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Identifying the ecological and societal consequences of a decline in *Buxus* forests in Europe and the Caucasus

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Abstract The potential impact of new invasive tree pests and diseases is usually quantified in economic terms. The ecological and social impacts are less often assessed. Using a comprehensive literature review we assess the potential ecological and social impact of two non-native invasive species (the box tree moth, *Cydalima perspectalis* and the fungus *Calonectria pseudonaviculata*) that threaten the survival of box tree, *Buxus* spp. in forests in Europe and the Caucasus. A total of 132 fungi, 12 chromista (algae), 98 invertebrate and 44 lichens were found to use *Buxus* spp. Of these, 43 fungi, 3 chromista and 18 invertebrate species have only been recorded on *Buxus* spp., suggesting that these species are obligate on *Buxus* spp. and are most at risk from in the loss of *Buxus* spp. due to these invasive pest and disease species. *Buxus* spp. was shown to be important for soil stability and water quality but there was no information on other ecosystem functions provided by *Buxus* spp. *Buxus* was found to be of considerable historical cultural importance but there was very limited information on current social values and uses. *Buxus* trees, wood and leaves are associated with different folklore and sacred rites which are still particularly important in the

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Caucasus. While we could not find any assessment of the economic value of *Buxus* forests the biodiversity, cultural and social values of *Buxus* identified here indicate that its loss could have major indirect and non-market economic effects. This work highlights the importance of studying the ecological and societal implications of biological invasions.

Keywords *Buxus balearica* · *Buxus longifolia* · *Buxus sempervirens* · *Calonectria pseudonaviculata* · *Cydalima perspectalis* · Non-native invasive

Introduction

Trees provide a range of ecosystem services including provisioning, cultural and regulation (Millennium Ecosystem Assessment 2005) and are also viewed as ecological keystone species due to their support for a range of species and their role in driving changes in ecosystem functioning (Ellison et al. 2005; Mitchell et al. 2007, 2010). Globally trees are increasingly threatened by a range of non-native plant pests and pathogens (Sturrock et al. 2011). Invasive non-native species are considered to be the most important threat to biodiversity after habitat loss (Mooney and Hobbs 2000) and the biosecurity threat from invasive plant pests and pathogens to native plant communities is now internationally recognised (Kenis et al. 2009; Potter et al. 2011; Dirzo et al. 2014; Klapwijk et al. 2016). Increased transportation of goods around the world together with the expanding trade in plants and plant products all aid the spread of invasive plant pests and pathogens (Anderson et al. 2004; Brasier 2008; Sutherland et al. 2008; Liebhold et al. 2012; Eschen et al. 2015). Trees that have nearly disappeared or are declining because of an invasive pest or a pathogen include, among others, American chestnut, *Castanea dentata*, in North America (by *Cryphonectria parasitica*), elms, *Ulmus* spp., in North America and Europe (by *Ophiostoma novo-ulmi*), ashes, *Fraxinus* spp. in North America (by *Agrilus planipennis*) and Europe (by *Hymenoscyphus fraxineus*) and Eastern hemlock, *Tsuga canadensis,* in North America (by *Adelges tsugae*) (Aukema et al. 2010; Santini et al. 2013).

The impact of the loss of a particular tree species due to disease may be quantified as a monetary value by assessing the economic importance of the tree species, usually in relation to timber and related products(e.g. Aukema et al. 2011). For example, when assessing the impact of *H. fraxineus* in the UK and the potential loss of *Fraxinus excelsior* the UK government estimated that *F. excelsior* has an estimated commercial value of around £22 million per year (Defra 2014). However, trees provide a wide range of other services in addition to timber, which cannot easily be assessed in monetary terms (Aukema et al. 2011; Kenis et al. 2017). In particular, the impact of tree diseases should also include ecological and cultural assessments. Due to the interactions and

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dependencies between species, assessing the cascading impacts of the loss of one species on the wider ecosystem (both species and function) can be difficult. This was done for European ash, *F. excelsior,* in the UK by Mitchell et al. (2014, 2016a), who developed a method for assessment of the ecological impacts tree diseases. The cultural implications of a loss of individual tree species are also beginning to be recognised (e.g. Urquhart et al. 2018). For example in North America the loss of *Fraxinus nigra* due to *Agrilus planipennis* will impact on the traditional basket making carried out by the indigenous North American Indians (Reo 2009; Diamond and Emery 2011; Willow 2011). However, there are few studies where a combined assessment of the ecological and societal implications of the loss of a tree species has been made. Here we aim to do this for *Buxus* spp. forests in Europe and the Caucasus.

In the Western Palaearctic area, the genus *Buxus* is represented by two to four closely related taxa: *B. sempervirens, B. balearica, B. colchica* and *B. hyrcana.* Although the last two are often considered as synonyms or sub-species of *B. sempervirens* (Di Domenico et al. 2011; 2012), in this paper, we use *B. colchica* and *B. hyrcana* to designate *Buxus* stands occurring in the Eastern Black Sea region and in the Western Caspian Sea region, respectively. The abundance and distribution of *Buxus* spp. in the Western Palaearctic has varied throughout history driven by changes in climate and human use (Çolak 2003; Shreekar 2011; Savill 2013). More recently, Western Palearctic *Buxus* spp. are declining due to the arrival of two non-native pests from East Asia, the box tree moth, *Cydalima perspectalis* (Walker 1859) (Lepidoptera: Crambidae) and the fungus *Calonectria pseudonaviculata* (Crous, J.Z. Groenew. & C.F. Hill) L. Lombard, M.J. Wingf. & Crous, (= *Cylindrocladium buxicola* Henricot) causing box blight. Both species have invaded most of Europe, Turkey and the Caucasus up to Iran (Gorgiladze et al. 2011; Gninenko et al. 2014, Lehtijärvi et al. 2014). They probably arrived on traded ornamental plants from Asia (Kenis et al. 2013; Tuniyev 2016; Matsiakh et al. in press). Since then, they have become major pests of ornamental *Buxus* trees in gardens, but they also represent a serious threat to wild *Buxus* spp. The blight was first observed in Western Europe in the late 1990s and in the Eastern Black Sea region (Turkey and Georgia) in 2010 when it started to destroy native *Buxus* stands, in particular in humid areas (Gorgiladze et al. 2011; Lehtijärvi et al. 2014). In Abkhazia, it was first reported in 2013 (Gasich et al. 2013) and, in Iran, in 2012 (Mirabolfathy et al. 2016). A recent molecular analysis showed that the invasive populations belonged to two closely-related species, the new species *Calonectria henricotiae* Gehesquière, Heungens and J.A. Crouch being present in Europe only (Gehesquière et al. 2016). The impact of *C. pseudonaviculata* on *Buxus* spp. depends on the climate. The blight causes the greatest damage, killing entire *Buxus* stands, at sites with high summer humidity and precipitation (Kenis et al. 2013). At sites with less favourable conditions the blight causes minor defoliation. The box tree moth was first reported in Germany and the Netherlands in 2007 and invaded most of Europe in just a few years (Kenis et al. 2013). It was first observed in a nursery in Sochi (Russia) on ornamental *Buxus* plants imported from Italy in 2012 (Tuniyev 2016). From Sochi it probably spread along the Black Sea coast to Abkhazia, as well as to Adjara and Samegrelo (Georgia). The first report of damage in natural *Buxus* tree stands in Georgia was from the Kintrishi Protected Area and the Mtirala National Park (Matsiakh 2014; Matsiakh et al. in press). The damage in these regions has been extensive (Kenis 2015) with the total destruction of ecologically and historically important stands of the highly valued *B. colchica* (Matsiakh 2016; Tuniyev 2016; Matsiakh et al. in press). In Europe as well, *C. perspectalis* has started destroying natural *B. sempervirens* stands, starting in Germany and Switzerland (John and Schumacher 2013; Kenis et al. 2013) and since 2015 in Southern France (M. Kenis unpublished). *C. perspectalis* has the greatest impact at sites where the temperature is warm enough for two or three generations to be produced in one year (Nacambo et al. 2014) causing severe defoliation sufficient to kill the tree. The damage is amplified by the habit of larvae to debark the trees when no leaves are available. A climate model showed that the moth has the potential to threaten all *Buxus* spp. stands in the Western Palaearctic region (Nacambo et al. 2014), causing concern for the survival of these tree species. While the impact of both *Cydalima perspectalis* and *Calonectria pseudonaviculata* is dependent on the climate both species have been shown to cause complete loss of *Buxus* spp. under optimal conditions (Matsiakh 2016). Therefore, a critical assessment of the ecological and societal impacts of the destruction of natural *Buxus* spp. stands is required.

Cydalima perspectalis and *Calonectria pseudonaviculata* will kill *Buxus* spp. planted as ornamental plants. *Buxus* spp. have been planted in gardens for centuries, particularly during the 16th and 17th centuries when topiary work was in vogue (Decocq et al. 2004). Nowadays, *Buxus* spp. are still important ornamental plant species and until recently, an enormous number of *Buxus* plants were imported to Europe and the Caucasus (e.g. over 1 million plants were imported from China to the Netherlands alone in 2010 (EPPO 2012)). In recent years, the trade has slowed down because of these two introduced pests, and *Buxus* trees in gardens and parks are starting to be removed and be replaced by other species (Henricot and Wedgwood 2013). While a decline in the health of *Buxus* plants will clearly impact on the horticultural trade and on the way gardens and parks with *Buxus* are managed, here we concentrate on assessing the potential ecological and societal consequences of the disappearance of natural *Buxus* spp. ecosystems. We focus on the loss of *Buxus* while acknowledging that in some situations *Cydalima perspectalis/Calonectria pseudonaviculata* will cause a decline in *Buxus* spp. abundance rather than its complete loss. In order to identify the impact of a loss of *Buxus* spp. we first identify its role ecologically and in society. Thus we aim to collate information on (1) the habitats where *Buxus* spp. occurs; (2) the role of *Buxus* spp. in woodland succession and hence its role in driving community composition; (3) specific ecosystem functions provided by *Buxus* spp. and (4) species which use *Buxus* spp., in particular identification of species which are obligate on *Buxus* spp., i.e. are only found on *Buxus* spp being specialised or monophagous on *Buxus* spp. If *Buxus* spp. are lost, they are likely to be replaced by species that currently co-occur with it. In order to assess how this may change the woodland composition we have a fifth ecological aim of identifying co-occurring species which may fill the gap left by *Buxus* spp. For the societal role of *Buxus* spp. we collate information on its use for (a) timber, (b) religious and sacred occasions and (c) other uses. For each of 1–5 and a–c above we use this information to identify the potential impacts of the loss of *Buxus* spp.

Methods

A literature review to identify the ecological and social importance of *Buxus* spp. was carried out using key-word driven searches on 'Buxus' undertaken in June–July 2016 in Web of Knowledge (http://wok.mimas.ac.uk/). The databases and timeframes covered by the Web of Knowledge search included Science Citation Index (1970–2016); Social Sciences Citation Index (1970–2016), Arts and Humanities Citation Index (1975–2016); Conference Proceedings Citation Index—Science edition (1990–2016); Conference Proceedings Citation Index—Social Science + Humanities edition (1990–2016). All the abstracts of those papers that contained information about *Buxus* were read and the papers obtained where possible. Information was also supplemented by grey literature, in particular from the Caucasus region where there was limited published information but considerable grey literature. The ecological information was categorized into the Sections "Habitats where *Buxus* spp. occur, *Buxus*'s role in woodland succession, Ecosystem processes and functions, Species that use *Buxus* spp., Comparison of *Buxus* and co-occurring species" outlined above and the cultural and social information into sections "Utilisation of *Buxus* wood, Religious and sacred significations, Other usages" as above.

Species that use *Buxus* spp. were also identified by searching existing databases and key taxonomic monographs etc. We confined our search to fungi, lichens and invertebrates that have been recorded on *Buxus* spp. and are known to occur in the Western Palaearctic (from Iran to Western Europe) and lichens using *Buxus* spp. in the UK. The main databases used for invertebrates were: Aphids on the world's plants database (http://www.aphidsonworldsplants.info); BRC Database of Insects and their Food Plants, (http://www.brc.ac.uk/dbif/invertebrates.aspx); The scalenet catalogue (http://scalenet.info/catalogue) and HOSTS - a Database of the World's Lepidopteran Hostplants (http://www.nhm.ac.uk/our-science/data/hostplants/). In addition Bolland et al. (1998) was used for information on spider mites. Most fungal records came from Farr and Rossman (2016), MycoBank (http://www.mycobank.org/) and Fungi of Ukraine (http://www.cybertruffle.org.uk/cgi-bin/nome.pl?organism=3745&glo=eng). All Lichen records came from the British Lichen Society's database. All databases were accessed during June 2016. A full list of all data sources is provided in Supplementary Excel file Annex 1. For each associated species the following was recorded: if it was a lichen/fungi or invertebrate, the taxonomic order and family; which *Buxus* spp. the associated species was found on, if the species was only recorded on *Buxus* spp. or not, the distribution of the species, the data source and if the species is known to occur in the Eastern Black Sea Region. The data was collated into an Excel database. Those species only recorded on *Buxus* spp. were considered potentially obligate species (i.e. species only occurring on *Buxus* spp.); however, due to low numbers of records this classification is uncertain. In addition the data sources used have incomplete coverage and hence the findings are likely to be underestimated.

A list of woody tree and shrub species with a canopy height of 2 m or more that co-occur with *Buxus* spp. in the Caucasus was developed from those lists in Matchutadze (2007), Akhalkatsi (2010, 2015) and Matchutadze et al. (2010, 2013, 2015), species that co-occur with *Buxus* spp. in south Russia and Abkhazia from Alper (1960) and Timukhin (2005) and species that co-occur with *Buxus* spp. in Europe from European Commission (2007). These lists were used to identify which species are likely to be the species that would naturally replace *Buxus* spp. if it goes locally extinct. The species were classified into deciduous/evergreen, if they formed the canopy or understorey (or both) and if they occurred on acidic or calcareous soils (or both). These sub-divisions were used to identify likely replacement species for *Buxus* spp. in different niches (understorey/canopy) and different soil types.

Results

The key word search on '*Buxus*' listed 474 papers containing the word *Buxus.* The results of this search are summarised below.

The ecological role of Buxus

Habitats where Buxus spp. occur

Buxus spp. play an important role as a tall understorey or small tree species within many forests types in Europe and the Caucasus. Stands occur through the southern half of Europe but are most dense in Southern France and Northern Spain (Di Domenico et al. 2012; Kenis et al. 2013). In cooler areas, *B. sempervirens* is a thermophilic and xerophilic species. However, in the warmer and drier areas of the Mediterranean region, it is more often found along the sides of streams in shaded situations (Lenoble and Broyer 1945). It usually grows on calcareous soils but it can also be found on more acidic soils, such as in Belgium and France (Lenoble and Broyer 1945; Duvigneaud 1969). Most *B. sempervirens* stands in Europe are found as understorey in beech or oak forests, but in some cases it can also form the canopy layer. It is characteristic of the phytosociological alliance *Quercion pubescenti-petraeae*. It is also found in the sub-alliance *Cephalanthero-Fagenion* and in the alliance *Carpinion betuli* (Grossenbacher 2012).

Within the European Union Habitats Directive *Buxus sempervirens* is listed as a characteristic species in five Annex 1 habitat types, two of which are priority habitat types: Endemic oro-Mediterranean heaths with gorse subtype Pyrenean hedgehog-heaths. *Junipero-Genistetum horridae;* Sub-Mediterranean and temperate scrub—Stable xerothermophilous formations with *Buxus sempervirens* on rock slopes; Medio-European limestone beech (*Fagus* spp.) forests of the *Cephalanthero-Fagion; Taxus baccata* woods of the British Isles (priority habitat) and Mediterranean *Taxus baccata* woods (priority habitat). Further east, *B. sempervirens,* is found as an understorey species in the Mediterranean Black Sea coast of Bulgaria, Romania and Turkey (Greller 2013) as well as in isolated spots in the Balkan Peninsula. For example, highly valued stands are found in Macedonia, where specific cultivars have been found, e.g. the "Vardar Valley" Boxwood (Del Tredici 2007).

In the Eastern Black Sea region, *B. colchica* forms part of the tall (up to 4 m) understorey, which is dominated by broadleaved evergreen shrubs and small trees in the Colchic Forest which are part of the Caucasian Deciduous Forests (Greller 2013). However, in this region, *B. colchica* can also form trees up to 15-19 m high and 40-50 cm diameter and reach more than 250 years old (Tuniyev 2016; Matchutadze et al. 2013). It grows favourably on calcareous soils but other soils are also suitable. *Buxus colchica* is extremely shade tolerant. Tuniyev (2016) provides a detailed description of the habitats occupied by *B. colchica* on the Russian and Abkhazian coasts of the Black Sea. The tree is found in five main habitats/

associations: *Fagus-Buxus* forests, *Carpinus-Buxus* forests, *Tilia-Buxus* forests, *Fagus-Carpinus-Buxus* forests, *Abies-Buxus* forests.

In Georgia, Akhalkatsi (2010, 2015) described five distinctive habitats for *B. colchica*: (1) The evergreen heaths of Kolkheti; (2) The limestone beech forests where *Buxus colchica* bushes are possible in the understorey; (3) *Fagus* spp. forests with Colchic understorey, where *B. colchica* creates the understorey with other woody shrubs; (4) boxwood forest where *B. colchica* occurs prior in the succession to the formation of *Carpinus betulus* and other broadleaved forests; (5) Colchic broad-leaved mixed forests.

Buxus hyrcana is one of the protected evergreen tree species distributed as compact mid-storey stands in about 80,000 ha of the preserved forests of the Caspian Sea region of Iran. *Buxus hyrcana* is placed in the *Querco-Buxetum* community and co-occurs with an upper storey dominated mainly by *Acer* spp., *Alnus* spp., *Celtis* spp. and *Diospyros* spp. *Buxus hyrcana* is considered a very important endemic species of Iran, with many 200 to 300 year old *Buxus* trees occurring in the historic shrine gardens throughout the Guilan and Mazandaran provinces.

Buxus balearica is a rather rare bush found around the Mediterranean Sea, in the Balearic Islands, southern Spain, Sardinia, Morocco, Algeria and Turkey (Di Domenico et al. 2012). It occurs in both deciduous and evergreen broadleaved forests (Balearic Islands, Sardinia) and in conifer woodlands (southern Spain). As with other *Buxus* spp., it is often found in canyons, river valleys and rocky cliffs, in sub-humid conditions (Di Domenico et al. 2012). To our knowledge neither the moth nor the blights have yet reached natural stands of *B. balearica* but tests have shown that *B. balearica* is a suitable host for *C. perspectalis* (Brua 2014) and personal observations by one of the authors have recorded *B. balearica* defoliated by the moth in the Buda Arboretum, Budapest, Hungary (G. Vetek, unpublished results).

Buxus's role in woodland succession

Buxus sempervirens is known to differentially influence establishment and survival of tree species thereby controlling future canopy composition and spatial structure (Dolezal et al. 2004). Dolezal et al. (2004) found that in the Central Pyrenees *Fagus sylvatica* will preferentially establish within *B. sempervirens* shrubs whereas *Abies alba* forms denser patches on sites with less *B. sempervirens* and its survival rate within *B. sempervirens* stands is significantly lower than outside them. The authors conclude that inhibition from *B. sempervirens* shrubs and interspecific competition prevent invading *A. alba* from dominating may therefore help in maintaining a mixed *Abies-Fagus* stand. A separate study comparing *Juniperus communis* and *B. sempervirens* concluded that *J. communis* shrubs are better safe sites for the establishment of *Quercus pubescens* and *F. sylvatica* seedlings than *B. sempervirens* shrubs (Kunstler et al. 2007). Thus from the limited data available it seems that *Buxus sempervirens* may drive the species composition of the canopy by providing differential safe sites depending on the canopy species and the other shrub species in the community. It is unknown if *B. colchica* influences the canopy composition in the same way.

Ecosystem processes and functions

Buxus spp. may play an important role in sediment trapping on steep slopes (Duvigneaud 1969). *Buxus sempervirens* is able to grow on steep crumbly slopes where other bigger tree species such as *Fagus sylvatica* would fall over (Savill 2013). Experiments have shown that *B. sempervirens* trapped 2.8 times more sediment than *Juniperus communis* and 1.5 times more sediment than *Pinus nigra*, although it trapped less sediment than the fourth species in the experiment *Lavandula angustifolia* (Burylo et al. 2012). *Buxus colchica* is known to perform similar functions being important in water storage via its role in protecting banks from erosion (Tugushi, 1972). There was no information available about the role of *Buxus* spp. in relation to any other ecosystem processes or functions.

Species that use Buxus spp

A total of 286 lichens, fungi, chromista and invertebrates were found to be associated with *Buxus spp.* (Supplementary material Annex 1). This included 132 fungi, of which 43 species have only been recorded on *Buxus* spp. The majority of the fungi belonged to the taxonomic classes Incertae sedis (17 species), Agaricomycetes (38 species), Dothideomycetes (42 species) and Sordariomycetes (31 species). The potentially obligate species belonged to the taxonomic classes Agaricomycetes (3 species), Dothideomycetes (18 species), Incertae sedis (2 species), Leotiomycetes (3 species), Pucciniomycetes (2 species), Sordariomycetes (13 species) and one species in each of the classes Hypocreales and Lecanoromycetes. Of the 12 Chromista species listed three are potentially obligate. Ninety-eight invertebrates were identified that use *Buxus* spp., of these 17 were only recorded on *Buxus* spp. The 98 invertebrate species included three Coleoptera species, one Diptera, 72 Hemiptera, nine Lepidoptera, two mesostigmatic mites, 10 prostigmatic mites and one Thysanopera species. The potentially obligate species (those only recorded on *Buxus* spp.) were largely *Hemiptera* (9 species) and *Prostigmatic* mites (6 species) with one species from each of the orders *Diptera, Lepidoptera* and *Thysanopera*. A total of 44 lichens have been recorded on *B. sempervirens* in the UK. None of them have only been recorded on *Buxus* spp.

Fagus sylvatica forests in Switzerland with *B. sempervirens* host a different fungal community compared to *F. sylvatica* forests without *B. sempervirens*. An unpublished study in North-Western Switzerland compared *Fagus* forests with and without a *B. sempervirens* understorey (Kenis et al. 2015). It suggested that stands with *B. sempervirens* hosted a different fungal community than stands without *B. sempervirens.* From the 97 fungi species found, four species were included in the Swiss red list of fungi (*Amanita caesarea, Aureoboletus gentilis, Cortinarius triumphans* and *Lactarius flavidus*), and they were all found exclusively in the *B. sempervirens* stands. Two other fungi species red-listed in Switzerland, *Marasmius buxi* and *Peniophora proxima,* not found in that study, are known to be exclusively found in *B. sempervirens*. In contrast, insect trapping (pitfall traps and bottle traps) failed to find significant differences between insect communities in the two habitats (Kenis et al. 2015). Other organisms, such as plants, birds, mammals, amphibians, soil organisms, etc., may be favoured or inhibited by the presence of *B. sempervirens* but comparative studies are lacking.

In addition to those species that directly use *Buxus* spp. there are a variety of species that are associated with the box forest habitat (e.g. birds, mammals, amphibians and reptiles) but do not directly live on *Buxus* spp. Identifying these species and assessing the impact of the loss of *Buxus* spp. on them is difficult due to lack of information. However, we did collate a list of 25 amphibian and reptile species that were associated with *Buxus colchica* in the Caucasus and Turkey (Table S2).

Comparison of Buxus and co-occurring species

Buxus spp. are slow growing, reaching maturity only after many years (Di Domenico et al. 2012). They are classed as a K strategy species (Çolak 2003), are long-lived and are a putative masting species showing substantial between-year variation (Lazaro and Traveset 2006; Lazaro et al. 2006). *Buxus* spp. are able to tolerate a high level of shade (Savill 2013) with the ability to grow as both an understorey species and as a canopy species (tall shrub/small tree) in more open conditions. In order to survive across this light gradient *B. sempervirens* exhibits both physiological and morphological plasticity (Letts et al. 2012). Individuals of *B. sempervirens* in situations experiencing high levels of light reduce light capture efficiency through high branch inclination and leaf clumping which increase the ratio of leaf area to silhouette area. *Buxus sempervirens* adjusts its branch and leaf morphology to alter light capture efficiency, thus preventing crown photo-inhibition in high light environments, but increasing light capture in understorey sites.

Seventy-five tree and tall shrub species that co-occur with *Buxus* spp. were identified (Table S1). *Buxus* spp. are unusual compared to many of the other co-occurring species in being an evergreen species that will form either a canopy or an understorey and grow as either a shrub or a tree on both calcareous and acidic soils. Thus different species are likely to replace *Buxus* spp. depending on the habitat (soil type) and niche *Buxus* spp. occupies (canopy or understorey) (Table 1). None of the co-occurring tree and shrub species that may replace *Buxus* spp. will match the traits of *Buxus* spp. listed above. Thus how the forest will change following the loss of *Buxus* spp. will depend on which species replace *Buxus* spp. Most of the co-occurring tree and shrub species are deciduous species, if these were to replace the evergreen *Buxus* spp it would result in a very different habitat being created. The majority of the co-occurring deciduous canopy and understorey species occur on either acidic or calcareous soils and include a range of *Acer* and *Salix* species. There are far fewer co-occurring evergreen species that might replace *Buxus* spp. as either a canopy or understorey species and the species

Table 1 Potential replacement species for *Buxus* based on species currently co-occurring with *Buxus*. See Table S1 for list of which species co-occur in which regions See Table S1 for authorities of names

	Acidic soils		Calcareous soils	
Evergreen-canopy	*Abies nordmanniana*	*Picea orientalis*	*Taxus baccata*	*Juniperus oxycedrus*
	Arbutus andrachne	*Pinus pinea*	*Arbutus andrachne*	*Pinus hamata*
	Pinus hamata	*Pinus sylvestris*		
Evergreen-understorey	*Ilex colchica*	*Prunus laurocerasus*	*Ilex colchica*	*Ligustrum vulgare*
	Ilex aquifolium	*Rhododendron ponticum*	*Ilex aquifolium*	*Taxus baccata*
	Juniperus communis	*Rhododendron ungernii*	*Laurus nobilis*	
	Ligustrum vulgare			
Deciduous-canopy	*Alnus glutinosa*	*Frangula alnus*	*Alnus glutinosa*	*Diospyros lotus*
	Castanea sativa	*Elaeagnus rhamnoides*	*Fagus orientalis*	*Ficus carica*
	Prunus mahaleb	*Malus orientalis*	*Fagus sylvatica*	*Fraxinus excelsior*
	Sorbus aria	*Ostrya carpinifolia*	*Prunus mahaleb*	*Elaeagnus rhamnoides*
	Acer campestre	*Prunus divaricata*	*Sorbus aria*	*Ostrya carpinifolia*
	Acer cappadocicum	*Pterocarya fraxinifolia*	*Acer campestre*	*Pyrus caucasica*
	Acer pseudoplatanus	*Quercus petraea subsp. iberica*	*Acer cappadocicum*	*Quercus petraea subsp. iberica*
	Acer sosnowskyi	*Salix alba*	*Acer platanoides*	*Salix elbursensis*
	Alnus glutinosa	*Salix caprea*	*Acer pseudoplatanus*	*Salix euxina*
	Alnus incana	*Salix elbursensis*	*Acer sosnowskyi*	*Salix triandra*
	Carpinus betulus	*Salix euxina*	*Alnus incana*	*Salix pentandroides*
	Carpinus orientalis	*Salix triandra*	*Carpinus betulus*	*Sorbus umbellata*
	Celtis australis	*Salix pentandroides*	*Carpinus orientalis*	*Tilia begoniifolia*
	Cerasus avium	*Ulmus minor*	*Celtis australis*	*Tilia platyphyllos*
	Diospyros lotus		*Cerasus avium*	*Ulmus glabra*
			Cornus sanguinea subsp. Australis	*Ulmus minor*
Deciduous-understorey	*Amelanchier ovalis*	*Euonymus leiophloeus*	*Amelanchier ovalis*	*Euonymus latifolius*
	Cornus mas	*Frangula alnus*	*Cornus mas*	*Euonymus leiophloea*
	Crataegus spp.,	*Elaeagnus rhamnoides*	*Crataegus spp.,*	*Elaeagnus rhamnoides*
	Rhododendron luteum	*Paliurus spina-christi*	*Staphylea colchica*	*Paliurus spina-christi*
	Staphylea colchica	*Prunus divaricata*	*Viburnum lantana*	*Philadelphus coronarius*
	Carpinus orientalis	*Rosa ssp*	*Viburnum opulus*	*Rosa ssp*
	Cotinus coggygria	*Rubus ssp*	*Carpinus orientalis*	*Rubus ssp*
	Cotoneaster integerrimus	*Sambucus nigra*	*Cotinus coggygria*	*Sambucus nigra*
			Cotoneaster integerrimus	*Sorbus umbellata*
			Euonymus europaeus	*Cornus sanguinea subsp. australis*

differ depending on the soil type. In calcaeous soils species such as *Taxus baccata, Ilex* spp., *Juiperus oxicedrus and Pinus hamata* are potential replacement species. On acidic soils *Pinus* species and *Rhododendron* species are potential replacements. *Arbutus andrachne* is one evergreen canopy species that may replace *Buxus* spp. on both calcareous and acidic soils.

The societal role of Buxus

Utilisation of Buxus wood

Buxus wood has been used since before antiquity for many purposes such as buttons, spoons, boxes, combs, handles of tools, pepper pots, and snuffboxes (Meiggs

1982; Decocq et al. 2004). The oldest writing-board ever recovered was in *Buxus* wood (14th century B.C.; Pendleton and Warnock 1990). Due to its slow growth, the wood is one of the heaviest and hardest of all European trees: 950 – 1200 kg m^{-3} (Savill 2013). Consequently, it has long been used in building tools such as hammerheads, nails and wooden joints (Di Domenico 2013) but also for mathematical instruments such as rulers, wood turning and tool handles (Fell 1998; Di Domenico 2013; Savill 2013). *Buxus* combs are particularly famous, e.g., in Ukraine, where they have been made since the 10th century from wood imported from the Caucasus (Kopytko 2003; Kabatov 2015).

In the 18th and 19th century, *Buxus* wood was used by engravers for the printing of illustrations. In particular, the famous British engraver Thomas Bewick (1753–1828) used metal-engraving tools to cut *Buxus* wood across the grain (as opposed to longitudinal cuts), which resulted in printing blocks that were much more durable than traditional wood blocks and in clear and accurate illustrations (Ivanov-Akhmetov 2013).

Buxus wood also provides good sound projection because it is free from the grain produced by the growth rings due to its slow growth (Savill 2013). This makes it suitable for crafting high quality musical instruments such as the classical oboe and the violin. In recent times, *Buxus* was largely replaced for musical instruments by tropical wood such as African blackwood (*Dalbergia melanoxylon*). However, African blackwood has recently become very scarce and, so, the demand for *Buxus* is increasing again (Savill 2013).

Buxus wood has also been extensively used in religious art, e.g. for bas-relief carving or for sculpting crosses, calices, patens, icons, rosaries and in the military sector to build bows, arrows and spears (Sabeti 2006). In Iran, *B. hyrcana* is used for similar items but also to make thin sheets on which the Koran or other books are written (Encyclopaedia Iranica 2017) as well as vessels and containers for milk and rose water for Iranian New Year days Festival (CAIS 2017).

The exportation of wood from *Buxus colchica* started in the antiquity when Greek colonies on the Eastern Black Sea shores and Turkey sent the wood to Greece and continued until now (Shkunov 2010; Savill 2013; Kravchenko 2014). The harvesting and shipping of box wood to Europe was particularly flourishing during the Genoese period (13th–15th centuries), an activity which is reflected in the historical toponymy of several Abkhazian localities (Bgazhba and Lakoba 2007). For example the historical name for the modern city of Gudauta in Western Abkhazia is "Cavo di Buxo" (Bgazhba and Lakoba 2007). This trade continued and in the 19th century c. 2340 tons of wood per a year were still exported worldwide from the Eastern Black Sea ports (Yacenko-Khemelevsky 1954).

Religious and sacred significations

Buxus spp. have been associated with different folk and sacred rites since antiquity (Brosse 1987 cited in Decocq et al. 2004). Their evergreen foliage symbolises the "perpetual life in the other world" leading to its use in religious festivals, particularly on Palm Sunday (Decocq et al. 2004). The association between Palm Sunday and *Buxus* tree is particularly strong in Georgia, where the holiday is named "Bzoba" (*Buxus* tree). This is also the reason why it is now often found growing naturally around old churches and other religious buildings, even in regions where it did not grow originally. In the Eastern Orthodox culture, *Buxus* is often planted in cemeteries and, because of its longevity, it symbolically means endurance, patience and perseverance (Shapravskiy 2011). In the old Ukrainian tradition, the evergreen branches of *Buxus* wood are still used to decorate Easter baskets as a symbol of eternal life (Wilczynski 2015). Also in Western Europe *B. sempervirens* shows a long-lasting link with human culture. In ancient civilisations it was a symbol of eternity, renewal and vigour, being found in burial sites and as coffins (Allison 1947; Di Domenico 2013). The Romans planted *B. sempervirens* all over Europe and there are even signs of plantations in the Neolithic age, probably more for sacred than ornamental purpose (Vernier 2010; Di Domenico 2013). In Abkhazia, alleys of *Buxus* trees were typically planted at the entrances of houses to remove the negative energy and provide good fortune and eternal life (Sabeti 2006).

Other usages

Buxus colchica is considered an excellent plant for honey production (Tuniyev 2016). Bark and leaves of

Buxus spp. contain various alkaloids (Atta-ur et al. 1992; Loru et al. 2000; Vachnadze et al. 2009; Leuthardt et al. 2013). Their infusions are used in cosmetics for hair reinforcement and in folk medicine to treat fever, rheumatism, arthritis, bile duct infections, diarrhoea and skin ulceration (Ait-Mohamed et al. 2011; Tuniyev 2016). In Morocco, decoctions of *B. balearica* are used against diabetes (Benkhnigue et al. 2014). *Buxus* spp. are also studied in modern medicine, e.g. for anti-acetylcholinesterase activities (Babar et al. 2006; Ata et al. 2010), immunosuppressive activities (Mesaik et al. 2010) and for anti-cancer properties (Ait-Mohamed et al. 2011).

In the Eastern Black Sea region, until very recently, dried *Buxus* leaves were commonly used to fill mattresses, especially for babies. Besides its repellent properties against blood-sucking arthropods, there was also a belief that the delicate and soft fragrance of dried *Buxus* leaves had a soothing and tonic effect on the body of the baby (Kuyek 2014). In Eastern European cultures, *Buxus* leaves were also used as one of the main components of wedding bouquets and wedding wreaths (Mikhaleva 2011; Pekarchuk 2014). The longevity of *Buxus* is acknowledged in the Abkhazian language where there is a set expression sounding as: "ashytc yiakhaanu" which translates as "the age of a box tree" which means that one is talking about something very ancient (R. Dbar, unpublished data).

Discussion

This study has shown that the non-native invasive species *Cydalima perspectalis* and *Calonectria pseudonaviculata* have the potential to have far wider impacts than just the loss of *Buxus* spp. These invasive species could indirectly cause ecological, social, cultural and religious changes due to the loss of *Buxus*. *Buxus* forests in Europe and the Caucasus are unique ecosystems that should be preserved. Interestingly, these ecosystems are rather poorly studied both ecologically and culturally. This prevented us from fully assessing the ecological and societal consequences of their disappearance, in particular on ecosystems functions, while many of the references to cultural importance were only available in the grey literature and referred to historical rather than current cultural values. We are not aware of any information available on the economic importance of the *Buxus* habitats. When a new pest/pathogen impacts an important resource the economics are often one of the first things assessed (cf ash dieback in the UK (Defra 2014)). This suggests that the *Buxus* habitats are perceived (possibly wrongly) as of low economic value as such an assessment has not yet been done. However the biodiversity, cultural and social values of *Buxus* identified here indicate that its loss could have major indirect and non-market economic effects.

The literature survey showed that the loss of natural *Buxus* spp. stands in Europe and the Caucasus could have important ecological consequences. The 63 species that have only been recorded on *Buxus* spp. may be obligate and therefore at risk of local extinction if *Buxus* spp. goes locally extinct. In addition, natural enemies of the insects and pathogens specific to *Buxus* spp. are also at risk. In general, these are not included in Annex 1, with a few exceptions, such as the predatory bug, *Anthocoris butleri*, which feeds exclusively on the psyllid *P. buxi* (Rabitsch 2008), and the predatory mite, *Typhlodromus olympicus*, preying on *Buxus*-feeding mites (de Moraes et al. 2004).

Compared to *Fraxinus excelsior*, which hosts, in the UK alone, 68 fungi (11 obligate) and 239 invertebrates (29 obligate) (Mitchell et al. 2014), *Buxus* spp. seem to host more fungi (but we have no data for the whole Western Palaearctic for *Fraxinus excelsior*) and less invertebrates. Indeed, before the arrival of *Cydalima perspectalis* and *Calonectria pseudonaviculata*, damage by insects was very rare but local fungi such as *Pseudonectria* (= *Volutella*) *buxi*, *Mycosphaerella buxicola* and *Puccinia buxi* were already causing problems to gardeners. Interestingly, of the 17 arthropods that appear specific to *Buxus* spp., six belong to Acari (Kenis pers comm.). Among arthropods, other occasional pests of *Buxus* spp. include the specific *Buxus* wood psyllid *Psylla buxi,* the *Buxus* leaf-mining gall-midge *Monarthropalpus flavus*, and the mites *Eurytetranychus latus* and *Aceria unguiculata.* Very few generalist arthropod pests actually damage *Buxus* spp., possibly because of the toxic alkaloids contained in the plants.

There are also likely to be a large number of species associated with the box forest habitat rather than with the *Buxus* plant directly, such as our list of amphibians and reptiles. The extent to which the loss of one tree/

shrub species from within the forest will impact on such species is unknown. Mitchell et al. (2016b) investigated how the ground flora of *Fraxinus excelsior* woodlands would change following the loss of *F. excelsior* and concluded that the impacts would change over time and be dependent on which species replace *F. excelsior*. We suggest that the same might be true in these box forests: the impact of a loss of *Buxus* on species associated with the *Buxus* habitat will depend on which tree/shrub species replace *Buxus*.

Cydalima perspectalis and *Calonectria pseudonaviculata* could indirectly lead to the loss of ecosystem services such as soil stability, water quality and an increase in flooding. The literature search highlighted the role of *Buxus* in soil stability. Soil erosion is a known problem in areas where *Buxus* spp. have been lost (Çolak and Rotherham 2006; Matchutadze 2007, Matchutadze et al. 2010, 2013). *Buxus sempervirens* can grow on loose, dry, crumbly soil on steep slopes where other, bigger trees, such as *Fagus sylvatica* become unstable and soon fall (Savill 2013). It is in such sites as these that *B. sempervirens* may play a key role in reducing soil erosion. Soil erosion problems are often linked to a decline in water quality (increased sediment load) and increased flooding (lack of water holding capacity in the soil). Thus the loss of *Buxus* spp. may not only result in increased soil erosion but also in a decline in water quality and an increase in flooding. There was no information on other ecosystem services and ecological functions provided by *Buxus* spp. and we were therefore unable to assess the relative ecological importance of *Buxus* spp. in nutrient cycling rates, decomposition rates and leaf litter quality and this is identified as a major knowledge gap.

If *Buxus* is lost, the gaps within the forests are likely to be filled by co-occurring species. If these co-occurring species differ in structure or traits from *Buxus*, this could have cascading effects on the forest function (e.g. leaf litter decomposition rates and nutrient cycling), the forest structure (e.g. with taller trees such as *Pinus sylvestris* establishing) and the forest community (e.g. changes in the biodiversity supported within the forest). Such changes have been recorded in other forest systems when the dominant tree species has been lost due to disease. Lovett et al. (2010) studied the impacts of 60 years of decline in *Fagus grandifolia* caused by the beech bark disease. *F. grandifolia* was replaced by *Acer saccharum* and the change in species composition resulted in increased litter decomposition, decreased soil C:N ratio and an increase in extractable nitrate in the soil and nitrate in the soil solution. There are many examples from N. America of a change in tree species composition, due to disease, resulting in changes in the biodiversity present. Specialist species associated with the diseased tree tend to decrease while generalists and species utilizing dead wood tend to increase (see examples in Rabenold et al. 1998; Koenig et al. 2013; Flower et al. 2014; Koenig & Liebhold 2017). Thus we would expect those species most closely associated with *Buxus* to decline following the loss of *Buxus* while species characteristic of disturbed habitats and generalists may increase. Most plant species that co-occur with *Buxus* are deciduous which will allow more light to the forest floor and may drive changes in the composition of the ground flora with the potential for vernal species to establish. Which species will replace *Buxus* spp. will depend on the niche within the forest that *Buxus* occupies (understorey or canopy species and successional stage), soil type, climate and propagule availability. While Table 1 splits the replacement species by soil type, mosaics of soil, such as acidic patches caused by *Taxus*-*Buxus* on limestone soils may allow a mixture of acidic and calcareous species to replace *Buxus* even within an area dominated by one soil type. If the loss of *Buxus* creates large areas of disturbance/bare ground *Buxus* may initially be replace with early successional species, or species characteristic of disturbed habitats (Rabenold et al. 1998) as happened in U.S. when *Betula lenta* replaced hemlock which was killed by the hemlock woolly adelgid (Adelges tsugae Annand) infestations (Tingley et al. 2002). Thus the loss of *Buxus* may reset the successional clock resulting in the species that replace *Buxus* changing over time due to successional processes.

There are many examples of studies of the social and cultural values of trees and forests (O'Brien & Morris 2013; Nordlund & Westin 2011) but few studies on the impacts of tree pests/pathogens on these values (Marzano et al. 2017). While this study attempted to review the impact of one tree pest and one pathogen on cultural and social values our study was limited due to lack of information. Interestingly our literature searches revealed little information on modern attitudes/values associated with *Buxus* forests although some of the traditional uses of *Buxus* continue to this day. Thus while this review highlights the potential loss of traditional values associated with *Buxus* spp. assessment of modern societal consequences is harder to make with only a couple of references to the potential use of *Buxus* spp. in modern medicine and musical instruments. This lack of current information could reflect a more general low level of stakeholder awareness of specific tree pests and diseases as found in studies of other trees/pests (Marzano et al. 2015; Urquhart et al. 2017). Without a better understanding of the modern societal values of *Buxus* spp. forests it is not easy to assess if the loss of *Buxus* spp. forests will lead to a corresponding loss of modern cultural and social values (De Bruin et al. 2014).

The role of social science in helping to address tree health has recently been highlighted (e.g. Marzano et al. 2017; Urquhart et al. 2018). Here we only review one area of the many aspects of social science related to tree health, focusing on the cultural values and traditional uses of *Buxus* forests and how they would be impacted if *Buxus* forests were lost. A better understanding of how people value these forests and the societal acceptability of management to control the blight/moth, the different stakeholders involved and the governance of the forests would all aid in working towards a better understanding of the impacts of *Cydalima perspectalis* and *Calonectria pseudonaviculata* and relevant mitigation measures. Therefore additional studies of both the ecological and social/cultural value of these *Buxus* spp. forests is required.

Most assessments of the potential impact of non-native plant pests and pathogens are confined to the economic impact. Assessments of future ecological impacts are usually restricted to descriptions of impacts observed in other invaded areas, when they exist, whereas there are only a few examples where cultural impacts have been included. This study has shown that the loss of a tree species can have huge ecological and cultural impacts which in turn could have major indirect and non-market economic effects. We argue that ecological and cultural impacts of biological invasions should be more regularly included in risk assessments.

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