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ORIGINAL PAPER

The role of planted forests in the provision of habitat: an Irish perspective

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Abstract The continued decline of natural forests globally has increased interest in the potential of planted forests to support biodiversity. Here, we examine the potential conservation benefits of plantation forests from an Irish perspective, a country where remaining natural forests are fragmented and degraded, and the majority of the forest area is comprised of non-native Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and Norway spruce (*Picea abies* (L.) Karst.) plantations. We examine the true value of Irish plantation forests to native biodiversity, relative to remaining natural forest fragments, and to prior and alternative land use to afforestation. We find that plantation forests provide a suitable surrogate habitat primarily for generalist species, as well as providing habitat for certain species of conservation concern. However, we find that plantation forests provide poor habitat for native forest specialists, and examine potential management strategies which may be employed to improve habitat provision services for this group.

Keywords Biodiversity · Forest generalist · Forest specialist · Habitat · Ireland · Plantation forests

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Introduction

Biodiversity is vital to human well-being and economic stability through the provision of essential ecosystem services. Numerous studies have stressed the importance of biodiversity in maintaining an adequate supply of ecosystem services (Díaz et al. 2006; Haines-Young and Potschin 2010; Balvanera et al. 2006). Biodiversity loss continues at an alarming rate, with no signs of significant slowing, and current rates of extinction being comparable to those seen in the fossil record during mass extinction events (Barnosky et al. 2011). There is a long standing view amongst many conservationists that biodiversity cannot be conserved through the use of natural reserves alone, and that conservation across multiple land uses is required to achieve the best outcome (Wilcove 1989). While the global expansion of plantation forests and the intensification of their management regimes pose a threat to biodiversity, considerable potential for conservation also exists in planted forests, particularly where natural woodlands are scarce or degraded, and where the alternative land cover is highly managed agriculture (Brockerhoff et al. 2008). Ireland provides an excellent case study for the potential value of plantation forests for biodiversity conservation, as natural forests are fragmented and account for less than 1 % of total land area, embedded in a matrix of highly managed agricultural land (Perrin and Daly 2010).

Ireland has a long history of human inhabitation, and anthropogenic influences have played a pivotal role in its complex forest history, with deforestation beginning as early as the Mesolithic period (Preece et al. 1986; Waddell 1998). However, the majority of Ireland's deforestation occurred from the 1600s onwards, spurred on by rapid domestic population growth and exportation of Irish timber to Britain. By the early 1900s, forest cover in Ireland had fallen to less than 1 % (Forest Service 2008). Following the formation of the Republic of Ireland in 1922, large scale planting has increased the forest area to just over 11 % of total land area (Fig. 1). However, native broadleaf species comprised only a minute percentage of this increase in forest area, and were largely ignored in favour of fast growing, exotic conifer species. Both Sitka spruce (*Picea sitchensis*) and Norway spruce (*Picea abies*) have been widely planted across Ireland, accounting for 59 and 10 % of current total growing stock respectively (Forest Forest Service 2013). This trend has largely been mirrored in Northern Ireland, where forest cover currently stands at 8 % and is fragmented across the country (Forest Service 2015). Despite attempts to increase forest area, Ireland remains one of the least forested EU member states, along with the Netherlands, Malta and the United Kingdom (EUROSTAT 2011). Ireland's modern forest landscape is very different to that of the past, with less than 100,000 ha of native woodland remaining, of which less than 20,000 ha is classified as ancient woodland, established prior to the 1600s (Perrin and Daly 2010). As such, Ireland depends on plantation forests for a whole spectrum of ecosystem goods and services which native woodlands are no longer capable of providing in sufficient quantities. Despite protection, remaining native woodlands across Ireland are under constant pressure from large mammal grazing (McEvoy et al. 2006; Perrin et al. 2006; 2011) and invasive plant species, primarily Rhododendron (*Rhododendron poniticum*), which has invaded large swathes of Killarney National Park, the most intact native woodland remaining in Ireland (Kelly 2005; Barron 2009). The importance of Ireland's native woodlands for conservation of forest biodiversity cannot be understated. However, in countries where native woodlands are limited and highly fragmented, plantation forests have been shown to provide habitat for forest associated species, as well as increasing overall biodiversity at a landscape scale (Stephens and Wagner 2007;

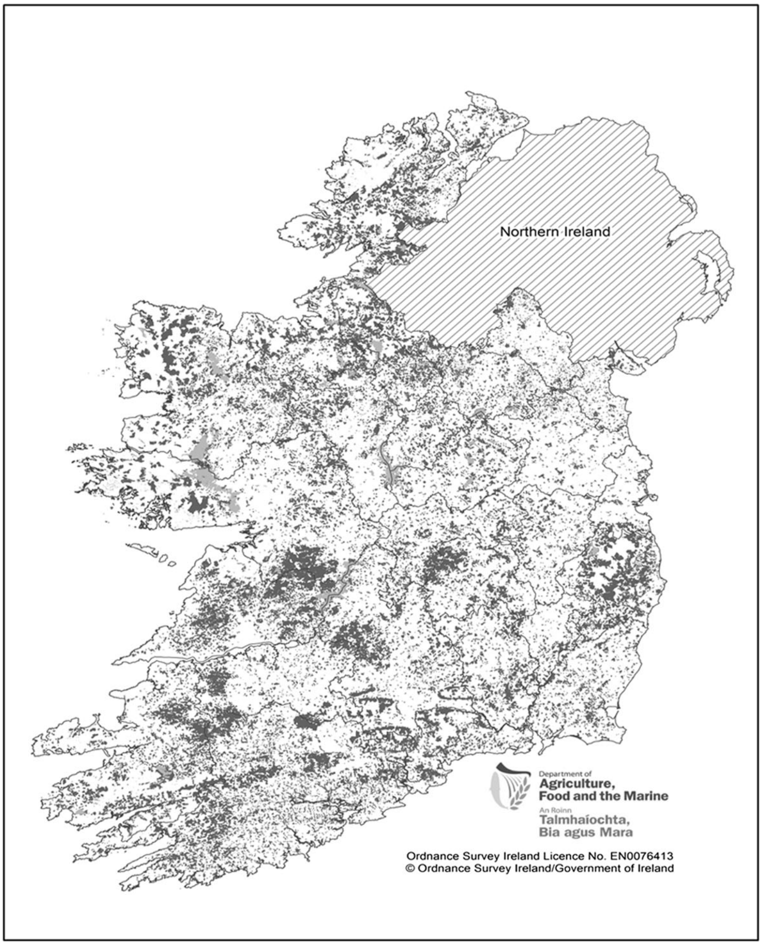

Fig. 1 National forest cover map of the Republic of Ireland (Department of Agriculture, Food and the Marine, 2012). Note, Ireland's forests represent ca. 11 % of total land area

Pawson et al. 2008; Coote et al. 2012). As such, we will examine the potential for plantation forests to provide habitat for native biodiversity.

However, when discussing plantation forests it is necessary to examine their impacts on biodiversity at a national level. From an Irish perspective, the conservation priorities in relation to plantations are twofold. First is the conservation of Ireland's forest biodiversity. As previously discussed, historical deforestation has decimated native woodland cover across Ireland (Mitchell 2000). As a result, the biodiversity value of these remaining semi-natural broadleaf woodlands are disproportionately high, providing habitat for a number of threatened forest species (Irwin et al. 2013). In regions such as Ireland, plantation forests are of greater value to forest biodiversity than regions which are dominated by semi-natural woodlands, particularly if managed in a sympathetic manner (Bremer and Farley 2010; Berndt et al. 2008). Secondly, it is also necessary to examine the potential biodiversity impacts of establishing plantation forests. Irish plantation forests do not directly negatively impact on forest biodiversity, as afforestation is carried out on open habitats rather than on previously forested land (Forest Forest Service 2013). However, it is first necessary to examine the impacts of such land use transitions on the biodiversity of open habitat species in order to determine the net impact on biodiversity.

Prior and alternative land use

Since large scale afforestation began across Ireland almost a century ago, plantation forests have traditionally been established on three primary habitat types, namely improved agricultural grassland, semi-natural wet grasslands and peatlands, including bogs and heaths (Smith et al. 2006). Increased afforestation rates are expected in Ireland over the next 30 years, as new strategies aim to increase forest cover to 18 % by 2046 (DAFM 2014). Therefore, establishing the impact of afforestation on the biodiversity of each of these habitats in important in determining the overall impact of plantation forests on biodiversity at a national level. Changes to biodiversity caused by afforestation of these habitats are examined below using three, well studied, indicator groups, namely plants, birds and spiders.

Agricultural land is the predominant land use in Ireland, accounting for approximately 61 % of the total landmass. The overwhelming majority of this consists of improved agricultural grasslands for grazing and silage production, accounting for over 90 % of all agricultural land in Ireland (O'Mara 2008). The biodiversity value of improved grassland is typically low, due to continued agricultural intensification across Europe (Reidsma et al. 2006). The intensive management regimes and high grazing pressure associated with improved grasslands has resulted in greatly reduced biodiversity, not only in terms of number of plant species, but also in the loss of faunal diversity, both at farm level and at the wider landscape level (Hopkins and Holz 2006). Plant communities of agriculturally improved grassland are largely dominated by one or two highly productive grass species, due to applications of fertilisers and herbicides (Benton et al. 2003). Few bird species directly utilise improved grasslands across Ireland for either feeding or breeding purposes, primarily due to the lack of suitable cover and food for generalist and woodland species (Wilson et al. 2012; Mcmahon et al. 2008). In contrast, hedgerows surrounding improved grasslands have been shown to be of greater importance to bird species. Moles and Breen (1995) recorded 32 bird species utilising hedgerows surrounding improved grasslands during the summer period and 47 species during the winter period. Spiders are the best studied group of invertebrates from an Irish context, and have been widely used as indicators for the invertebrate community of the habitat as a whole. The spider communities of improved grasslands have also been shown to be poor, lacking specialist open habitat spiders. Irish improved grasslands are largely dominated by pioneer species associated with heavily disturbed habitats, a trend replicated in the UK (Cole et al. 2005). This was largely attributed to the intensive management regime associated with such habitats (Oxbrough et al. 2006b, 2007). As with birds, hedgerows surrounding grassland pastures have been shown to provide habitat for a range of generalist invertebrates, representing a large proportion of the spider diversity in agricultural habitats (Oxbrough et al. 2007). Similar trends have been recorded for other invertebrate groups, such as ground beetles, where improved grasslands are largely dominated by generalist species with good dispersal ability, at the expense of specialists (Rainio and Niemelä 2003). Due to the low species richness of the habitat, afforestation of improved grasslands with exotic conifers is likely to result in a net increase in biodiversity, if carried out correctly. Immediately following planting of improved grassland sites, Buscardo et al. (2008) found a significant increased frequency of competitive grasses commonly found in both wooded and unwooded habitats, as well as a reduced frequency of less competitive ruderal grasses, typically associated with open habitats. This can largely be attributed to the removal of grazing pressure, resulting in changes to the competitive balance between species (Stránská 2004). This resulted in a significant increase in bryophyte species richness, as new species colonised new habitat in the shade beneath taller, ungrazed grass species. As improved grasslands are fundamentally species poor habitats in relation to vegetation, afforestation has little short-term negative impacts on diversity (Buscardo et al. 2008). Afforestation was also shown to be beneficial to ground spiders, at least in the short term, as species richness increased, particularly the species richness of those associated with low vegetation (Oxbrough et al. 2006b). In relation to bird species, afforestation of improved grasslands has been shown to be largely positive. Data collected by Wilson et al. (2012) suggested that the planting of conifers on improved grassland would benefit both generalist and woodland bird species by providing greater shrub cover and foraging habitats. Open habitat specialists are typically lacking from improved grassland habitats, and generalist species which occupy the surrounding hedgerows will also use forests (Pithon et al. 2005). However, many studies cited above suggest the importance of retaining prior features associated with improved grassland during afforestation, particularly hedgerows, which harbour a large amount of improved grassland biodiversity (Oxbrough et al. 2006b; Buscardo et al. 2008; Wilson et al. 2012). Creating a buffer zone of open space around such hedgerows during planting would ensure they are not shaded out as the plantation forest matures, ensuring continuous shrub cover and increasing the prevalence of native tree species (Buscardo et al. 2008), benefiting both bird and invertebrate diversity throughout the forest cycle (Oxbrough et al. 2005; Wilson et al. 2012). Although retaining existing habitats such as hedgerows has been included in the forest biodiversity guidelines, it remains unclear to what extent this is currently practiced (Forest Service 2000).

In contrast to improved grassland, which is of high agricultural value but of low biodiversity value, unimproved wet grasslands are typically of low agricultural value but of far greater importance to open habitat biodiversity. Wet grasslands are semi-natural ecosystems, often found on poor draining soils which periodically flood. Although used for seasonal grazing purposes, the management regime of these habitats is far less intensive than improved grasslands (Fossit 2002). Plant biodiversity of wet grasslands are higher than that of improved grasslands, with initial studies recording a mean of 25.7 plant species/4 m^2 plot (Eakin 1995), many of which were open wet habitat specialists (Buscardo et al., 2008). Spider diversity of wet grasslands was shown to be higher than that of improved grassland, with 114 species recorded compared to 91 species. In addition, wet grasslands had a greater number of species typically associated with wet habitat conditions, with both *Gnathonarium dentatum* and *Pardosa amentata* being significantly more abundant than in other survey habitats (Oxbrough et al. 2007). Studies examining other wet grasslands around Ireland found a significantly higher number of all common agricultural species occupying wet grassland habitats, compared to improved grasslands. This can be largely attributed to the higher carrying capacity of the hedgerows surrounding wet grasslands, which had over twice as much hedgerow habitat available, compared to improved grasslands, again emphasising the importance of retaining residual habitats during the afforestation process (Wilson et al. 2012).

Despite their importance to biodiversity, wet grassland habitats are at risk, largely due to their lack of formal protection at a national level (Buscardo et al. 2008). Since the turn of the millennium, planting of semi-natural wet grasslands has substantially increased, in both relative and absolute terms, and account for a higher proportion of planting over the past 15 years than any other time (Wilson et al. 2012). Wet grasslands afforestation has a negative impact on biodiversity, particularly for species which prefer wet conditions. Following afforestation of wet grasslands, changes to plant communities were similar to those seen in improved grassland, although less marked due to a lower pre-afforestation grazing and fertilisation pressure. However, drainage of the habitat in preparation for afforestation resulted in a significant decrease in the frequency of wet habitat species, and an associated increase in competitive grasses. Differences in plant species richness between planted and unplanted wet grasslands were shown to be not significant at a scale of 100 m^2, as drainage ditches provided a temporary habitat with reduced competition for both vascular plants and bryophytes (Buscardo et al. 2008). Ground spider diversity was reduced following afforestation of wet grassland habitats, with a particular reduction in the number of rare species and wetland specialists. This may be due to the application of fertilisers, however soil drainage is also likely to have a significant impact (Oxbrough et al. 2006b). Soil moisture content has been shown to exert a positive influence of ground spider density directly (Kajak et al. 2000), as well as indirectly through changes in the vegetation (Cattin et al. 2003). Patterns for other invertebrate groups have not yet been studied in great detail, and therefore little information is currently available. While afforestation is unlikely to have a significantly negative impact on common species associated with wet grasslands, particularly if existing hedgerows are retained, afforestation of these habitats poses a threat to open habitat specialists. Specialist species such as the meadow pipit (*Anthus pratensis*) and skylark (*Alauda arvensis*) utilise wet grasslands in agricultural areas (Wilson et al. 2012); however, they are absent from plantation forests due to the lack of sufficient open space (Wilson et al. 2006). It is evident that the afforestation of wet grassland habitats is a suboptimal choice in terms of biodiversity conservation, with soil drainage and reduction of open space resulting in the probable loss of a number of rare and specialist species incapable of utilising forest habitats.

However, plantation forests cannot be viewed only in relation to the prior habitat, but also the alternative land use in the absence of afforestation (Newmaster et al. 2006; Brockerhoff et al. 2008). In the case of semi-natural wet grasslands, their low agricultural productivity often results in land abandonment. If wet grasslands remain unplanted, their biodiversity value is contingent on maintaining grazing levels. Should grazing levels fall below the necessary level on such marginal agricultural land, tree and shrub layers will no longer be suppressed and a closed canopy woodland would develop over a longer temporal scale. This would result in the loss of habitat for a number of open habitat species, particularly birds (Scozzafava and De Sanctis 2006). Abandonment of semi-natural grasslands has been a major driver in the decline of biodiversity in the Burren region in the west of Ireland, due to scrub encroachment (Moles et al. 2005; Parr et al. 2009). While there are no studies which directly compare the two scenarios, it is likely that over a long temporal scale, the impact of abandonment on wet grassland habitats is on par with that of afforestation.

While both improved grasslands and wet grasslands are still being utilised for afforestation, the afforestation of upland peatlands has ceased, with almost no planting on intact peatland occurring since the establishment of Coilte in 1988, the semi-state body in charge of all public forests. However, over 44 % of the total forest estate in the Republic of Ireland is currently established on peatland sites (Forest Service 2013). Although it is unknown to what extent plantation were established on intact functioning peatland, relative to degraded peatland, the impact of historical afforestation on peatland biodiversity is undeniable (Black et al. 2008). Afforestation has replaced the distinctive plant communities which characterise Irish peatlands (Sottocornola et al. 2009), with international studies demonstrating a significant reduction in the frequency and richness of specialist ombrotrophic species (Lachance et al. 2005). This can largely be attributed to changes in shade and soil moisture following afforestation, two environmental parameters which are highly important in determining the distribution of peatland vegetation (Lachance and Lavoie 2004; Breeuwer et al. 2009). Studies examining the impact of afforestation on peatland spiders show that while there are no significant changes to species richness, species composition was heavily impacted. Planted peatland sites were distinguished by significant reductions in rare specialist wetland species, being replaced by more generalist fauna (Oxbrough et al. 2006b). Again, this can largely be attributed to soil drainage prior to afforestation, which has been shown to be a significant influence on spider distribution (Usher 1992; Laine et al. 1995). While peatlands tend to have a low bird diversity, they are primarily inhabited by open habitat specialists, which are negatively impacted by afforestation. Hen harrier (*Circus cyaneus*), red grouse (*Lagopus lagopus scoticus*), stonechat (*Saxicola torquata*) and whinchat (*Saxicola rubetra*), all of which are upland open habitat specialists are commonly recorded on peatland sites prior to afforestation. However, they are typically absent from subsequent peatland plantations, due to the lack of a low vegetation layer during the later stages of the forest cycle, which these species are heavily reliant on (Wilson et al. 2006; Wilson et al. 2012).

While it is evident that afforestation has had a considerable negative impact on peatland biodiversity, it is necessary to examine the potential alternative land use of peatland, in the absence of afforestation. Industrial peat extraction continues in both the Republic and Northern Ireland, producing over 540,000 tons of peat sod annually for domestic use and commercial sale (Bullock et al. 2012). Over 100,000 ha have already undergone mechanical extraction, and a further 70,000 ha remain in production, primarily raised peat bogs in the midlands (Renou-Wilson and Byrne 2015). This has produced a vast area of cutaway peatlands, where all peat has been extracted. In their basic state, the biodiversity value of cutaway peatlands is extremely low, with studies showing sites being devoid of typical peatland vegetation and associated biodiversity following the cessation of harvesting (Lavoie et al. 2003). Active restoration is necessary to restore biodiversity to cutaway peatlands (Rochefort et al. 1997, 2003). While the majority of Irish cutaway peatland has been utilised as wind farm sites or subsequently afforested (Renou et al. 2006), restoration has been attempted in a number of locations, with mixed success. Attempts at restoration in North West Ireland succeeded in revegetating the site; however, the plant communities bear little resemblance to typical Atlantic blanket bog. Common rush (*Juncus effuses*), which is commonly associated with disturbed peat soil, was dominant, and *Sphagnum* moss species only developed in areas where the water table remained high (Farrell and Doyle 2003). It cannot be stated that afforestation of intact peatland is preferable to industrial extraction as both result in a significant negative impact to peatland biodiversity. Numerous studies of peatland plantation forests have demonstrated that almost no biodiversity associated with peatlands is retained following canopy closure (Oxbrough et al. 2006b; Wilson et al. 2006), while small fragments of intact peatland within peat production areas provide habitat for a small amount of peatland biodiversity (Farrell and Doyle 2003). Neither event can be classed as favourable, as both result in the complete loss peatland biodiversity of high conservation concern. However, in cases where restoration of cutaway sites has been attempted and failed, well managed plantation forests may provide a greater benefit to biodiversity as a whole, compared to leaving the site bare

(Renou et al. 2006). This is all entirely retrospective, as current policy strictly forbids the afforestation of peatlands, and the practice has been all but phased out (Black et al. 2008).

As has been suggested in other studies, the biodiversity value of plantation forests in highly variable, and depends heavily on the type of land use which it is replacing. If replacing functioning natural ecosystems, be they wet grasslands or peatlands, the net result of afforestation to overall biodiversity is likely to be negative. If, however, plantation forests are planted on already degraded ecosystems, such as improved grassland pasture or cutaway peat bog, the net impact on biodiversity is more likely to be positive (Bremer and Farley 2010). However, biodiversity value is heavily dependent on a number of forest management factors, which must be examined further (Brockerhoff et al. 2008).

Irish plantation forests and habitat provision

While examining the impact of plantation forests on biodiversity in relation to both the past and potential alternative land use is important, objectively determining the biodiversity value of plantation forests requires assessing it on its own merits. In regions where natural forest cover is lacking, studies have shown that plantation forests can act as a potential surrogate habitat for forest associated plant and animal species (Berndt et al. 2008). This is particularly true in the case of Ireland, where fragmented native woodland accounts for approximately 1 % of total land area, both in the Republic and Northern Ireland (Haines-Young et al. 2000; Cross 2012).

There is considerable evidence that native forests are a superior habitat to plantation forests for native species. Regardless of management strategies, studies have shown that native forests will most often support a higher species richness and abundance of native species, relative to plantation forests, both in Ireland (Irwin et al. 2014; Pedley et al. 2014) and elsewhere (Lindenmayer and Hobbs 2004; Brockerhoff et al. 2008). It must be stressed that this difference between plantation and semi-natural forests is not as a direct result of the excessive use of exotic conifer species in Irish plantations. The biodiversity of Irish plantations comprised primarily of native ash (*Fraxinus excelsior*) was shown to differ greatly from semi-natural ash woodlands, supporting significantly fewer woodland plant species, indicating both the importance of forest structure. Furthermore, it indicates that importance of land use prior to afforestation. Even native plantation forests show a lack of native forest biodiversity, likely due to the lack of nearby native woodland from which propagules could originate (Brockerhoff et al. 2008; Coote et al. 2012). Due to its geographical separation from mainland Europe and recent glaciation events, Ireland has retained only a small number of forest specialists that still occur in Europe and Great Britain (Fuller et al. 2007; Kelly 2008). Therefore, the differences in species richness between native and plantation forests are less marked than elsewhere, as both forests are primarily inhabited by generalist species, capable of utilising a wide range of available habitats (Irwin et al. 2014). However, directly comparing the two forest types is not appropriate from an Irish standpoint, as plantation forests have not replaced native woodland, as has occurred in other regions (Stephens and Wagner 2007). While not comparing the two in absolute terms, the high biodiversity value of Irelands remaining native woodland provides a valuable reference point against which plantation forests can be examined. This information can be utilised further to improve the conservation value of plantations, through altering forest management strategies to meet environmental objectives (Irwin et al. 2013).

A number of Irish studies have examined biodiversity of mature plantation forests, primarily Sitka spruce and Norway spruce, and assessed their conservation value in relation to remaining unmanaged woodlands. Invertebrate species richness varied considerably between forest types depending on taxa. The species richness of both ground dwelling beetles and canopy dwelling spiders was found to be similar to that of native woodlands, largely reflecting the lack of specialists, specifically adapted to forest habitats (Irwin et al. 2014). Studies have suggested that spiders in particular are more heavily influenced by availability of suitable prey and habitat structure, rather than any one particular species of tree (Halaj et al. 2000; Purchart et al. 2013). In contrast, the species richness of canopy dwelling beetles was shown to be consistently and significantly greater in oak and ash woodlands, relative to plantation forests. As such beetles are more specialised than spiders, with more diverse foraging strategies, and previous studies have shown that they are heavily impacted by plantation forest management strategies (Wiezik et al. 2007). Similar results have been shown by Pedley et al. (2014), with native woodlands supporting over double the number of beetle species, as well as supporting twice as many Diptera and Hemiptera families. The total abundance of invertebrates in Sitka spruce plantations was shown to be significantly higher than that of native woodlands; however, this was largely due to dominance by ultra-abundant aphids (Aphididae) and midges (Ceratopogonidae and Chironomidae). Again, species richness of canopy dwelling spiders showed little divergence between forest types, with the abundance of aphids as prey making plantation forests suitable habitat for generalist spider species. This demonstrates that many invertebrates are incapable of utilising plantation forests, although whether this is as a result of the presence of individual tree species, or due to the overall canopy structure, is difficult to determine (Pedley et al. 2014).

The plant communities of either Sitka spruce or Norway spruce plantations typically show little similarity to that of native woodlands, either structurally or functionally (French et al. 2008; Coote et al. 2012), a trend which has also been noted in other plantation forest types, both in the UK and North America (Humphrey et al. 2002b; Aubin et al. 2008). The lower species richness of bryophytes and vascular plants within plantation forests can largely be attributed to the lack of light penetration once full canopy closure occurs (Irwin et al. 2014). Coniferous plantation forests also lack the understory vegetation layer seen in native woodlands, which is of particular importance to foraging and nesting birds (Coote et al. 2012).

Given Irelands primarily generalist bird fauna, there is considerable potential for plantation forests to act as an effective habitat. Studies have shown that much of the generalist bird fauna that characterise native oak and ash woodlands are also present in Sitka spruce plantations, both at mid-rotation and the mature phase (Sweeney et al. 2010c). This supports the theory that plantation forests act as a complementary habitat for generalist birds (Irwin et al. 2014). However, distinctive differences remain between plantations and native woodlands. Irish plantation forests have a much lower carrying capacity, relative to native woodlands, with the majority of species present in lower densities. A small number of species dominate plantation forests, with coal tit (*Parus ater*) and goldcrest (*Regulus regulus*) accounting for over 60 % of total bird density (Sweeney et al. 2010c). Although both these species occur in other, non-arboreal habitats across Ireland, they are particularly associated with plantation forests. This can be attributed to their diet, with both species feeding on small Hemiptera and Collembola invertebrates, which are common in plantation forests (Snow et al. 1997). A number of other species which were recorded in plantation forests were typically associated with non-crop broadleaf vegetation, rather than conifers, with the densities of these species being significantly greater in native woodlands. These include blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*), which are primarily, although not exclusively, associated with native broadleaf woodlands (Sweeney et al. 2010c; Wilson et al. 2010). The lack of understory vegetation and low structural diversity of plantation forests following canopy closure contributes to their poorer habitat quality relative to unmanaged heterogeneous native woodlands (Smith et al. 2009). Without sufficient understory vegetation, birds in plantation forests lack nesting and foraging opportunities, thereby resulting in a far lower carrying capacity (Quine et al. 2007; Sweeney et al. 2010c).

Determining the contribution of plantation forests to the conservation of rare or endangered species is another important aspect in assessing their biodiversity value (Carnus et al. 2006). This is particularly true from an Irish context, as plantation forests make up over 90 % of national forest cover (Cross 2012). As part of a national assessment, all major forest types were surveyed and associated biodiversity recorded, including a number of species of national conservation concern. Although plantation forests were shown to provide habitat for species of conservation concern from multiple different taxa, betony (*Stachys officinalis*) was the only species which was typically associated with long established woodland in Ireland, although it is also associated with calcareous grasslands and hedgerows (Perrin et al. 2008) (Table 1). Although plantation forests supported a number of species of conservation concern which were not recorded in native woodlands, these species were typically associated with other habitats. For example, *Athous campyloides*, a beetle species on the UK Red List, is typically associated with dry calcareous grassland, yet was found in a number of different forest types (Buckland 2009). Furthermore, while two birds of conservation concern, the linnet (*Carduelis cannabina*) and grasshopper warbler (*Locustella naevia*) were both recorded in the early successional stages of plantation forests (4–8 years), they were entirely absent from mature plantations

Table 1 Species of conservation concern recorded in Irish plantation forests (after Irwin et al. 2013)

Species name	Common name	Conservation status	Taxa	Native woodland associated species
Stachys officinalis	Wood betony	Notable	Vascular plant	Yes
Daltonia splachnoides	Irish Daltonia	Near threatened (Europe) Least concern (Ireland)	Mosses	No
Sphagnum girgensohnii	Common green peat moss	Near threatened	Mosses	No
Plagiothecium laetum	–	Vulnerable	Mosses	No
Malthodes guttifer	–	UK red list	Invertebrate	No
Orchesia minor	–	UK red list	Invertebrate	No
Athous campyloides	–	UK red list	Invertebrate	No
Stenichnus poweri	–	UK red list	Invertebrate	No
Carduelis cannabina	Common linnet	Irish amber list	Bird	No
Locustella naevia	Grasshopper warbler	Irish amber list	Bird	No

following canopy closure. Although plantation forests provide habitat for species of conservation concern from multiple taxa, the majority of forest associated species of conservation concern were only recorded in native woodlands (Irwin et al. 2013).

Despite Irelands primarily generalist fauna, it is evident that plantation forests provide poor quality habitat for a wide range of taxa, and while a number of species of conservation concern were recorded in plantation forests, almost none of these are species typically associated with native woodlands. While it is important to stress that plantations do not actually negatively impact on native forest biodiversity, as plantation forests have not replaced native woodlands, the above finding suggest that plantation forests only provide some limited benefits to native biodiversity in their current state. However, there exists considerable potential further improve the biodiversity value of these plantations through altering management regimes.

Biodiversity and forest management

The provision of all ecosystem services, including habitat provision, can be altered either positively or negative by management decisions (De Groot et al. 2010; Deal et al. 2012). In this respect, plantation forests are neither inherently positive nor negative in respect to biodiversity, rather it is the way in which they are managed which ultimately determines the biodiversity value (Brockerhoff et al. 2008). Although there is still considerable uncertainty as to the mechanisms of ecological change in Irish plantation forests, and the management practices which may potentially influence them, a number of core management decisions must be considered (Oxbrough et al. 2014).

The choice of which tree species are planted and in what percentage, has received the greatest amount of attention in promoting habitat provision in plantation forests (Hartley 2002). This is particularly important from an Irish perspective, due to the heavy reliance on a select few fast growing conifer species for wood production. Although there has been a growing movement across Europe in recent decades to diversify tree species of plantation forests, Ireland remains behind the trend, with Sitka spruce remaining the dominant tree species in the Irish forest landscape (Forest Europe 2011; Forest Service 2013). Although planting a mix of native species may prove beneficial from a biodiversity standpoint, this is often not a commercially viable option. This is indeed true in the case of Ireland, where slow growth rates make native broadleaves unsuitable (Horgan et al. 2003). Instead, it is necessary to examine the potential biodiversity benefits of including native species as secondary species in the plantation setting.

The dominance of conifers in plantation forests has not been entirely negative. Monocultures have offered some benefits to biodiversity, providing vital habitat for the protected red squirrel (*Sciurus vulgaris*) and pine marten (*Martes martes*), both species of conservation concern which typically perform poorly in broadleaf dominated forests. Excessive broadleaf vegetation in areas where these species occur is strongly discouraged (Teangana et al. 2000; O'Mahony et al. 2006; Irwin et al. 2013). However, as has been discussed previously, it is evident that Sitka spruce or Norway spruce dominated plantations provide poor habitat for a range of native forest species. Effort has been made to improve the habitat provision of commercial plantation forests in Ireland. Under revised guidelines, first rotation plantations must consist of 10 % broadleaf species, while second rotation forests must also consist of 10 % diverse conifers (any conifers excluding Sitka spruce and Norway spruce) (Forest Service 2000). However, research into the impact of mixed species plantations in Ireland has shown that the strategy has little benefit to biodiversity, at least not in the manner which is currently being carried out. Sweeney et al. (2010a) examined the bird communities of Norway spruce monocultures, as well as Norway spruce mixed with 20–40 % native oak (*Quercus*) and Scots pine (*Pinus sylvestris*) at sites across both the Republic and Northern Ireland. No significant differences were found in the composition of bird communities, with only slight differences shown between forest types. Of 25 species recorded, 23 were detected in pure Norway spruce, 20 in Oak mixes and 22 in Scots pine mixes. Furthermore, there was no significant difference in species richness or Simpson's diversity for birds between monoculture and mixed forests. Interestingly, the bird density of Norway spruce/Scots pine mixed forests was significantly higher than that of monoculture forests or oak mixes. However, this can be attributed to the ecological state of the forest, rather than the actual tree species per se. The slower growth rate of Scots pine relative to Norway spruce creates a more open canopy structure, allowing for increased light penetration and the establishment of non-crop vegetation and the development of an understory. This in turn positively influences bird density, through providing greater nesting and foraging opportunity than monoculture forests (Sweeney et al. 2010a; Wilson et al. 2010). Despite the presence of oak, a number of species which are typically more associated with native broadleaf forests such as the longtailed tit (*Aegithalos caudatus*) and Eurasian treecreeper (*Certhia familiaris*) were recorded in greater density in the Scots pine mixes. This is largely due to the manner in which the trees were planted. All trees were planted intimately, evenly spread throughout the stands, rather than in clumps or rows, resulting in the faster growing Norway spruce overshadowing and suppressing the oak. If oak mixes were planted in clumps, out of direct competition with the primary species, the influence which they exert over bird communities may be greater (Joyce 2002; Sweeney et al. 2010a). Arthropod diversity was examined at the same sites, with similar results. Arthropod communities showed no significant differences, with species richness, assemblage structure and number of specialist species similar across all forest types. This suggests that mixed species planting at a low ratios (15–40 %) is of limited benefit to biodiversity, as no differences in the environmental conditions were noted between forest types. It remains unclear what proportion of native trees is necessary to have a significant impact on biodiversity in Irish non-native conifer plantations (Oxbrough et al. 2012).

In addition to improving the proportion of native trees in plantations, there are a number of other changes to forest management strategies which can improve the biodiversity value of plantation forests, and can be implemented in a shorter timescale. In general, studies have shown that increasing thinning intensity has a positive impact on biodiversity (Kalies et al. 2010; Verschuyl et al. 2011). Irish studies have shown a link between thinning intensity and increased vascular plant species richness, as a result of releasing previously monopolised resources, primarily light. However, this is accompanied by a decline in both bryophytes and lichens, as both typically prefer heavily shaded conditions (Dhubháin et al. 2005; Iremonger et al. 2006). There is a lack of information relating to thinning and other organisms from an Irish perspective, however some general trends can be determined from international research. The overall impact of thinning on invertebrate communities appears to be positive, with heavier thinning regimes resulting in significantly greater increases in species richness and diversity of herbivores and predators (Warriner et al. 2002; Yi 2007). In such studies, thinning regime were "determined by the percent of unthinned (control) stand basal area or trees per hectare remaining in thinned (treatment) stands", with heavy thinning being defined as 0–33 % remaining (Verschuyl et al. 2011). Irish studies carried out have already demonstrated that failure to thin stands sufficiently can result in a few invertebrates species dominating the community (Day and Carthy 1988). Heavy thinning is particularly beneficial for saprophytic invertebrates, primarily due to the large input of dead wood into the ecosystem during the process, rather than the any subsequent increase in light penetration. (Bishop et al. 2009; Nadeau et al. 2015). Furthermore, thinning also appears to be beneficial for small mammals, as improved understory growth following thinning has been shown to result in increased population densities of several species, through greater availability of shelter. However, increased densities in mammal populations are generally short term, typically reverting to pre-thinning levels within 3–5 years (Garman et al. 2001; Suzuki and Hayes 2003). Furthermore, population levels of certain small mammals are negatively impacted by heavier thinning regimes (<123 trees per ha) due to loss of cover, meaning the conservation benefits of thinning need to be examined at a site by site basis (Garman et al. 2001). It should be noted that experiments on small mammals have not been carried out in Irish plantations, and extrapolating results for mammal species present in Irish forests is not possible at this time. Typical rates of commercial thinning within plantation forests of 20–30 % are of little benefit for improving bird diversity, as canopy closure reoccurs within a few years (Calladine et al. 2009; Hansson 2001). For most bird species, significant effects over a long term can only be detected at above 50 % canopy removal (Burgess 2014). While continuous rigorous thinning has been suggested as a method for improving forest habitat for the hen harrier (*Circus cyaneus*), an open habitat specialist which typically only utilises plantations during the pre-thicket stage (Wilson et al. 2005, 2009), the overall benefits of traditional commercial thinning on bird species are likely insignificant. Although heavier thinning has been shown to be of benefit to some taxa, changing current management practices may prove difficult, due to the increased risk of wind throw, which is a prevalent threat across Ireland (Dhubhain et al. 2001; Joyce and O'Carroll 2002).

However, it is necessary to take a broader look at the forest landscape as a whole to further improve the biodiversity value of plantation forests. Areas of Biodiversity Enhancement (ABE's) are an important factor in the provision of habitat by plantation forests, and include a range of associated forest features such as roadside verges, forest rides and unplanted glades. Under current guidelines, approximately 15 % of forest area must be treated with particular regard to biodiversity, including 5–10 % open space and 5–10 % retained habitat features (Forest Service 2000). Considerable research has been carried out into the impact of ABE's on plantation forest biodiversity in Ireland, examining vegetation, invertebrates and bird communities (Mullen et al. 2003; Gittings et al. 2006; Coote et al. 2007; Smith et al. 2007; Wilson et al. 2010). Open spaces have been shown to support significantly higher numbers of open habitat and ruderal vascular plant species (17.9 $\pm$ 1.4 species), relative to closed canopy areas, although increased light levels typically result in fewer bryophytes being supported (6.0 $\pm$ 0.7). However, to make significant impact, studies have shown that roads must be a minimum of 15 m in width, while glades require a minimum of 625–900 m^2 due to the influence of surrounding canopy shade (Coote et al. 2007; Smith et al. 2007). Further studies have shown the benefit of open space to invertebrates such as spiders and hoverflies. Open spaces support a unique spider fauna which is typically absent from closed canopies. Of all habitats, glades supported the greatest total species richness and greatest species richness of open habitat associated species. As well as supporting open habitat spider species, forest road verges have also been shown to provide habitat for a number of species which are of conservation concern (Oxbrough et al. 2006a; Fuller et al. 2013). The importance of open space is even greater to hoverflies compared to spiders in plantation forests, with over 80 % of species recorded within the forest associated with open habitat rather than closed canopies, with significantly higher species richness being recorded in glades relative to roadside verges (Gittings et al. 2006). Due to the large ranges of open habitat specialists, it is unlikely that open space available within plantations would be sufficient to support such bird species. Regardless, open space remains an important factor in improving the overall bird diversity of Irish forests, through providing areas where non-crop broadleaf vegetation can develop (Wilson et al. 2010). While certain species, such as the sparrowhawk (*Accipiter nisus*), merlin (*Falco columbarius*) and raven (*Corvus corax*) are capable of nesting within plantations, they often do not due to lack of available open habitat in which to forage. Therefore, retaining open habitats, both at the forest level and at the overall landscape level remains critical to promoting the use of plantations by these species (O'Halloran et al. 2002). Incorporating sufficient open space during the afforestation phase is a key aspect of improving the biodiversity of Irish plantation forests. In already established plantations, where open space is limited, creating open space may be an option. However, this decision must be made with due consideration for potential wind damage which may occur as a result of removing trees.

The method by which mature plantation forests are harvested is key to maintaining habitat provision services between concurrent forest cycles. Conventional clear felling, where all trees within an area are uniformly cut down, is the principle harvesting method used in Ireland at present. However, this is typically carried out focussing on economic and operational considerations (Wilson and Wilson 2001) without due consideration for the potential impacts that the harvesting method has on habitat provision services (Pawson et al. 2006). From an Irish perspective, the aim is not to eliminate the use of clear felling for forest harvesting, rather to manage the forest landscape in a manner that reduces negative impacts of clear felling on biodiversity. Clear felling can also have a positive effect on biodiversity, providing greater species richness through the colonisation of the temporary open space provided by open space species (Rosenvald and Lohmus 2008). Plant diversity increases following the removal of the canopy, and also allows for the germination of the existing seed bank (Brockerhoff et al. 2003; Roberts and Zhu 2002). Significant changes to the community composition of carabid beetles and ground spiders have been recorded following clear felling, with increased species richness occurring as open habitat species colonise newly harvested sites (Fahy and Gormally 1998; Huber et al. 2007). It is also important to note that a certain amount of clear felling is recommended for Irish plantation to provide habitat for open habitat specialist birds of conservation concern, most notably the nightjar (*Caprimulgidae*) and hen harrier. Both of these species react positively to large areas of clear fell harvesting (O'Halloran et al. 2002). In general, young clear fell sites tend to support a greater diversity of shrubland birds, due to the increase in low shrub cover following the removal of the canopy. Diversifying harvesting regimes within forests is likely to have greatest benefit to bird diversity, as different approaches support different groups of species (Calladine et al. 2015). Unlike natural disturbance events (primarily windthrow in an Irish context), the lack of remnant forest patches following clear felling creates a homogeneous habitat devoid of resources, placing constraints on forest biodiversity. A number of management decisions can be taken, spatially ranging from stand to landscape level to aid in maintaining forest biodiversity following harvesting.

In both Ireland and the UK, there has been increased interest in the use of continuous cover forestry (CCF), as an environmentally sound, low-impact harvesting method, by maintaining forest cover at one or more levels at all times, eliminating clear felling (Mason et al. 1999). However, numerous studies have being carried out that show such methods are of only limited use in Ireland due to a combination of factors including high risk of windthrow and poor natural regeneration, typically below 20 % (Dhubháin et al. 2005;

Dhubháin 2010). One study in Northern Ireland demonstrated that successful regeneration is possible within second rotation coniferous plantations but the method can only be implemented at certain preselected sites (Cooper et al. 2008). It is necessary to examine alternative methods to address the negative biodiversity impact of forest harvesting at a national scale.

Although the use of CCF in Ireland is likely to be limited at best, other actions can be taken to help maintain habitat provision services of plantation forests following harvesting. The Forest Biodiversity Guidelines have stressed the importance of managing forests in rotation, creating a diversity of age structures at a spatial scale. Therefore, provided that the area of clear felling is not too extensive, adjacent mature stands are capable of acting as a refuge for displaced biodiversity. Furthermore, mature stands can act as a source of propagules to colonise younger forest stands where necessary (Forest Service 2000). Creating a mosaic of stand ages at a landscape level is likely to have the greatest positive impact on biodiversity, as the value of any given stand to different taxa changes along with the forest cycle (Smith et al. 2009). For example, mature stands confer the greatest benefit to spiders, due to greater structural complexity and a greater amount of deadwood (Oxbrough et al. 2005), while young pre-thicket stands provide greater benefit to bird species, due to greater shrub cover available for nesting and foraging sites (Wilson et al. 2006, 2009). Creating a mosaic of stand ages, both at the forest and landscape level, has been shown to be highly beneficial to forest biodiversity by maintaining suitable habitat for multiple taxa, across both spatial and temporal scale (Lindenmayer et al. 2006) A number of strategies are also available to ensure clear felled stands continue to provide some degree of habitat provision following harvesting. The deadwood component of Irish plantation forests is typically poor throughout the forest cycle, approximately 40–50 % of the volume recorded in native woodlands, as it often actively removed (Sweeney et al. 2010b). This trend continues post harvesting, as the majority of harvesting residue removed from site and utilised as biofuel (Hoyne and Thomas 2001; Kent et al. 2011). Given the documented importance of deadwood to biodiversity in Sitka spruce plantation forests across the British Isles (Humphrey et al. 2002a; Oxbrough et al. 2005), leaving debris on site following harvesting is likely to provide some benefit to biodiversity (Gunnarsson et al. 2004). On a similar note, structural retention of a number of mature trees during the harvesting phase, both live trees and standing deadwood, has been recommended to improve bird diversity on clear fell sites, particularly benefiting secondary cavity nesting species, such as tits (O'Halloran et al. 2002; Baker et al. 2015). However, forest managers are slow to adopt any strategy which includes retaining deadwood, due to a potential increase in the risk of bark beetle outbreaks as well as safety concerns in the case of standing deadwood.

Forest age and biodiversity

The age of a forest or stand has a strong influence on its habitat provision services. As productive plantations are ultimately grown to be harvested, the age at which harvesting occurs can have significant impacts on biodiversity (Brockerhoff et al. 2008). As with thinning, the age at which plantations are harvested is decided based on economic factors, with the financial age of maturity typically occurring much earlier than the ecologically optimum age of greatest biodiversity (Hartley 2002). For Sitka spruce plantations in Ireland, financial maturity is typically reached at between 38 and 50 years, depending on site conditions (Philips 2011). However, a number of studies have suggested that extending the rotation length would create more structurally complex stands to benefit plantation forest biodiversity, while also improving the provision of other ecosystems services (Bertomeu and Romero 2001; Carnus et al. 2006; Lindenmayer et al. 2006). Older plantations are typically of greater benefit to biodiversity, as they are far more structurally complex than newly established plantations, which benefits forest species. Furthermore, colonisation of older plantation by forest species is likely to have progressed further than in young plantations if the previous land use was not forest (Brockerhoff et al. 2008). However, for Irish plantation forests, simply increasing the rotation length is unlikely to provide significant benefits to forest biodiversity, in the absence of active management of forest structure, aimed at improving conditions for forest species. Therefore, the management practices discussed previously would need to be implemented, along with extending the age at which trees are eventually harvested. However, the economic loss associated with lengthening the rotation time of forests must be considered, along with the benefit to biodiversity. Private forest managers, which make up a considerable proportion of the Irish forest estate, may be reluctant to implement management strategies aimed at improving biodiversity, as increasing the length of time before trees are harvested is often viewed as an unacceptable risk, which incurs a financial cost on their part (Taylor and Fortson 1991).

Conclusions

Ireland's long history of deforestation of native woodlands has resulted in a real and significant loss in the provision of forest ecosystem services. Both in the Republic and Northern Ireland, native woodlands are scarce, degraded, and imbedded in a matrix of intensively managed agricultural pasture. As a result, productive plantation forests, initially planted for the sole purpose of wood production, must provide the wide range of ecosystem services which are no longer being provided by native woodlands. While it has been shown that Irish plantation forests provide habitat for a number of forest species, including species of significant conservation concern, it is evident that the current state of Irish plantations is not optimal for biodiversity conservation. However, a number of management options exist which can be utilised to improve plantation forests biodiversity value. These steps begin at the afforestation phase, ensuring plantations are established on degraded, low biodiversity habitats, and retaining any complementary habitats such as hedgerows. Beyond this, a wide range of sympathetic management practices can be considered, at spatial and temporal scale, ranging from stand level to landscape level. However, these management decisions must be based on solid scientific research. Although the forest biodiversity guidelines represent a good starting point for improving plantation forest biodiversity value, it is clear that the usefulness of many management actions is not sufficiently supported by evidence. More research is necessary to determine the optimal mixed species ratio, thinning regime and rotation length to maximise biodiversity conservation within plantation forests. Furthermore, while there has been considerable research into plantation forest biodiversity in Ireland, this has primarily focused on the stand and forest level. As afforestation continues across Ireland in order to meet the sustainability objectives of EU 2020, further research is required to determine the impact of plantation forests at the overall landscape level, and their influence on adjacent habitats.

While this review has focused almost entirely on the island of Ireland, the fundamental principles of managing plantations for the purpose of conservation, in unison with production, hold true at a global level. As plantation forests continue to expand rapidly at a global level, and natural forest cover declines, the Irish situation may be replicated in other regions across the world, where exotic plantations become dominant within the forest landscape. However, this may prove beneficial to forest biodiversity if forests are sustainably managed to fulfil multiple roles, rather than solely for the production of timber and biofuel. In this regard, there must be meaningful engagement from all forest stakeholders, from conservationists to managers, to ensure that management changes are implemented successfully without unacceptable economic losses.

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