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How to define nativeness in organisms with high dispersal capacities? A comment on Essl *et al.*

ABSTRACT

Essl and colleagues documented worldwide invasion patterns in bryophytes, which so far have been neglected in invasion biology. In the absence of historical evidence, Essl and colleagues used criteria such as anomalous geographical distribution, preference for disturbed habitats, and indirect associations with some means of human transport as criteria to identify aliens. Because bryophytes exhibit high long-distance dispersal capabilities, disjunct distribution patterns are, however, the rule rather than the exception in the group. In our opinion, none of the previously proposed criteria to characterize aliens can be satisfactorily applied to groups like bryophytes, for which historical and fossil records are extremely scarce. We suggest that, in order to validate the conclusions of Essl and colleagues, further taxonomic and phylogeographical studies are needed. This is especially true for island floras, for which recent critical taxonomic work and updated checklists, which compose the primary source of information for biodiversity, are largely missing.

Keywords Bryophytes, genetic diversity, genetic structure, invasive species, long-distance dispersal, nativeness.

Invasive species are increasingly viewed as a significant component of global change and one of the major drivers of current biodiversity loss (Didham *et al.*, 2007). In this context, nativeness has become the *sine qua non* invoked by many management policies, plans and actions to justify intervening on prevailing ecosystem processes (Chew & Hamilton, 2011). Although the distribution of alien species urgently needs to be documented for risk assessments, such information remains scarce in some geographical areas and taxonomic groups (Vilà *et al.*, 1999). In particular, although the socio-economical and ecological impact caused by bryophyte invasions is minor compared with other taxonomic groups, alien bryophytes threaten habitats that are often of high conservation relevance, affecting other cryptogams, but also invertebrates, vertebrates, and vascular plant seedlings (Essl *et al.*, 2014a).

Based on a spatial analysis of the distribution of alien bryophyte species worldwide, Essl *et al.* (2014b) concluded that 'bryophyte invasions exhibit marked biogeographic patterns on a global scale [. . .], with islands being clearly more prone to invasion' (p. 9), 'regions in the Southern Hemisphere have higher numbers of naturalized bryophytes' (p. 1), and that 'naturalizations occur more frequently in regions of the complementary hemisphere than in regions of their native hemisphere' (p. 1). These findings raise intriguing questions about the historical, evolutionary and ecological mechanisms underlying these patterns.

The distinction between native and introduced biotas presents, however, unique challenges (Bean, 2007). Comparative analyses using information previously published in floras and checklists, therefore, 'crucially depend on the quality of assessment of particular species with respect to their taxonomic identity, time of immigration and invasion status' (Pyšek, 2003, p. 499). The distinction between native and introduced plants and animals is especially problematic in organisms with high long-distance dispersal capacities (Bean, 2007) and for which, like bryophytes, historical records are mostly lacking. Here, we reappraise the problem associated with the criteria that can be employed to identify alien species in highly mobile organisms.

As pointed out by Essl *et al.* (2014b), direct evidence of introduction is available only for a limited number of bryophytes. Essl *et al.* (2013, 2014a,b) hence used criteria, such as the lack of historical records, anomalous geographical distribution, preference for disturbed habitats, and association with some means of human transport, to define alien species. Both experimental (Lönnell *et al.*, 2012, 2014) and phylogeographical (e.g. Szövényi *et al.*, 2012; Lewis *et al.*, 2014; and references therein) studies have, however, demonstrated the high long-distance dispersal capacities of bryophytes. Using spore-trapping experiments, Sundberg (2013) estimated that about 1% of the regional spore rain has a transcontinental origin. Disjunct distribution patterns are, therefore, the rule rather than the exception in bryophytes (Medina *et al.*, 2011), challenging the use of such a criterion for identifying aliens.

The disjunct distribution criterion led Essl *et al.* to qualify taxa with striking range disjunctions, such as the moss *Syntrichia bogotensis* and the liverwort *Plagiochila retrorsa*, which are primarily distributed in the Neotropics, as alien species in Macaronesia. Approximately 3.5% of the Macaronesian mosses and 8% of the Macaronesian liverworts exhibit range disjunctions between Macaronesia and tropical areas that are identical to those exhibited by *S. bogotensis* and *P. retrorsa* (Vanderpoorten *et al.*, 2011), and could therefore be assigned as aliens based on the disjunct distribution criterion. Such an assessment is, however, contradicted by two lines of evidence. First, *P. retrorsa* occurs in pristine laurel forest environments in steep north-facing slopes (Rycroft *et al.*, 2001). Most of the disjunct species between the Neotropics and Macaronesia similarly occur in the same (macro-)habitat (Vanderpoorten *et al.*, 2011). While alien species can sometimes also invade more or less pristine environments (Carter, 2014), they tend to primarily occur in disturbed habitats (Bean, 2007; Essl *et al.*, 2013). Although occurrence in disturbed habitats does not necessarily point to an alien status (Hassel *et al.*, 2005), habitat specificity for pristine environments does not point to an alien status either. Second, population genetic analyses on the Northeastern Atlantic bryophyte flora indicate that islands have played a key role as a stepping-stone for transoceanic migrants between tropical regions and Europe during the Pleistocene (Patiño *et al.*, 2015).

In our opinion, therefore, and apart from the very few cases, such as *Campylopus introflexus*, *Orthodontium lineare* and *Lophocolea semiteres* (Stieperaere, 1994; Hassel & Söderström, 2005), for which historical evidence is available, assigning an alien status to bryophyte species based on criteria such as the anomaly of the disjunction can be misleading. This is especially true in poorly known oceanic archipelagos, such as St Helena and even Hawaii, which lack a recent and critical evaluation of their bryophyte floras, but were identified by Essl *et al.* (2014a,b,

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Fig. 1) as alien hotspots. What would be, for instance, the rationale for identifying such cosmopolitan species as *Tortula muralis* and *Bryum argenteum*, for which molecular phylogeographies point to an almost complete absence of geographical structure in patterns of genetic variation at the global scale (Werner & Guerra, 2004; Pisa *et al.*, 2014), as aliens in St Helena, but not in other archipelagos (Essl *et al.*, 2013, Appendix S2)? Unfortunately, none of the previously proposed criteria to characterize nativeness can be satisfactorily applied to groups like bryophytes, wherein historical and fossil records are extremely scarce.

During the process of human-mediated introductions, invasive species experience founding events, which leave strong imprints in their genetic structure (Dlugosch & Parker, 2008). Genetic diversity, genetic structure and estimated time since founding events derived from the analysis of neutral genetic markers can, thus, be employed to seek evidence as to the native status of populations of uncertain origin (e.g. Fussi *et al.*, 2012; Bell *et al.*, 2013; Fuentes-Utrilla *et al.*, 2014). For example, the moss *Sphagnum subnitens* exhibits a strikingly disjunct distribution between Europe, North America and New Zealand, where it is mostly restricted to disturbed habitats. The absence of private alleles, extremely low genetic diversity, and sharing of alleles with European plants, led Karlin *et al.* (2011) to conclude that the species underwent a recent founding event in New Zealand from European migrants sometime prior to the 1970s, most likely by human-mediated introduction, confirming its status as an alien by Essl *et al.* (2013, 2014a).

While defining nativeness in organisms that are not deliberately introduced, and for which the fossil record is extremely scarce, is an exceedingly challenging task, we suggest that population genetic analyses can represent a useful tool based upon a series of criteria such as the timing of founding events, genetic diversity, and local patterns of genetic structure, to help distinguish native from alien populations. We suggest that such an approach would represent a useful test of hypotheses regarding patterns of invasion inferred from distribution data, which have most recently been proposed for long-neglected groups in invasion biology, like bryophytes (Essl *et al.*, 2013, 2014a,b). This is especially true on oceanic islands, where recent critical taxonomic work and modern, up-to-date checklists, which compose the primary source of information for biodiversity studies, are largely missing.

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Identifying alien bryophytes taking into account uncertainties: a reply to Patiño & Vanderpoorten (2015)

ABSTRACT

Recently, Patiño & Vanderpoorten (2015, *Journal of Biogeography*, **42**, doi:10.1111/jbi.12492) commented on our manuscripts about patterns and processes of global bryophyte invasions. In particular, they argued that the criteria we have used to identify alien bryophytes (i.e. anomalous geographical distribution, preference for disturbed habitats, indirect associations with some means of human transport) are insufficient in the absence of further evidence. We fully agree with this statement. Consequently, we had used the above-mentioned criteria only for the identification of 'cryptogenic' (i.e. probable alien) species and have stated this explicitly in our manuscripts. Thus, we conclude that Patiño & Vanderpoorten (2015) have drawn misleading conclusions on the way we defined aliens. Nevertheless, we acknowledge that given the excellent long-distance dispersal capacities of bryophytes, diverging opinions between different experts on the native, alien or cryptogenic status of a particular bryophyte species in a given region do sometimes exist.

Keywords Alien species, bryophyte biogeography, cryptogenic species, invasion, nativeness, naturalization, non-native, species distribution.

Until recently, bryophyte invasions have received little attention in invasion ecology (Pyšek *et al.*, 2008). To improve knowledge on this taxonomic group we have compiled data on bryophyte invasions in 82 regions (countries, federal states, islands) from all over the globe and subsequently analysed macroecological patterns in this dataset (Essl *et al.*, 2013, 2014a,b).

In a recent correspondence, Patiño & Vanderpoorten (2015) have questioned the criteria we supposedly had applied to identify bryophytes as aliens in particular regions. Specifically, the authors argue that '... anomalous geographical distribution, preference for disturbed habitats, and associations with some means of human transport' are insufficient criteria for identifying alien species in the absence of further evidence.

We fully agree with the argument that identifying alien species in taxonomic groups for which historical data are scarce and which have effective means of natural long-distance dispersal (Vanderpoorten *et al.*, 2011; Lewis *et al.*, 2014) is a daunting task. Consequently, we not only applaud a claim for a conservative approach (Pyšek, 2003) but also think that we have applied such a conservative approach. First, we only included regions where we considered documentation of alien status reliable: to ensure that available expert knowledge of alien and cryptogenic bryophyte occurrences is properly accounted for, we contacted approximately 25 regional bryologists who reviewed the data for their region of expertise (see Acknowledgements in Essl *et al.*, 2013).

Second, we made use of the concept of 'cryptogenic' species. In biogeographically less well-known taxonomic groups such as bryophytes, there is often a substantial proportion of species which may be considered alien for a range of possible reasons (i.e. lack of old records, association with anthropogenic ecosystems, anomalous distribution), although a definite assessment is not yet possible (cf. Söderström, 1992). For such suspicious aliens, the term 'cryptogenic' has been proposed (Carlton, 1996). The recognition of cryptogenic species has several benefits. In particular, it allows for a separate analysis of this group to look for possible differences with well-documented aliens (Essl *et al.*, 2014b). Moreover, it flags species for which additional research for assessing their biogeographical status is needed.

We underline that the criteria criticized by Patiño & Vanderpoorten (2015) and cited above have only been used for the identification of such cryptogenic species and not for aliens in the strict sense. The identification of alien bryophytes required further well-documented evidence such as molecular studies, observed introduction events, association with introduction pathways (e.g. occurrence as an epiphyte on ornamental plants, or as a weed in horticultural supplies), or robust floristic or biogeographical evidence provided by regional bryofloras, bryological studies or experts. Similarly, the availability of several complementary indications of non-native status, such as new occurrences of conspicuous bryophyte species which have previously been absent from bryologically well-researched regions outside their native ranges and which are restricted to anthropogenic habitats, in combination also qualified a species for assignment of alien status in our analyses.