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RESEARCH ARTICLE

Spatial targeting of woodland creation can reduce the colonisation credit of woodland plants

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Abstract

1. Colonisation credit refers to the temporal lag between positive conservation actions and species' responses and may be one of the reasons we fail to meet short-term conservation targets. This is particularly evident in woodlands which take decades to develop and harbour slow colonising species. Given global objectives to increase woodland cover, it is important to know the timeframe within which colonisation credit will be fulfilled.
2. The colonisation of woodland plants was examined in recent woodlands, created between 15 and 80 years ago, and located adjacent or isolated from existing ancient woodlands. Colonisation credit was calculated as the proportion of understory woodland plant species in the nearest ancient woodland which had not colonised recent woodlands. Looking at individual species traits also allowed us to tease apart their impact on the species colonisation and establishment ability.
3. Spatial adjacency between created and ancient woodland reduced colonisation credit by an average of 28%, and more mature created woodlands (50–80 years old) had fulfilled 24% more of their colonisation credit on average than younger created woodlands (15–21 years old). However, mature woodlands created adjacent to ancient woodlands had still only been colonised by an average of 72% of the available species pool.
4. Plants which had reached adjacent created woodlands were dispersed by a range of mechanisms, where those that had reached more isolated sites were largely dispersed by birds or mammals. Low community weighted mean shade tolerance, high community weighted nutrient affiliation, and the dominance of *Hedera helix* suggest that competition from dominant natives may be preventing certain species establishing in new woodlands.
5. This research demonstrates the need to account for appropriate time-lags when setting biodiversity targets, with most sites still displaying colonisation credit decades after they were created. The results also indicate that spatially targeting woodland creation adjacent to species-rich mature woodlands should be prioritised. Still, poor local habitat conditions may lead to the dominance of specific competitors which prevent a range of other species from establishing. Local

management interventions such as translocations and tree thinning may ameliorate this but further research is needed.

KEYWORDS
colonisation credit, dispersal mechanisms, ecological time-lags, restoration ecology, woodland creation, woodland plants

1 | INTRODUCTION

Ecological time-lags—the delays in ecological responses to landscape change—have been observed globally across a range of ecosystems (Jackson & Sax, 2010; Kuussaari et al., 2009; Lira et al., 2019). Colonisation credit refers to the temporal lag between positive conservation action, such as habitat creation and restoration, and species' response (Jackson & Sax, 2010). This credit has been observed in a wide range of species and ecosystems, and found to operate over a broad range of spatial and temporal scales (Lira et al., 2019). Colonisation credit is driven by a range of mechanisms, but is especially evident in small populations of specialist species which struggle to reach slow developing habitat (Lira et al., 2019).

Woodland (used here as a synonym for forest) is a habitat particularly affected by long time-lags, especially colonisation credits. This is because trees take decades to develop structurally (Fuentes-Montemayor et al., 2021), and woodland specialist species are particularly slow colonisers (Brouwers & Newton, 2009; Honnay et al., 1999). There are global efforts to create and restore woodland habitat (Bonn Challenge, 2019), however, due to the slow development of woodland and the isolated nature of remnant woodland patches (Haddad et al., 2015), long time-lags between woodland creation and biodiversity benefits should be expected. Woodland understory herbaceous plants are an interesting case study in this regard. Due to their adaptations of shade tolerance, long life, and large seeds (Whigham, 2004), these plants rely on woodlands to out compete landscape generalists which would otherwise dominate. Woodland plant species are also exceptionally slow colonisers of newly created woodlands, as diaspores struggle to reach isolated patches (Honnay, Verheyen, et al., 2002). Further, initial biodiversity increases in plant communities after woodland creation may represent different communities to those resulting after decades of woodland development. After woodland creation, light demanding landscape generalists have been shown to quickly colonise. However, it is expected that these will slowly be outcompeted by shade tolerant woodland specialist plants before dying out and being completely replaced (Harmer et al., 2001). This means that any short-term biodiversity increases may not persist in the long term and may not signal any later colonisation by woodland specialist plants. It has been suggested that colonisation credit could be masking our ability to observe progress towards conservation success (Watts et al., 2020). Thus, a greater understanding of the drivers of colonisation credit will give us an opportunity to account for future species' responses and to intervene to reduce these temporal lags and speed up the realisation of biodiversity benefits.

There is a rich history of study looking at how specialist plants colonise recently created woodlands (Brunet & Von Oheimb, 1998; Honnay, Bossuyt, et al., 2002; Peterken & Game, 1984), and more recently colonisation credit has been explicitly considered (Brunet et al., 2021; Kolk et al., 2017). Calculating the colonisation credit of woodland understory plants could be done in many ways, including comparing the observed species richness to that of nearby suitable habitat, or by modelling species richness against past and present landscape patterns (Lira et al., 2019). Naaf and Kolk (2015) inferred from recent woodlands in Germany that some colonisation credit in isolated woodlands remained after centuries, when compared to similar ancient woodlands in the area. Recently, Brunet et al. (2021) showed how this process is sped up in recent woodlands contiguous to ancient neighbours, although after 80 years colonisation credit was still not fulfilled. As these studies were large scale, they compared the species richness of recent woodlands to a baseline species richness of nearby ancient woodlands. Thus, woodlands were deemed to have fulfilled their colonisation credit if they had an equal species richness to their older neighbouring woodlands, although species identities and community composition could be different.

The present research attempts to further unpick the colonisation credit of recent woodlands by focusing on species identity and whether the species present in ancient woodlands have either succeeded or failed to colonise nearby recent woodlands. The dispersal mechanisms and habitat requirements of these plants are then further explored. From this we can identify which traits may be limiting species colonising and establishing in more or less isolated recent woodlands. We used an approach aligned with a natural experiment design by using paired blocks of planted woodlands within the Isle of Wight, each containing an 'adjacent created woodland' and an 'isolated created woodland'. Adjacent created woodlands were recent woodlands created adjacent to an ancient woodland (assumed to be in existence since the year 1600) (Spencer & Kirby, 1992), where isolated created woodlands were recent woodlands created at least 100 m away from any ancient woodland. Adjacent and isolated created woodlands were always of similar age within blocks but varied in age between blocks with a range of 15 and 80 years. This allowed us to observe how quickly colonisation credit can be fulfilled, and how the spatial proximity of adjacent ancient woodlands might speed this up. We expected the colonisation credit of recent woodlands to take decades to fulfil due to the slow colonisation time of most woodland plants and the length of time it takes new woodlands to develop. We were not sure if connecting newly created woodlands to existing source woodlands would ameliorate this fully, but we did expect colonisation credit to be higher in younger isolated created woodlands and lower in older adjacent created woodlands. Lastly, we expected the colonisation of woodland plants in isolated woodlands to be driven by mammals and birds as their primary dispersal vector, where adjacent created woodlands may have been colonised by plants with a range of long and shorter distance dispersal mechanisms.

2 | MATERIALS AND METHODS

2.1 | Study region and site selection

The study took place on the Isle of Wight in the south of England, where there have been recent efforts to spatially target woodland creation to extend ancient existing woodland (Quine & Watts, 2009) along with ongoing untargeted woodland creation. Taken together, these approximate a natural experimental design: with approximately equal areas of woodland planted either adjacent to or isolated from ancient woodland sites. There is also no wild deer population on the Isle of Wight, which significantly reduces the grazing pressure on recently planted woodlands. Woodlands were planted with native broadleaf species similar to those found in the nearby ancient woodlands. Planted species included *Fraxinus excelsior*, *Fagus sylvatica*, *Acer campestre*, *Quercus robur* and *Corylus avellana*. But many of the woodlands had subsequently been colonised by *Salix viminalis* and *Crataegus monogyna*.

Woodlands were selected in blocks of three, each block including one ancient woodland, one recent woodland planted adjacent to the ancient woodland, and a second recent woodland of a similar age and size planted in isolation (on average 494 m from the source woodland, range: 129–887 m). The ages of recent woodlands were discerned using historical maps and ranged between 80 and 15 years old, where their sizes ranged between 0.2 and 2 ha. In total, eight blocks were identified (Figure 1), although one ('America') only included an ancient woodland and an adjacent created woodland, as the isolated counterpart was not found to be wooded on arrival. Due to proximity, the ancient woodland of 'Great park a' was used as the counterpart to the isolated woodland of 'Great park b' (Figure 1). Recent woodlands were separated into two age categories; mature created woodlands were those planted between 1940 and 1970 (50–80 years old), whereas young created woodlands were those planted between 1999 and 2005 (15–21 years old), relatively few woodlands were planted between 1970 and 1999 and so these are not represented here. The study sites ranged between 2 and 87 m a.s.l., with an average summer temperature between 13°C and 20°C, an average winter temperature between 3°C and 9°C and average precipitation of around 870 mm (Met Office, 2020). The northern half of the island is largely made up of clays where the southern half is made up of sandstones.

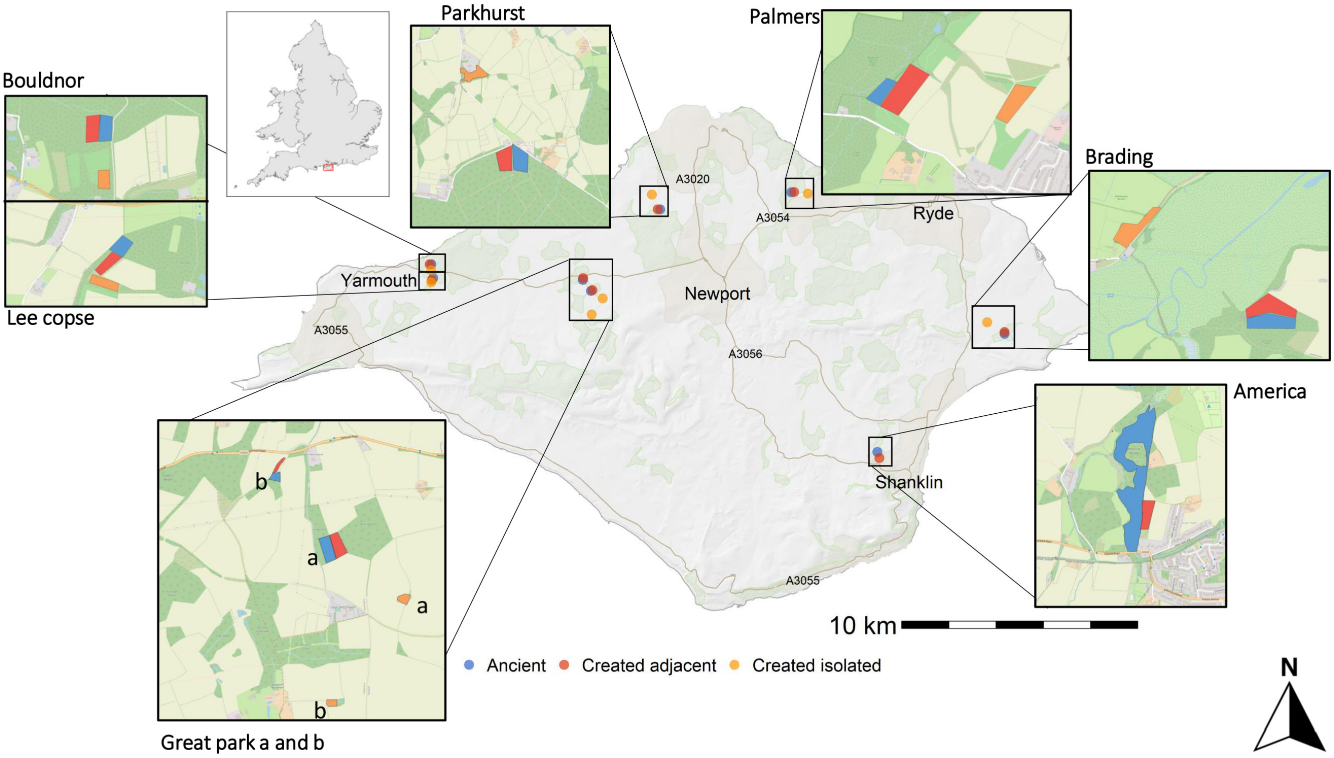

FIGURE 1 Map of the 23 study sites in the Isle of Wight made up of 8 ancient woodlands and 15 recent woodlands. These are organised into eight blocs. Mature woodlands first appeared on maps between 1940 and 1970, where young woodlands first appeared around the start of the new millennium (1999–2005). The base map is provided by the OS zoomstack, where dark green patches represent other woodland.

2.2 | Field surveys

Field surveys were carried out in July 2021. All woodlands were sampled systematically using six 1 m^2 quadrats. In adjacent created woodlands, two quadrats were placed at 25% and 75% of the length of the edge adjacent to the source woodland 15 m in towards the centre, two were placed 20 m either side of the woodland centroid, parallel to the adjacent edge, and two were placed 15 m in from the far edge opposite the quadrats near the adjacent woodland. In isolated created woodlands the same pattern was used mimicking the orientation of the adjacent created woodland. Where source woodlands were significantly bigger than the adjacent created woodland, far quadrats in the source woodland were placed equidistant to the far quadrats in the adjacent created woodland. Within each quadrat all vascular non-woody plants were recorded along with their percentage cover, estimated subjectively by dividing the quadrat into 20 cm^2 cells to aid the observer. Docks and brambles were aggregated into *Rumex* and *Rubus* spp. respectively. Plant species were separated into woodland plants or non-woodland plants and assigned an Ellenberg Light (L) Nitrogen (N) and pH values based on their habitat preferences as defined by PLANTATT (Hill et al., 2004). The mean seed weight and dispersal strategy of each plant was also recorded from the EcoFlora database (Fitter & Peat, 1994). The described field work required no licences or permissions.

2.3 | Statistical analysis

Data were analysed using R version 4.1.0 (R Core Team, 2021). Woodland level analyses were performed by aggregating the quadrats of each plot, and generalised linear mixed models (GLMMs) were constructed using the *lme4* package (Bates et al., 2014) with block as a random intercept.

2.3.1 | Colonisation credit

Colonisation credit was analysed using a GLMM assuming a binomial error distribution. Here, the number of plants available in the ancient woodland acted as the number of trials, and the number of plants shared between the recent woodland and the ancient woodland acted as successful colonisations. This model included the age of the recent woodland as a categorical predictor variable including young created woodlands and mature created woodlands (described above), and whether the recent woodland was created adjacent to the ancient woodland or isolated from the ancient woodland as a second categorial predictor variable. An interaction term between the two predictor variables (age and distance) was also tested. The isolated woodland of the block 'Great park b' was paired with the ancient woodland of 'Great park a' due to it being closer to this than the ancient woodland of 'Great park b'.

2.3.2 | Community weighted mean trait value

The community weighted mean (CWM) L, N and pH values were calculated for each created woodland to test how plant communities vary in functional diversity. These values were calculated using all understory plant species to get a picture of local habitat conditions that may be preventing the establishment of understory woodland plant species. The methods of Garnier et al. (2004) were followed to calculate these values, by summing the proportional cover of all species multiplied by their respective trait value. LMMs were then built with binary predictor of adjacency to an ancient woodland and a categorical predictor of woodland age (young or mature). Ancient woodlands were not included in the statistical analysis, although they are included in the result plots for reference. The CWM seed weight (mg) value was calculated for just woodland understory plants in the recent woodlands, this was to assess if heavier seeds were limiting the dispersal of certain woodland species. This was tested using an LMM with the same predictor variables as described above (adjacency and age).

3 | RESULTS

In total, 48 understory herbaceous plant species were found; of these 28 were recorded in source woodlands, 28 were recorded in created adjacent woodlands and 23 were recorded in created isolated woods. There were 19 woodland plant species found; 17 of these were recorded in ancient woodlands, 13 were recorded in recent adjacent woodlands and 8 were recorded in recent isolated woodlands. There was an average of 5.25 woodland plant species in ancient woodlands and 2.8 in created woodlands. Species numbers are summarised across adjacency status and age groups in Table 1. Many of the recent sites were dominated

TABLE 1 Showing the distribution of plants across different age and isolation categories. Plants are also subset into woodland plants. Young woodlands were created between 1995 and 2001, where mature woodlands were created between 1940 and 1970. Adjacent woodlands were created adjacent to an ancient woodland, where isolated woodlands were not.

	Ancient woodland	Mature created adjacent woodland	Young created adjacent woodland	Mature created isolated woodland	Young created isolated woodland
Total plant species richness	28	22	27	12	23
Woodland plant species richness	17	10	6	6	5

by ivy (*Hedera helix*), but other more specialist woodland plants such as *Hyacinthoides non-scripta* had also colonised at lower rates (Figure 2).

There was no significant interaction between the age of woodlands and their adjacency to ancient woodlands when predicting colonisation credit, and so this term was removed from the model. Mature created woodlands had fulfilled 24% more of their colonisation credit than young created woodlands ($p=0.05$, SE$=0.49$, $z=1.9$). However, mature created woodlands had still only fulfilled 58% of their colonisation credit on average. Colonisation credit was significantly reduced by adjacency on average by 28% (Figure 3), this was only significant at the 10% level ($p=0.06$, SE$=0.48$, $z=1.86$). Even mature adjacent created woodlands had only fulfilled 72% of their colonisation credit on average. One mature adjacent created woodland did have a colonisation credit of zero, although this resided next to a particularly depauperate ancient woodland. Of the 19 woodland plant species used in this analysis, seven were dispersed by mammals and/or birds, two were dispersed by ants, four by wind and six were unspecialised. Of the 16 species found in adjacent recent woodlands only six were dispersed by animals, the others were either self-dispersed, carried by wind or carried by ants. In contrast, six out of the eight species found in isolated woodlands were dispersed by mammals or birds.

The CWM L value was not significantly affected by adjacency ($p=0.87$, $t=0.16$, df$=8.59$) or age ($p=0.21$, $t=-161$, df$=7.60$). Interestingly young adjacent created woodlands had a lower CWM L value than young isolated created woodlands, where mature adjacent created woodlands had a higher CWM L value than mature isolated created woodlands, although this interaction was not significant (Figure 4). CWM N and pH values were significantly affected by adjacency but not woodland age. Woodlands created adjacent to ancient woodlands had lower N values ($p=0.008$, $t=-3.63$, df$=6.8$) (Figure 5) and lower pH values ($p=0.01$, $t=-3.45$, df$=5.8$) (Figure 6). Neither of these values were significantly affected by woodland age. CWM seed weight (mg) was not significantly affected by age or adjacency.

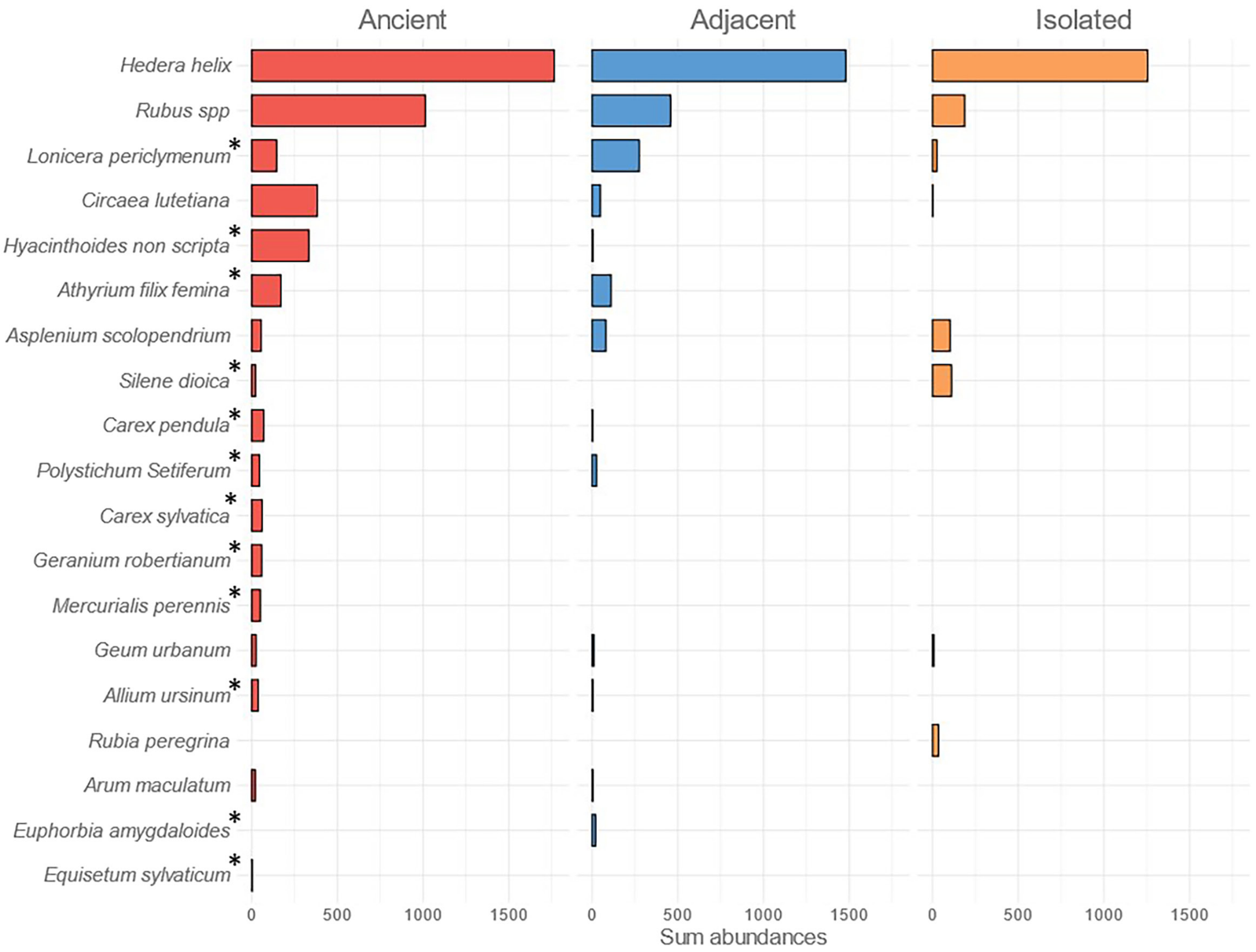

FIGURE 2 Sum abundances of woodland plant species found across recent woodlands separated by age and the degree of isolation. This plot also shows the dominance of Hedera helix in more mature woodlands.

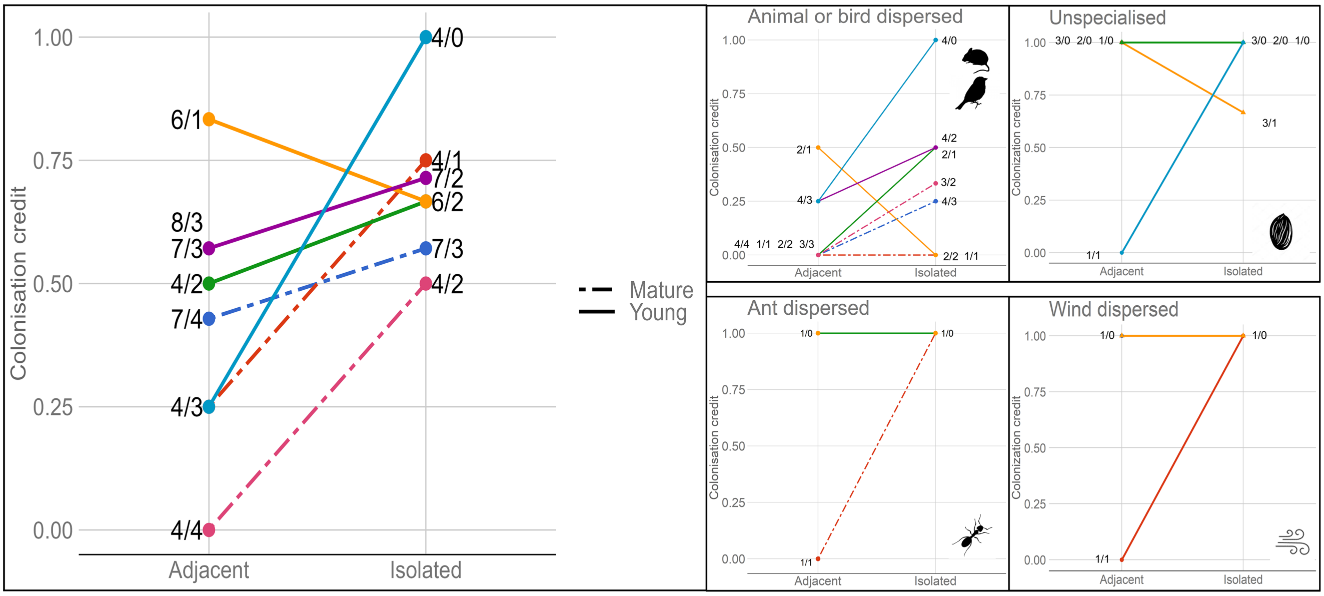

FIGURE 3 Pairwise colonisation credit between recent woodlands planted adjacent to an ancient woodland and those planted in isolation. These were separated into mature (50–80 years old) and young (16–22 years old) as denoted by shape. Numbers left of the forward slash are the amount of woodland plant species available in the nearby ancient woodland, where numbers right of the forward slash are the amount of these species that have made it to the created woodland. Adjacent woodlands had a significantly lower colonisation credit than isolated woodlands. These were separated into dispersal types also, mammals and birds, ants, wind and unspecialised.

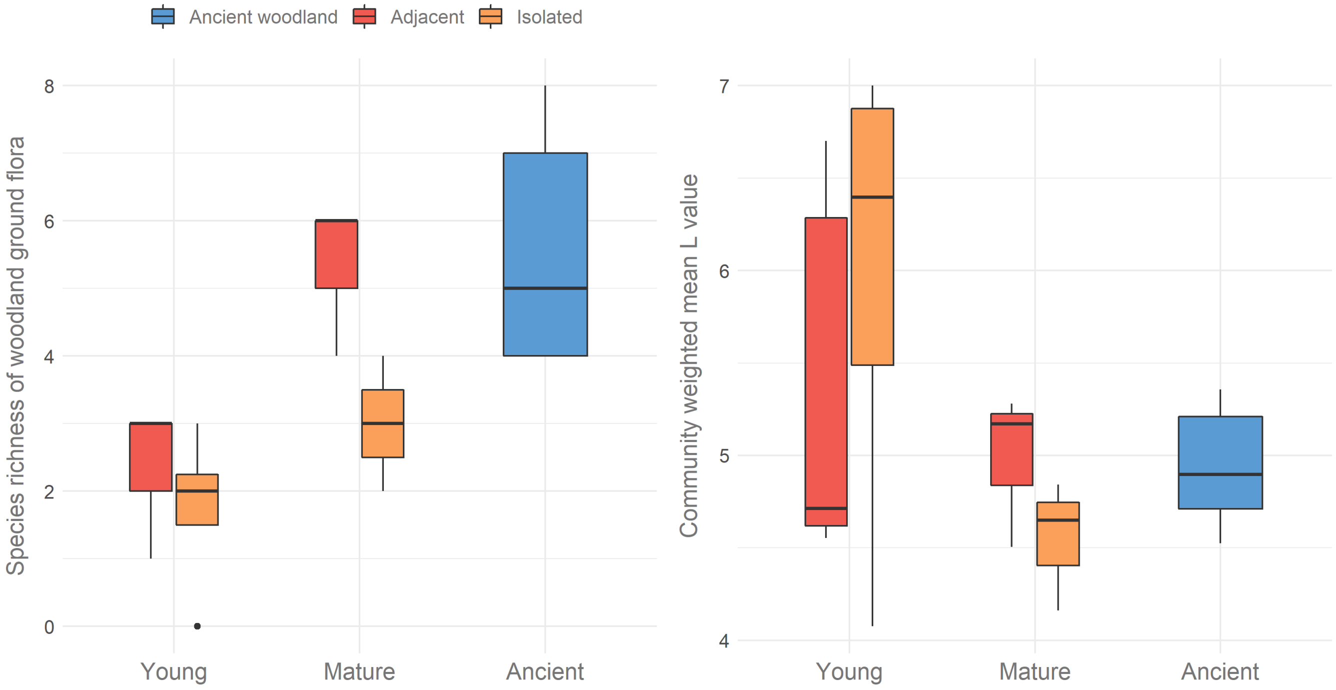

FIGURE 4 The community weighted mean Ellenberg L value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50–80 years of age, and ancient woodlands are believed to have existed since the 1600s.

4 | DISCUSSION

Using the approach of a natural experiment design this study has shown that the colonisation credit of woodland plants remains up to 80 years after woodland creation. Creating woodlands adjacent to ancient woodland sources does speed up this process partially (though only significant at the 10% level) but is not enough to completely fulfil colonisation credit within a meaningful timeframe. These results concur with other work looking at ecological time lags in temperate woodlands: Naaf and Kolk (2015) found that

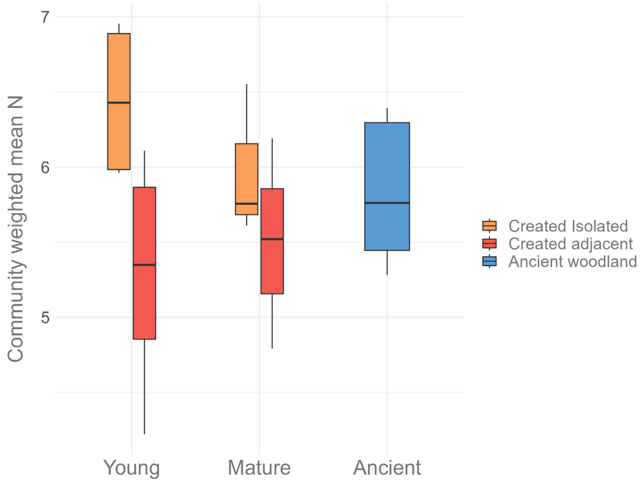

FIGURE 5 The community weighted mean Ellenberg N value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50–80 years of age, and ancient woodlands are believed to have existed since the 1600s.

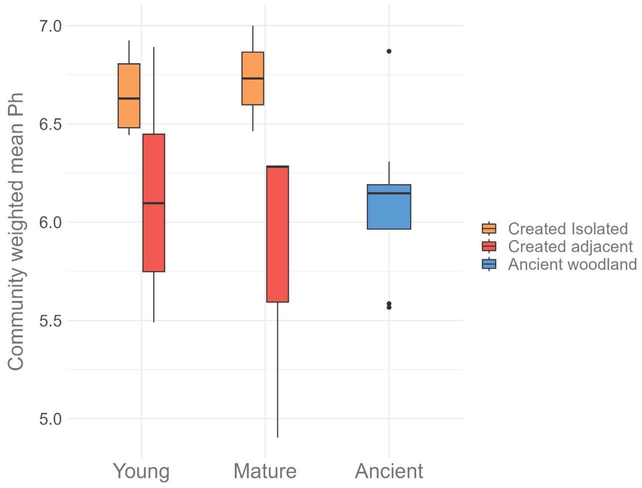

FIGURE 6 The community weighted mean Ellenberg pH value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50–80 years of age, and ancient woodlands are believed to have existed since the 1600s.

colonisation credit could last centuries. This extended colonisation credit is a testament to the importance of considering ecological lags when judging conservation outcomes (Watts et al., 2020), and means that other markers of success may be needed to judge whether management interventions will be necessary in the long-term. These results may also mean that further management is needed to increase understory woodland plant species richness after woodland creation.

The colonisation of woodland plants into recently created woodlands could be limited by two factors: (1) habitat suitability, and (2) dispersal distances. Woodlands take decades to develop structurally and young created woodlands often have higher stem densities and provide more shade than ancient woodland counterparts (Fuentes-Montemayor et al., 2021). Woodland plants need the shade provided by woodland canopies to outcompete landscape generalists (Whigham, 2004), however too much shade can lead to the overcrowding by native dominants such as *Hedera helix* (Marrs et al., 2013). Woodland plants are also extremely slow dispersers (Honnay, Bossuyt, et al., 2002; Whigham, 2004), and so dispersal limitations are also likely to cause the slow colonisation of recent woodlands, particularly in isolated patches. General principles suggest that woodlands closer to ancient woodland sources would fulfil their colonisation credit faster than those planted in isolation, and this was true to an extent. However, even in mature adjacent created woodlands there was still a substantial colonisation credit. This alongside the dominance of *Salix viminalis* suggests that habitat quality in recent woodlands may be limiting their colonisation credit being fulfilled.

The dominance of a particularly shade-tolerant species which outcompetes other potential woodland species could be considered a negative milestone in restoration timelines. Many of the recent woodlands in this study had been completely dominated by *Salix viminalis* which blocked out almost all light. As a result, ivy (*Hedera helix*) dominated the ground of most recent woodlands. This is supported by the low CWM L values of the more mature created woodlands, where ivy was often ubiquitous across the ground. Creating woodlands adjacent to existing source woodlands did counteract this slightly by providing more plant species to compete against the ivy. This explains why the CWM L values in mature created woodlands were higher if they were created adjacent to an existing ancient woodland. Young adjacent created woodlands had a lower CWM L value than their isolated counterparts, this was expected because the adjacent source woodland was providing the shade which the early-stage canopy of the created woodland could not (Harmer et al., 2001). It has been shown that traditional management techniques such as coppicing significantly increase the abundance and richness of woodland plant species in the understory (Barkham, 1992; Fuller & Warren, 1993; Kirby et al., 2017). Some of the woodlands of this study are too young to be coppiced, however, thinning to counteract the overshading of *Salix viminalis* could increase the biodiversity of ground flora by allowing a more diverse range of plants to compete with the ivy (Kirby & Thomas, 2017). The dominance of plants such as ivy, or the presence of trees which block out light may be a good milestone to assess this by.

The high CWM N and pH values of isolated woodlands also point to more generalist plant species outcompeting woodland specialists. Woodland plants have been shown to favour medium nutrient levels and neutral pH conditions (Hermy et al., 1999), this is also demonstrated by the CWM N and pH values of ancient woodlands in this study (Figures 5 and 6). In isolated woodlands the presence of nitrophilous competitors such as *Urtica dioica* alongside the low abundance of specialist woodland plants leads to higher CWM N and pH values. These values may be lower in adjacent created woodlands as more woodland plants are able to reach them to compete against landscape generalists.

Plants dispersed by mammals and birds were routinely reaching adjacent *and* isolated created sites, where plants dispersed by wind, ants or their own mechanisms tended to only reach adjacent sites. This suggests that dispersal mechanisms also limit the fulfilment of colonisation credit, as mammals and birds can disperse plant species over long distances (Brunet & Von Oheimb, 1998). Watts et al. (2020) suggest the use of 'milestone species' to assess whether a restoration action is on course to fulfil its potential. In the case of new woodlands, initial milestone species could be those with longer ranged dispersal mechanisms, as these are expected to reach new habitat sooner. Later and perhaps more important milestone species would be those dispersed by short range dispersal mechanisms. If, after some years these have not made it to a newly created site, it is likely that they never will as the site is too isolated. In this case further management interventions may be needed, these could take the form of translocations or seeding. These interventions have been shown to increase the establishment of native plant species in restored sites (Orrock et al., 2023), and have also been shown to influence the structure of non-plant species communities (Paraskevopoulos et al., 2023).

The source woodlands included in this study happened to be relatively species poor. This could either be a result of the lack of recent management that has shaped ancient woodlands over the centuries, or the small nature of these isolated fragments (Rackham, 2008). The species pool available to colonise new habitat patches is known to play an important role in how a focal site is colonised (Cornell & Harrison, 2014). Catano et al. (2021) found that seeding a restored site with a larger species pool steepens the species area curve due the spatial aggregation of new species. This further supports the use of seeding or translocation interventions when recent woodlands are not being colonised. If the cause of this is not the isolation of the new woodland but in fact the poor species pool available, then management interventions may be the only way to increase diversity in a recent woodland.

5 | CONCLUSIONS

The colonisation credit of specialist plants in recently created woodlands takes decades to fulfil and remains up to 80 years after creation. Spatially targeting woodland creation adjacent to existing ancient woodlands does reduce colonisation credit faster but does not fulfil it in a meaningful time frame. The use of a natural experimental design allowed us to focus in on which species are driving these long time-lags after woodland creation. Early signs of success after creating a new woodland may be the arrival of specialist plants which are dispersed by long-range mechanisms. These species should make it to more isolated sites as they are less dispersal limited. What *would* limit these species is poor local habitat conditions, overshading may cause more shade tolerant species to dominate the woodland floor, and under shading may mean that landscape generalists move in an outcompete woodland species. If there are conditions such as these, extra management interventions may be needed such a thinning or supplementary tree planting. The arrival of species dispersed over shorter distances may be an appropriate second milestone from which to judge woodland creation by. If these species arrive and establish it would suggest that dispersal distance is not a limiting factor in fulfilling colonisation credit. If these species do not start to arrive when habitat conditions are suitable it may suggest the need for management interventions such as translocations.

Ecological time-lags in woodland ecosystems are exceptionally long, these must be considered when planning restoration projects, and success needs to be judged over appropriate timeframes or by identifiable early milestones.

AUTHOR CONTRIBUTIONS

The study was initially conceived by Samuel Hughes and Kevin Watts on a trip to the isle of wight to scope potential sites. Samuel Hughes, Kevin Watts, Guy Ziv and Bill Kunin all significantly contributed to study design. Samuel Hughes collected and analysed the data. All authors contributed to and approved manuscript drafts.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data behind this research is archived in UK CEH Environmental Information Data Centre: https://doi.org/10.5285/7c2b2878-1d15-4ddd-9d7e-cf50bd65f652 (Hughes et al., 2023).

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