the native area – i.e. "anthropogenically induced-adaptation to invade" – (Hufbauer et al. 2011) gives it the same competitive advantage that occurs in the same way, both in its natural range and in areas of introduction. A similar evolutionary process has been demonstrated for the Colorado potato beetle (Forister et al. 2007). Thus, these examples show that the distinction between natives and non-natives cannot be based on a supposed difference in the mode of competition either.

2) The existence of cryptogenic species (i.e. species that cannot be reliably demonstrated as being either introduced or native) (Carlton 1996) and pseudoindigenous species (i.e. introduced species that are mistakenly considered as native to a location) show the sometimes uncertain nature of determining the origin of a species. Yet, some of them become dominant rapidly within their habitat(s). The uncertainty about their origin could thus result in wrongly qualifying this phenomenon as "range expansion" sensu Richardson et al. (2011) – instead of "biological invasion" – when in fact, it is a question of a pseudoindigenous species or of a cryptogenic species, considered by default as native (Carlton 2009).

3) The demographic explosion and the dominance of a species may not occur immediately after its introduction, but only after a time lag that is always of indeterminate length. After how long can an introduced species be considered, or has to be considered native? If this question does not receive a clear answer so as to clearly define this other limit between native and non-native species (Simberloff 2012 for further information on the major issues regarding

such a categorization), perhaps it would be more appropriate to discard an uncertain dichotomy which is then totally inoperative on a practical level.

Conclusion

We believe that arbitrary dichotomies (i.e. natives vs non-natives; and among non-natives, those transported by humans vs other vectors) inopportunistically complicate the analysis of the phenomenon of biological invasion and have weak justifications both from theoretical and practical viewpoints.

Our analysis does not reveal any process or mechanism that is not already known and therefore eliminates any justification for the autonomy of invasion ecology. We concur with the conclusions of Mark Davis (2009) who advocates the emergence of a wider disciplinary field which he calls SPRED ecology (i.e. ecology of SPecies REDistribution), which would permit a more integrated study of all species on the move, whether due to climate change, land use change, human transport, or a combination of these and other factors.

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