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The invasive moss *Campylopus introflexus* (Hedw.) Brid. (Bryophyta) spreads further into South-Eastern Europe

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Abstract – *Campylopus introflexus* (Hedw.) Brid. is the most widespread invasive moss species in Europe. Originating from the Southern Hemisphere, it is nowadays causing serious changes in coastal sand habitats of Western Europe and invading various anthropogenic habitats in Central Europe. In South-Eastern Europe, the species was initially found in Croatia in 2013, in the Dinaric region in the karst plain Vrhovinsko polje, on leached bare soil and pine bark remnants. In 2015, another stand of similar size was found in the peri-Pannonian region, on Mt Papuk, on a gneiss cliff in an acidophilous sessile oak forest. These two localities are on the South-Eastern frontline of the species' invasion within Europe. The oldest individuals were three to four years old, and sporophytes were not found. At the moment, it seems that the invasive moss is not a threat to native flora in the Dinaric region. Nevertheless, special attention should be given to the peri-Pannonian and Eastern Balkan regions, since its expansion could threaten the habitats of native moss and lichen species growing in similar acidic forests. Since the bryoflora of South-Eastern Europe is still largely undersampled, directed surveys and monitoring programs should be promptly established.

Alien moss species / Biological invasion / Croatia / Dinaric region / peri-Pannonian region

INTRODUCTION

Invasion patterns of bryophytes have been largely neglected in invasion biology, and historical data are very scarce and incomplete. Therefore, many controversies in approaches and definitions exist (Essl *et al.*, 2013, 2014, 2015; Patiño & Vanderpoorten, 2015) and consequently, differences in the number of

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invasive species adduced. Using their own criteria, Essl *et al.* (2014, 2015) recognized 139 alien bryophyte species worldwide. On a European level, 1.8% of all bryophyte species are alien or 2.5%, if cryptogenic species (those with unclear histories of occurrence in Europe) are included (Essl *et al.*, 2013). In total, 58 species are quoted in the DAISIE database (2017). Only five alien and three cryptogenic species have invaded more than five European countries (Mikulášková *et al.*, 2012). According to Razgulyaeva *et al.* (2001), only three species can be recognized as truly invasive: *Campylopus introflexus* (Hedw.) Brid., *Orthodontium lineare* Schwägr. and *Scopelophila cataractae* (Mitt.) Broth. The first two are among the very few, for which historical evidence of invasion is available (Stieperaere, 1994; Hassel & Söderström, 2005; Patiño & Vanderpoorten, 2015).

Campylopus introflexus, in Europe an alien invasive species, is native in the Southern Hemisphere: South America, southern Africa, Australia and New Zealand (Frahm, 1984). It has spread worldwide, affecting the composition of resident species (Essl *et al.*, 2014). Invasion of this species in Europe started in Great Britain (Fig. 1), where it was first recorded in 1941 (Richards, 1963). A detailed overview of literature

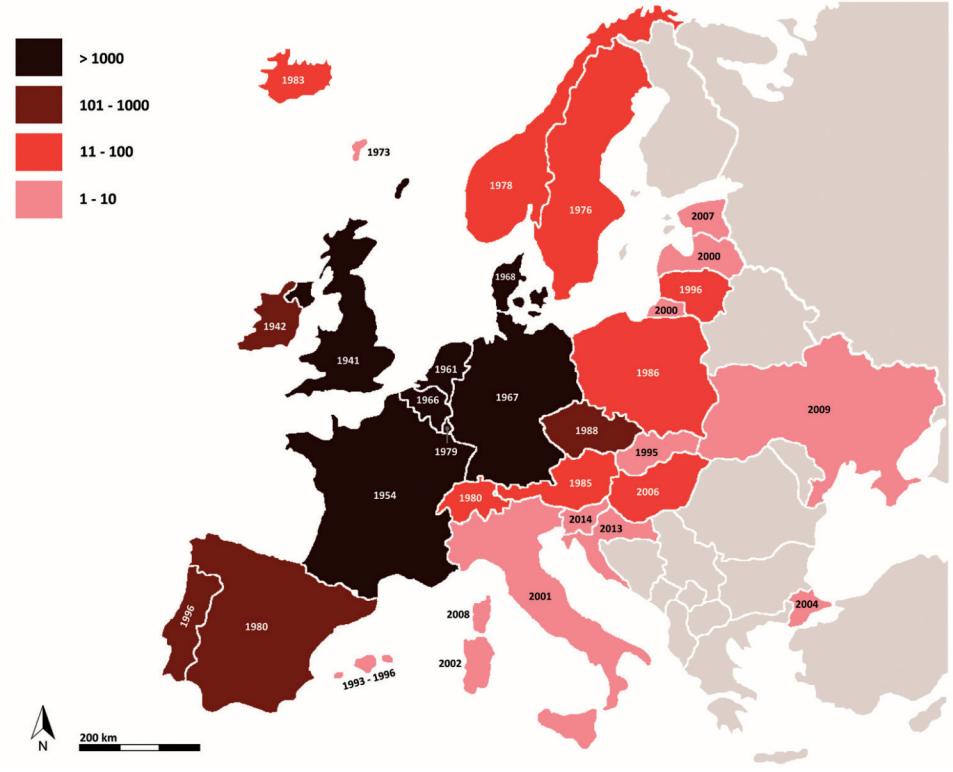

Fig. 1. Historical review of *Campylopus introflexus* invasion through Europe. Data on first records are according to the *Invasive Species Compendium* database, accessed on 15th June 2017, except for Italy – Cortini Pedrotti C., 2001, Sardinia – Cogoni *et al*., 2002, Corsica – Sotiaux *et al.*, 2008, Estonia – Vellak *et al*., 2009, Ukraine – Lobachevska & Sokhahchak, 2010 and Slovenia – Szűcs & Bidló, 2014. Classes of abundance (number of localities) are presented on a logarithmic scale (rare – 1-10 localities; sparse – 11-100 localities; common – 101-1000 localities and very common – > 1000 localities) and are based on general and national databases, literature and personal communications.

dealing with first occurrences in European countries is accessible through the CABI database (2016), from which it is evident that by the end of the 1960s *C. introflexus* had spread throughout Western Europe and during the next two decades further in many countries of Central and Northern Europe. In Eastern Europe it was firstly recorded in the 1980s (Poland), while in Latvia and Russia (Kaliningrad Province) it was noticed in 2000. The tendency for it to spread eastwards is well documented in Poland (Fudali *et al.*, 2009; Górski *et al.*, 2016). Some of the most recently invaded countries are Italy (Cortini Pedrotti, 2001), Hungary (Szűcs & Erzberger, 2007), Ukraine (Lobachevska & Sokhahchak, 2010) and Slovenia (Szűcs & Bidló, 2014). This moss currently occurs in 27 countries and the recent status of its distribution throughout Europe is presented by Hodgetts (2015).

The pattern of its spread from Western Europe eastwards suggests that long distance spreading by spores is more important for initial colonization, and that the importance of asexual reproduction increases in subsequent short distance-spreading (Mikulášková *et al.*, 2012). In some countries, the distribution of *C. introflexus* is well documented; in the Netherlands (BLWG Verspeidingsatlas mossen, 2016) and Germany (Moose Deutschland, 2016) the species has been recorded in almost all mapping units, in Hungary it was found in 13 of 2832 mapping units (Szűcs *et al.*, 2014), while in the Czech Republic over 100 localities are known (Mikulášková *et al.*, 2012).

With several experimental studies, the impacts of *C. introflexus* are the best-studied among invasive bryophytes (Essl *et al.*, 2014). Nevertheless, in most parts of Europe its invasion intensity and ecology are still insufficiently known. The existing data indicate that the species behaves differently in Western and Central Europe. In Western Europe, i.e. in parts of Europe with an oceanic climate (Netherlands, Belgium, Germany), *C. introflexus* colonizes a wide spectrum of habitats and is capable of forming dense mats. The negative impact of invasion by *C. introflexus* was first pointed out for the coastal dunes of the Netherlands (van der Meulen *et al.*, 1987). Accordingly, the majority of studies in Western Europe have been concentrated on sandy habitats and related nutrient-poor grasslands, where it is a threat to native flora (Hasse, 2007; Daniëls *et al.*, 2008; Klinck, 2009; Sparrius & Kooijman, 2011). *C. introflexus* may alter the ecosystem structure and functioning of dunes by stabilizing soils, binding leaf litter, altering decay rates, and creating microhabitats which affect the composition of microfaunal communities (Klinck, 2009; Vogels *et al.*, 2005; Schimerl, 2011; Schimerl *et al.*, 2011; Schimerl & Buchhlolz, 2013; Van Turnhout, 2005; Pehle & Schimerl, 2015). For Central Europe, the most data are available from the Czech Republic, where the distribution of *C. introflexus* ranges from colline to montane belt (210-1140 m a. s. l.); the most frequently invaded habitats are the edges of spruce plantations and pine forests, forest clearings and bare areas in damaged peat bogs (Mikulášková *et al.*, 2012). All of these habitats are influenced by human disturbance, including bare acidic soils where vascular plant competition is low, thus being favorable for *C. introflexus* growth. However, findings from Hungary (Csiky *et al.*, 2014, 2015; Szűcs *et al.*, 2014) suggest that anthropogenic disturbance is not required for colonization, since bare acidic soil surfaces suitable for colonization can commonly be formed naturally or due to animal disturbance. In the easternmost frontline of the invasion (Kaliningrad Province, Russia), the species was recorded in small patches on humus litter in an open *Betula pendula-B. pubescens-Pinus sylvestris* forest (Razgulyaeva *et al.*, 2001). Repečkienė *et al.* (2015) concluded that *C. introflexus* may negatively affect fungal diversity and the seasonal succession and structure of fungal communities in Lithuanian peatlands, which can have negative influence on natural restoration of

plant cover. By contrast, a study on peatlands in Latvia (Priede & Mežaka, 2016) showed that *C. introflexus* is a common pioneer species in vacuum-harvested peatlands and that it has a minor impact on vegetation diversity and cannot be considered as the threat to peatlands.

In North America, the species was firstly recorded in 1967 and now occurs primarily in coastal areas in the western part of the continent. As in Central Europe, many of the populations are associated with anthropogenic environments but relatively undisturbed sites are also invaded (Carter, 2014).

Using ecological niche models and ordination techniques, Mateo *et al.* (2015) compared the macroclimatic niches of *C. introflexus* in its native range (Southern Hemisphere) and in its invasion area (Northern Hemisphere). They found no evidence for niche expansion in the invaded range. The species occurs in the invaded area under climate conditions similar to those in the native range. The models indicated a possible threat of *C. introflexus* for Central and Eastern Europe, North America and eastern Asia.

In our study we introduce the first two occurrences of *C. introflexus* in Croatia, which are in the South-Eastern frontline of invasion within Europe.

MATERIALS AND METHODS

Study area

Croatia is situated in South-Eastern Europe at the meeting point of several (bio)geographical regions: peri-Pannonian, Dinaric and Mediterranean. In this study, two different geographic situations were studied in terms of bryophytes: the karst plain Vrhovinsko polje in Dinaric, and Mt Papuk in peri-Pannonian region.

Vrhovinsko polje is located on the southern edge of Mt Mala Kapela, just alongside the eastern border of Plitvička jezera National Park, in a belt of beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.) forests. Vrhovinsko polje is a typical karst plain with its lowest, central part periodically flooded during winter and early spring. It is covered with diverse grassland vegetation, with many plant communities, determined mainly by moisture and pH. In terms of the diversity of flora and grassland communities, it is one of the richest and most diverse karst plains in Croatia. Parts of the field are used as arable land, where predominantly barley and wheat are grown. Paths and field edges are characterized by patches of bare soil and low ruderal vegetation. The neighbouring slopes of Mt Mala Kapela are covered by natural and climax beech-fir forests, as well as by old plantations of *Pinus nigra* J.F. Arnold and *P. sylvestris* L. The climate is moderately warm and humid, with warm summers. The average annual precipitation is 1550 mm with maxima in spring and autumn, and snow cover from November to March. The coldest month is January with an average temperature of 2.2°C, while the warmest is July with an average of 17.4°C. The annual average is 7.9°C (Zaninović, 2008). Geological bedrock is manly limestone, but mostly bearing deep deposits of leached and acidic soils.

Mt Papuk, with peaks higher than 900 m a. s. l., is the largest mountain of the peri-Pannonian region of north-eastern Croatia (Slavonia region). Almost the entire Papuk area (33600 ha) has been protected as a nature park since 1999, and since recently, as a NATURA 2000 site (Anonymous, 2013). Due to the high geological diversity and various types of rocks (e.g. igneous, sediment and

metamorphic) Papuk belongs to the European Geoparks network and the Unesco-assisted Geoparks network. The open and exposed rocky habitats, although rather small in extent, are of great importance for biodiversity. Ninety-five percent of the area is covered with forests, dominated by acidophilous beech communities. The climate is temperate, moderately warm without an explicit dry period. Depending on the elevation, the annual mean temperature varies between 8 and 11°C, and annual precipitation between 800 and 1300 mm (Zaninović, 2008). The bryophyte flora of Papuk is very rich, counting 190 species (Alegro *et al.* in prep.), with several species unique for Croatia.

Data collection

In 2013, a complete survey of bryophyte flora of Vrhovinsko polje field was conducted, and a comprehensive list of vascular plants was compiled. The specimens are deposited in the Bryophyte Herbarium of the Hungarian Natural History Museum, Budapest (BP) and the Herbarium Croaticum of University of Zagreb (ZA).

In 2015, during a field survey in the Mt Papuk area, vascular plants, bryophytes and lichens of several habitats were studied. The collected specimens are placed in the Herbarium of the University of Pécs (JPU) and ZA.

The species was identified with stereomicroscope and light microsope, using Smith (2004), Frey *et al.* (2006) and Brugués & Guerra (2006). Distributional data regarding history of invasion and invasion intensity across the Europe were gathered through various databases, literature and personal communications (Fig. 1).

In the text below, dominant species are marked with bold fonts within the species lists.

RESULTS

The first finding of *Campylopus introflexus* in Croatia and South-Eastern Europe was in the central part of the Vrhovinsko polje field (Fig. 2), on a raised area, out of reach of flood water. In this particular locality, deposits of soils are very deep, which isolates the surface from the limestone bedrock. Soil is dry, powder-like and leached, bearing acidophilous flora with low demands for nutrients (e.g. ***Agrostis capillaris*** L[1]., ***Aira elegantissima*** Schur, *Chamaecytisus supinus* (L.) Link, *Danthonia decumbens* (L.) DC., *Helianthemum ovatum* Dun., ***Linum catharticum*** L., and *Luzula campestris* (L.) DC.). *C. introflexus* grows outside closed grassland vegetation on anthropogenically influenced patches of bare soil, and on *Pinus nigra* logs, colonizing partially decayed bark. The surface occupied by *C. introflexus* is not larger than 2 m^2, and the moss itself is scattered in several dozen cushions of a few square decimetres. Plants are typically developed, vigorous, greyish green, but without sporophytes. According to the growing sections, the oldest plants were three years old, and on the edges of cushions two and one year old stems were abundant. Other bryophytes present in the vicinity are the following: *Bryum alpinum* Huds. *ex* With., ***Homalothecium lutescens*** (Hedw.) H. Rob., *Pleuridium acuminatum* Lindb., *Pogonatum urnigerum* (Hedw.) P. Beauv., ***Polytrichum piliferum*** Hedw.,

1. In bold are the most frequent species.

Fig. 2. Locations of *Campylopus introflexus* in Croatia.

Pseudoscleropodium purum (Hedw.) M. Fleisch. and *Weissia brachycarpa* (Nees & Hornsch.) Jur. The complete bryophyte species list of Vrhovinsko polje is published in Alegro *et al.* (2014).

The second locality, Sokolina, is situated in the southern part of the Papuk mountain, north of the settlement of Velika (Fig. 2), on a bare gneiss cliff with a north-eastern facing, 10° steep slope at the top, rising above an acidophilous oak forest. Expansion of the stand is 2 m × 0.5 m, while the largest contiguous patch is approx. 0.5 m^2. The compact cushions of this moss grow on very thin and dry debris of bedrock and dead organic matter. *C. introflexus* is presumed to spread to the detriment of the dominant *Polytrichum piliferum* Hedw. and other native moss species in the locality. Due to the bedrock and the low demands of nutrients, only a few, mainly acidophilous, plant species occur in this habitat (e.g. *Betula pendula* Roth, *Deschampsia flexuosa* (L.) Trin., *Fagus sylvatica* L., *Genista pilosa* L., *Hieracium pavichii* Heuff., *Juniperus communis* L., *Molinia arundinacea* Schrank, ***Quercus petraea* agg.**, ***Vaccinium myrtillus*** L. and *Vulpia myuros* (L.) C.C. Gmel.). Other lichens and bryophytes present within the studied sample (plot size 2 m^2) are the following: *Cladonia arbuscula* (Wallr.) Flot. (new for Papuk), *Cladonia coccifera* (L.) Willd. (new for Croatia), *Cladonia furcata* (Huds.) Schrad., *Cladonia gracilis* (L.) Willd., *Cladonia macilenta* Hoffm., *Cladonia pyxidata* (L.) Hoffm., *Cladonia rangiferina* (L.) Web. *ex* Wigg., *Cladonia squamosa* (Scop.) Hoffm., *Cladonia uncialis* (L.) Web. *ex* Wigg., *Cladonia cervicornis* (Ach.) Flot. subsp. *verticillata* (Hoffm.) Ahti (new for Papuk), *Cynodontium polycarpum* (Hedw.) Schimp., *Dicranum scoparium* Hedw., *Dicranum spurium* Hedw., *Polytrichum formosum*

Hedw. and ***Polytrichum piliferum*** Hedw. According to the growing sections, the oldest *Campylopus introflexus* stems in this stand are four years old and contain no sporophytes.

Campylopus introflexus from both sites could be easily distinguished from similar species *C. pilifer* through hair-points reflexed at right angles. Plants from Vrhovinsko polje have, in some specimens even very conspicuously, ribbed dorsal surface of the costa, and in plants from Papuk it is much smoother, with weakly exerted ribs. In both cases ribs are only one cell high, which distinguishes it from *C. pilifer*, which has 3-4 cells high lamellae on dorsal surface of the costa.

Voucher specimens: Croatia, Vrhovinsko polje, 44°49'13.78"N, 15°29'23.81"E, 770 m, 27 July 2013, *B. Papp, A. Alegro & V. Šegota* (ZA44934); Papuk Mt, Sokolina, ; 45°29'37.84"N, 17°36'28.51"E, 524 m, 18 July 2015, 45°29'37.84"N, 17°36'28.51"E, 524 m, *J. Csiky, J. Deme., D. Kovács & D. Purger* (ZA44935); repeated collection on 16 Oct. 2015, A. Alegro & V. Šegota (ZA44936).

DISCUSSION

Two localities of *Campylopus introflexus* in Croatia, at a distance of 160 km from each other, have provided the first known records in the Western Balkans. The nearest known localities are in Central Europe: Slovenia (Szűcs & Bidló, 2014), *ca* 200 km from Vrhovinsko polje, and southern Hungary (Szűcs *et al.*, 2014), *ca* 75 km from Mt Papuk. Ecological requirements of the species are very similar to those in the Czech Republic, where it "invades dry, nutrient-poor acidic soils in a range of vegetation types, and is most common in coniferous forest plantations and drained bogs, where it colonizes open patches resulting from anthropogenic disturbance where there is little competition from other plants" (Mikulášková *et al.*, 2012). In Hungary, it was found in pine plantations, mixed deciduous-coniferous forests, acidophilous oak woodlands and man-made habitats. Older records mainly indicate decayed pine woods as habitats of this species, but the species was recently found on acidic soils as well (Szűcs *et al.*, 2014). In Slovenia, it was found on trampled sites with acidic soil, in a mixed deciduous forest (*Quercus petraea, Fagus sylvatica*), near a planted *Pinus sylvestris* forest stand (Szűcs & Bidló, 2014).

In Croatia *Campylopus introflexus* was found in similar conditions, on patches of open, leached and nutrient-poor soil, and remnants of pine bark. However, in the case of Vrhovinsko polje, the main difference is that the habitat is fully open, located within the grassland area, while the closest pine stands are several hundred metres to a kilometre away. Since the species was found not only on bare soil, but also on remnants of pine bark introduced into the site, the nearby stands of *Pinus nigra-P. sylvestris* were searched for *C. introflexus*, but with no success. Hence, it is not clear whether *C. introflexus* first invaded patches of open soils and secondarily overgrew the remnants of pine bark, or was introduced by the pine tree remnants. Since it was not found in the pine forest, it is quite possible that the pine bark does not originate from the nearby pine stands, if the bark is indeed the medium of introduction.

In the case of Mt Papuk, the *Campylopus introflexus* habitat is quite similar to the localities in southern Hungary. In the acidothermophilous sessile oak forests with open canopy and rocky outcrops, the medium of introduction can be either wind or vertebrates. Prominent cliffs are the best lookout points in a forested area.

Birds and game prefer these isolated and insulated places for resting, therefore, these localities may become the centre for the dissemination of zoochory-spread plants as well.

The current threat from *Campylopus introflexus* to the native flora in Central Europe is small (Mikulášková *et al.*, 2012), since the potentially invaded plant communities are widespread and composed of common species. Likewise, a low threat to native flora can be assumed for the Dinaric region, but it should be kept in mind that this conclusion is based on only one known locality. The main reason for such an assumption is the fact that in a large grassland area with a range of plant communities, *C. introflexus* was restricted to patches of bare soil resulting from anthropogenic disturbance. Another limiting factor for the further spreading of the species is the relatively rare occurrence of acidic soils in the Dinaric region of Croatia, where carbonates dominate. Furthermore, in a cultivation experiment, the lime-enriched substrate inhibited the growth of protonemata, and most of the gametophores died within six months on such a substrate (Mikulášková *et al.*, 2012). Therefore, the invasion scenario known from Western Europe (Equihua & Usher, 1993; Biermann & Daniëls, 1997), is unlikely to happen in the Dinaric region of Croatia. However, in the peri-Pannonian region, where there are small and critically endangered remnants of continental sands with loose stands of *Festuca vaginata* Waldst. & Kit. *ex* Willd. and *Corynephorus canescens* (L.) P. Beauv., invasion by this moss species could be harmful for native flora. Similarly, a few very restricted coastal sandy areas with critically endangered flora in the Mediterranean region of Croatia could be influenced by *C. introflexus*.

In the South-Transdanubian region of Hungary, lowland habitats with psammophytic vegetation have not been invaded by *Campylopus introflexus* yet. This invasive moss has the largest stands in this part of Hungary, but instead of lowland sandy habitats it prefers disturbed acidic forest soils on sandstone in the colline and submontane regions influenced by a sub-Mediterranean or sub-Atlantic climate (Szűcs *et al.*, 2014; Csiky *et al.*, 2015). These habitats are very rich in regionally rare lichen and bryophyte species (Lőkös, 2010; Papp, 2010; Csiky *et al.*, 2015; Deme *et al.*, 2015) and therefore the expansion of *C. introflexus* is a potential threat to their populations in the Mecsek Mountains, as it has reduced species diversity of lichens and some lower plants in Western Europe (Biermann & Daniëls, 1997; Kettner-Oostra & Sýkora, 2004, 2008; Hasse & Daniëls, 2006; Daniëls, 2008). Likewise, in the Papuk area, in the vicinity of the acidophilous oak forest with *C. introflexus,* several rare lichen, bryophyte and vascular plant species occur (e.g. *Asplenium adiantum-nigrum* L., *Dibaeis baeomyces* (L. f.) Rambold & Hertel, *Dicranum spurium* Hedw., *Hieracium pavichii* Heuff., *Spiraea chamaedryfolia* L., *Vulpia bromoides* (L.) Gray). It should be stressed that such habitats on Mt Papuk are not anthropogenic, but natural open habitats of rocky forest fringes, cliffs and rock outcrops. They are localized, occupying a limited surface, which makes them very sensitive to and threatened by colonization of alien species. Since such geological situations with acidic metamorphic rocks are common in the mountain region of the Eastern Balkans (Reed *et al.*, 2004), the spead of *C. introflexus* towards the southeast is very likely.

The findings in Croatia confirm the pattern of invasion of *Campylopus introflexus* from Western Europe eastwards (Mikulášková *et al.*, 2012), but also indicate a further spread toward the south. It can be concluded that *C. introflexus* has started to invade South-Eastern Europe, occupying open habitats with bare soils. However, it is still too early for a definitive conclusion, since the bryoflora of South-Eastern Europe is still largely undersampled and insufficiently studied. When the

ecology of *C. introflexus* in Central and Western Europe is considered, it seems that the species will not be a serious threat to the native flora in the Dinaric region. However, special attention should be given to the possible invasion of this species on specific rare, acidophilous habitats resembling those in Western Europe or southern Hungary, in the peri-Pannonian region. According to the special conditions in the Mt Papuk area, the spread of *C. introflexus* is very likely to the acidic metamorphic outcrops in the mountain region of the Eastern Balkans (Moesian provinces) too. Since there is no evidence that plants with sporophytes have been found at the nearest locations in neighbouring countries, we might conclude that zoochory and anthropochory are the dominant types of dispersal in the Western Balkans. Therefore, directed surveys and monitoring programs should be established promptly in South-Eastern Europe. Pest control in this stage seems to be still premature.

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