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How are anthropogenic pressures facilitating the invasion of *Campylopus introflexus* (Dicranaceae, Bryopsida) in mainland Portugal?

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Abstract – *Campylopus introflexus*, listed as one of the 100 worst alien taxa in Europe, is an example of a recent introduction in this region. It became an invasive species in Portugal only twenty years ago, but is now known from more than 200 localities, where it occupies extensive areas and numerous microhabitats.

Several studies have highlighted the methodological deficiencies for understanding the expansion of *Campylopus introflexus*, and some have already explored the reproductive strategies, hybridization processes and abiotic factors (geological and climatic parameters) influencing this species' ability to invade native species' habitats. In the present work, we specifically focused on the spatial patterns of its invasion in mainland Portugal, which can be linked to human-related parameters that reflect land occupation, management or abandonment. Specifically, we have studied the link between all distribution records (presence and absence data) known for this species in Portugal until 2016, and parameters expressing human presence or pressure.

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Our findings show that the highest occurrence of this invader corresponds to areas with higher levels of human population density and in oceanic areas where land management is dominated by non-native tree-plantations. Conversely, *C. introflexus* expansion is hindered by dryland farming or agricultural practices that rely on fire which, consequently, promote natural or human-induced aridity and/or result in increasingly arid landscapes.

Invasive species/ fire/ aridity/ non-native tree plantations/ Human Impact Index/ mosses, bryophyta

INTRODUCTION

Campylopus introflexus (Hedw.) Brid. is a widespread moss in the Southern hemisphere, where it occurs in southern areas of South America and Africa, parts of Australia, as well as in islands of the Pacific and Indian oceans (Söderström, 1992; Klinck, 2010). Considered to be one of the 100 worst alien species in Europe (Delivering Alien Invasive Species Inventories for Europe, http://www.europe-aliens.org/default.do), *C. introflexus* is one of the few classic examples of a recently introduced taxon in Europe (Øvstedal, 1978; Stech & Dohrmann, 2004). Its presence has been associated with a certain amount of environmental disturbance (Söderstrom, 1992; Sparrius & Kooijman, 2011; Repeckiene *et al.,* 2012). In its turn, this invader introduces changes that alter other bryophyte and vascular plant communities. For instance, *C. introflexus* produces a significant negative effect (60% reduction) on the germination of *Calluna vulgaris* on moss carpets (Equihua & Usher, 1993).

The expansion of *Campylopus introflexus* is complex to explain, due to possible interactions between ecological, population, reproduction and genetic factors among closely related species. The reproductive strategy of *C. introflexus* is very successful in comparison to related taxa, such as *C. pilifer* Brid., since it involves faster growth rates, profuse ramification and frequency of gametangia, and a massive spore investment, contributing to its competitive advantage whenever the niche of the two species overlap (Hugonnot, 2017). However, on the other hand, the possibility of hybridization and the described intermediate forms of *Campylopus introflexus* and *C. pilifer* (Frahm & Stech, 2006; Gama *et al.*, 2017) is currently an established ecological problem that hinders the comprehension of the expansion pathways of this alien.

In Europe, *Campylopus introflexus* was first recorded in 1941, in Sussex, South East England. However, in mainland Europe, it was only discovered in 1954 in France (Størmer, 1958). The European southern limit of its distribution is not mainland Portugal, since this species is also present in western Macaronesia, the Azores (Sérgio & Schumacker, 2001) and Madeira Island (Stech *et al.,* 2007). Its presence in North Africa remains doubtful, with reports in Morocco and Algeria and a single locality in Libya (Ros *et al.,* 2013). Its known northern distribution limit is Norway and Sweden, and to the East the species has been recorded in Estonia, Slovakia and Turkey (Klinck, 2010; Blockeel *et al.,* 2009). In recent years Szucs & Bidlo (in Ellis *et al.*, 2014) have reported it from Slovenia.

The distribution of this species in the Iberian Peninsula was outlined by Casas *et al.* (1989), and was first reported in Portugal in 1996 (Sérgio, 1997) from northern Lisbon. Subsequently, it was recorded in another four localities in the north of the country (Sérgio *et al.*, 2003) and extensive fieldwork conducted across the country after 2003 recorded numerous new localities totalling approximately 40 new areas subject to Atlantic influence. Currently, it is known to occur in about 200 localities in the country. In Spain, its high establishment and expansion rates are also worrying; it has been reported from numerous new localities in the provinces of Barcelona and Girona (Benjumea *et al.*, 2013).

Studies providing a comprehensive assessment of the environmental and anthropogenic factors driving bryophyte communities and invasions are scarce. Only recently, Essl *et al.* (2015) tested how species' attributes and environmental and anthropogenic factors can affect bryophyte invasions worldwide, while Mateo *et al.* (2015) aimed to determine the potential of spread of invasive bryophytes, showing that their expansion appears to be constrained by climatic conditions, since these invaders only occur under climate conditions that are similar to those currently prevailing in their native ranges. These particular studies provide insights on a global level. At a regional scale, Portela *et al.* (2017) proposed a framework to monitor the cumulative effects of several anthropogenic pressures on the distribution of bryophyte communities in modified riverscapes.

It is now widely accepted that the current global change, including overall climate warming and changes in land use, results from human action with a heavy ecological impact (Vitousek, 1994). Human-facilitated dispersal has been repeatedly shown to be the most important vector for the spread of invasive species, including bryophytes (Essl *et al.,* 2015; Mateo *et al.,* 2015). *Campylopus introflexus*, as with other alien plants, responds positively to a higher frequency or intensity of anthropogenic disturbances (Vicente *et al.*, 2011). We acknowledge that climate-driven changes affect bryophyte distribution. For instance, as global air temperature changes, even by a few degrees, the habitats in which bryophytes thrive will also change and, eventually, facilitate xerophytes such as *Campylopus* species, as has been found for other bryophytes [see Sérgio *et al.* (2011) for *Sematophyllum substrumulosum*].

At the same time, it is well established that human activities not only facilitate plant invasions, but also shape their invasion mechanisms. However, not many publications address the social factors influencing invasion dynamics (Kueffer, 2017). In this work, we hypothesize that an increased distribution of *C. introflexus* might be a consequence of human-induced changes, especially when these affect the microhabitat level (e.g. nutrient cycles and soil moisture changes following human-driven disturbances). Therefore, we intend to explore, not the advantageous traits of *C. introflexus* that allow its adaptation to climate-driven changes, but the invasion patterns that might be linked to the influence of humans, whose socioeconomic activities determine land management and abandonment, or greatly increase the pressure on the least-invaded habitats (Kueffer, 2017).

Considering the context of its known Portuguese localities, our research focused on the following questions:

1. Can geographic, land-use or anthropogenic factors be related to increased *Campylopus introflexus* presence?

2. Among the studied parameters, which are the ones that most influence *Campylopus introflexus* occurrence?

3. Can a derived socio-economic Index (Index of Human Impact) be useful in explaining the ability of *Campylopus introflexus* to progress to new areas in Portugal?

MATERIAL AND METHODS

Field procedures and data sources

The majority of *Campylopus introflexus* records were gathered during intensive fieldwork performed in a heavy metal monitoring study in mainland Portugal (Figueira *et al.,* 2002). Bryophytes were surveyed on 178 sites, located in a 30 × 30 km grid, set up at a national scale, but intensified in large urban or industrial areas to a 10 × 10 km grid (Figueira *et al.,* 2002; Reis *et al.,* 2010). At each site, *C. introflexus* presence/absence was established after a thorough examination of overall biodiversity (at least in an area of 50 × 50 m and all available habitats were studied). Data on species absence were based on field prospection, which was continuously updated for 10 years (*ca* 55 localities inspected from 2006 to 2016). These data were compiled along with other published occurrences (Sérgio *et al.,* 2003), together with additional records obtained from specimens until 2016 in the Herbaria of Lisbon (LISU) and Porto University (PO).

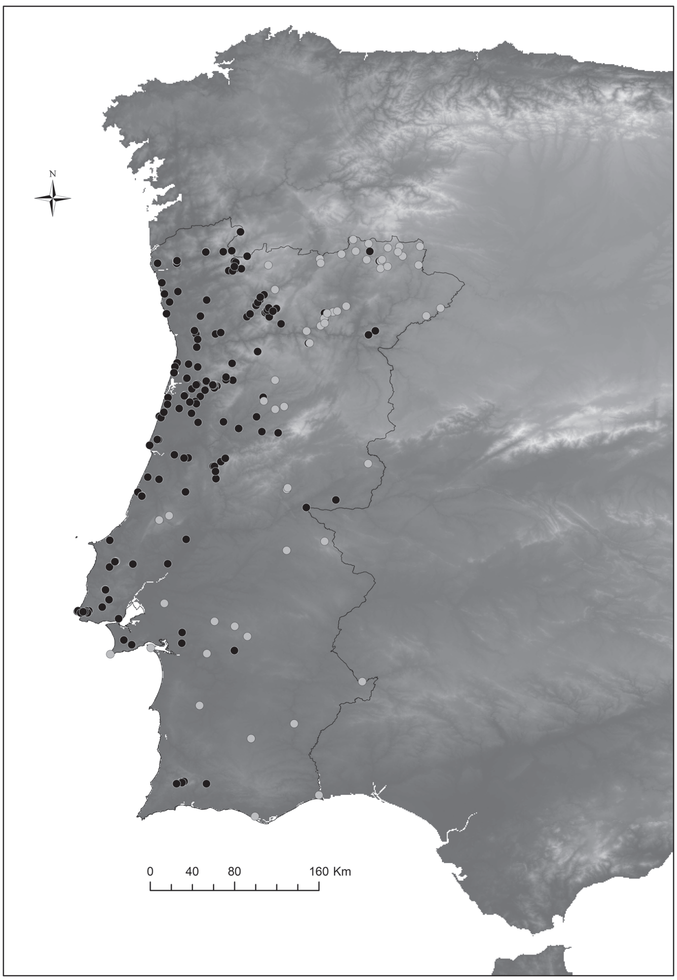

Fig. 1. *Campylopus introflexus* distribution: records of occurrence and absence in mainland Portugal. Grey scale: altitudinal level (lighter grey indicates higher altitude). (● Presences in Portugal from 1996 until 2016 based on LISU and PO herbarium samples. ⊙ Absences.)

Species data and parameters. All available Portuguese records (presence and absence) of *Campylopus introflexus* were georeferenced and integrated in a database: gathering *ca* 200 presences and 55 absences from different localities in mainland Portugal, until 2016 (Fig. 1). To establish to what extent human influence could be linked to the presence/absence of *C. introflexus,* we selected the following geographic (1-2), anthropogenic (3-5) and land-use (6) parameters available online:

1. Altitude (**AL**) (meters).
2. Longitude (**LO**) (degrees).
3. Population Density (**PD**) (n° inhabitants/km^2 by district – 2008 Census); Decennial Number/Square kilometre. Source: Statistics Portugal, Population and housing census, www.ine.pt.
4. Burnt Forest Area (ha) (**BA**) occurring from 2001 to 2010. Source: http://www.icnf.pt/portal/florestas/dfci/inc/estat-sgif.
5. Fuel Consumption (**FC**). Source: Annual domestic petrol consumption per inhabitant – toe/hab. www.ine.pt.
6. **COS** (land use and land cover in mainland Portugal). Source: http://mapas.dgterritorio.pt/geoportal/catalogo.html. All the variables were tested and then the following 4 with highest significance were selected:
   - **COS211** – Dryland farming
   - **COS223** – Olive groves
   - **COS323** – Sclerophytic vegetation
   - **COS324** – Open forests, clear-cutting and new plantations

Parameter correlations and Index of Human Impact (IHI). Spearman correlations were calculated to assess the correlation between the presence/absence of *Campylopus introflexus* and the geographic variables. The statistical analyses were performed using the software IBM SPSS Statistics 23.0. IBM® SPSS® Statistics 23.0.

The creation of an Index of Human Impact (IHI), a subjective index, was adapted from Gombert *et al.* (2004), and from Sérgio *et al.* (2016) who used this Index to study floristic changes of epiphytic flora in the Tagus region. To calculate IHI, we verified, for each *Campylopus introflexus* record, which were the three quantitative parameters with the most significant and highest Spearman correlation with the occurrence of this species. Subsequently, and considering the three most important parameters for the total of *C. introflexus* localities, we assigned a class from one to four to the top 3 parameters to obtain the IHI (Table 1). Since a positive and significant correlation was found between several parameters and the presence of *C. introflexus*, we selected the top three to correlate to its overall presence: PD, FC and BA (Table 1).

Finally, the IHI Index was calculated using the following formula:

$$IHI = PD (FC + BA)$$

Table 1. Value of each quantitative parameter in classes (1 to 4) from all points of occurrence of *Campylopus introflexus,* used for the calculation of the Index of Human Impact (IHI)

Parameter /Classes	*1*	*2*	*3*	*4*
PD- Population's density. n°/km^2 (Census 2008)	0-9	10-99	100-499	> 500
FC- Fuel consumption toe/hab (2011 to 2013)	0-999	1000-4999	5000-19999	> 20000
BA- Forest Burnt Area ha (2001 to 2010)	0-40	50-99	100-999	> 1000

Table 2. Spearman correlations between *Campylopus introflexus* presence/absence data and geographic parameters, socio-economic statistics, land use and land cover (COS) and the Index of Human Impact (IHI) (*p*-values: * = 0.05; ** = 0.01; *** = 0.001)

Parameters	*Spearman r*	*95% confidence interval*	*p-value*
Longitude (LO)	– 0.5183	– 0.6052 to – 0.4191	***
Altitude (AL)	– 0.1768	– 0.2968 to – 0.05121	**
Forest burnt area (BA)	– 0.1166	– 0.2398 to 0.01028	*
Population's density (PD)	0.4546	0.3480 to 0.5497	***
Fuel consumption (FC)	0.1941	0.06910 to 0.3131	**
COS211 – Dryland farming	– 0.2376	– 0.3537 to – 0.1144	***
COS223 – Olive groves	– 0.1638	– 0.2846 to – 0.03790	**
COS323 – Sclerophytic vegetation	– 0.1319	– 0.2544 to – 0.005301	*
COS 324 – Open Forests, cuts and new plantations	0.1463	0.01994 to 0.2680	*
Index of Human Impact (IHI)	0.242	0.136 to 0.338	**

RESULTS

Distribution of *Campylopus introflexus*

The distribution of this species in Portugal clearly shows a geographic tendency towards coastal areas of the mainland, and its quasi-absence in the inland areas.

Parameter correlations and Index of Human Impact (IHI). Table 2 shows the results of Spearman correlations between *Campylopus introflexus* presence or absence in the field and information on geographic, land-use or on quantitative socio-economic statistics indicating human influence. The top three parameters that were most significantly correlated with the presence of *C. introflexus* were Longitude (LO), Population density (PD) and Dryland farming (COS211) (Table 2).

When calculating the IHI, we obtained Index values for *C. introflexus* localities ranging from 2 (low IHI) to 28 (high IHI). The results of the Index of Human Impact (IHI) (Fig. 2) reveal that the localities where the presence of this moss was confirmed until 2016 tend to show a higher IHI than the localities of consistent absence over ten years (2006-2016) for this species.

DISCUSSION

Longitude, as a geographical proxy of the largest environmental axis that distinguishes the opposing geological and climatic characteristics between coastal and inland Portugal, had the strongest (negative) correlation with *Campylopus introflexus* presence. On the other hand, the presence of *C. introflexus* positively correlates with denser human occupation and fuel consumption, and the species

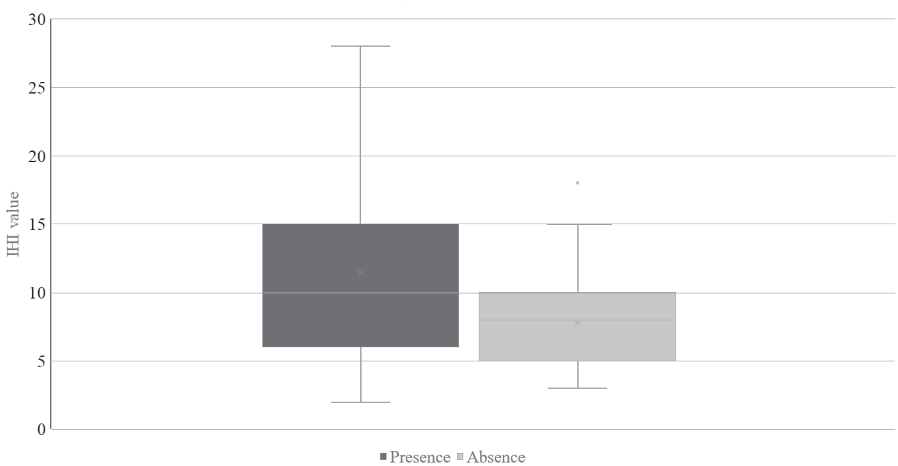

Fig. 2. Index of Human Impact (IHI) values for localities with presence and absence of *Campylopus introflexus* confirmed until 2016 (absence confirmed along ten years (2006-2016).

tends to establish itself in areas subject to Atlantic influence, although it avoids the highest altitudes (negative correlation with altitude). In fact, this spatial pattern is also reproduced by human populations, which settle in a much denser pattern in coastal and lowland areas of the country (Sousa Gomes, 2013). This type of human occupation creates an asymmetrical exploitation of soil resources in the country and, therefore, a more intensive coastal land change, use intensity and degradation. The fact that we also found a positive and significant correlation with parameter COS 324 (Open Forests, clear-cutting and new plantations) substantiates what we repeatedly observe in the field: the quick soil colonization of *C. introflexus* in open forests, clearings or new plantations. This evidence is particularly true in *Eucalyptus* plantations, which are exceedingly present in the coastal areas of Portugal. Effective dispersers and invaders like *C. introflexus* (with small and highly numerous spores and brood bodies) quickly establish in the freshly exposed soils of plantations, especially in the coastal areas of the country, where the disrupted soil, in the shade of the plantation's canopy, is often an excellent microhabitat for this species.

We consider that human population density and land use intensity might not be the sole factors influencing this species' distribution, since according to our results, *C. introflexus* is negatively correlated with the driest cultivated areas (dryland farming (COS211)), olive groves (COS223) and dry natural habitats (sclerophytic vegetation (COS323)), in agreement with Hugonnot's (2017) findings. Although a decrease in soil moisture might facilitate *C. introflexus* expansion to a certain point, this species appears unable to invade the driest rocky environments, without soil or shade, which, instead, are colonized by *Campylopus pilifer* and other xerophytes (e.g. *Grimmia* and *Racomitrium* spp.). In fact, a close look at a Portuguese natural aridity index map (Sanjuan *et al.,* 2011), shows a clear tendency for aridity to decrease towards the northwestern region of the territory, the same spatial direction in which *C. introflexus* becomes a successful invader.

Extreme dryness can also correspond to post-fire situations, which also seem significantly unsuitable for *C. introflexus* invasion. In Portugal, it is very common that burnt areas correspond to forest and abandoned agricultural lands transformed into unmanaged landscapes where low population density, high level of population ageing, and very fire-prone vegetation coincide (Nunes & Lourenço, 2017). This has led to a dramatic increase in the magnitude and frequency of wildfires, as well as to post-fire hydrological and erosion processes. These sustain very arid areas that remain unreachable to invaders that are limited by extreme dryness, such as *C. introflexus*. In fact, at a global scale, harsh environments that are cold, dry, shaded, or nutrient poor are often refugia of biodiversity and, to date, little affected by invasions (Kueffer, 2017).

The socio-economic IHI calculated in this work combines different anthropogenic variables and aims to simplify, synthesize and directly express a gradient of human impact and anthropogenic pressure. It identifies a tendency between the presence of this invasive species and localities with highest IHI (between 15 and 28). Although this index is significantly but not very strongly positively correlated, its application to the whole country would make it possible to elaborate a preliminary map of areas susceptible to invasion in mainland Portugal. However, the precise identification of areas of occurrence of this species should also consider comprehensive geological and climatic approaches, which is beyond the goals of this analysis, and should be a starting point for future studies.

Our results demonstrate that the invasion of *Campylopus introflexus* results from the opposing synergetic dynamics of anthropogenic factors. Fire and agricultural practices promote dryness and hinder *C. introflexus* from colonizing natural or human-changed landscapes, while dense human populations and non-native forest plantations strengthen the invasion potential of this moss. The results of this study demonstrate the importance of interdisciplinary approaches in complex socioecological systems, which can include guidelines related to the role of human population in promoting biological invasion.

To check if climate-driven or anthropogenic-induced factors promote invasion by *Campylopus introflexus,* we suggest, whenever possible, to monitor the progress of this species' invasion by selecting monitoring sites in the areas where we registered its absence in the 10-year lifespan of our study.

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