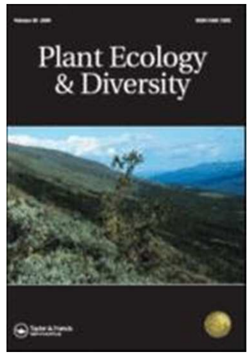

Transplanting the leafy liverwort Herbertus hutchinsiae: A suitable conservation tool to maintain oceanic-montane liverwort-rich heath?

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Abstract

Background: Translocating plants for conservation purposes can be a useful tool to enhance existing populations, restore lost populations, or create new ones, but has rarely been done for bryophytes, especially liverworts.

Aims: Here, the leafy liverwort *Herbertus hutchinsiae*, a representative species of oceanic-montane liverwort-rich heath, was translocated to unoccupied habitat within its current range, to establish whether its restricted distribution is due to habitat- or dispersal limitation.

Methods: Feasibility of establishing new populations outside the current distribution range was assessed, to test the suitability of the species for assisted colonisation. Furthermore, transplants were grown at degraded sites where the species had declined to assess potential for restoration.

Results: Although maximal growth rates occurred within-range, transplants grew at all sites, indicating that the species could be dispersal limited; a conclusion supported by distribution modelling.

Conclusions: Assisted colonisation is thus an option for this species to overcome dispersal limitation and to track future climate space. Reinforcement of populations at degraded sites is only recommended if the pressure causing the degradation has been removed. These findings provide an evidence base for practical conservation management.

Keywords: assisted colonisation, bryophytes, dispersal limitation, population reinforcement, reintroduction.

Introduction

Environmental change alters plant communities (e.g., Stevens et al. 2004; Smart et al. 2006), with climate change being a major issue in global biodiversity changes (Hannah et al. 2007), but other environmental drivers also playing their part. While the overall climate in British Isles has become warmer and wetter (Barnett et al. 2006), the vegetation of the UK uplands (all areas above enclosed farmland and generally above ca. 300 m a.s.l.) has also been subjected to overgrazing, anthropogenic burning and atmospheric deposition of nitrogen and sulphur (Barnett et al. 2006; RoTAP 2012). When these interacting drivers cause habitat degradation and fragmentation, this can have very negative effects on some species, particularly specialist species with low dispersal and colonisation abilities (Travis 2003) and species populations with low genetic diversity that may not be able to adapt to environmental changes *in situ* (Skelly et al. 2007).

Translocation (hereafter transplantation) may offer a management opportunity for these specialist species to aid their dispersal, increase existing populations or treat inbreeding depression ('reinforcement': IUCN/SSC 2013), and also to 'reintroduce' a species to areas within its range where it previously existed but has disappeared (IUCN/SSC 2013). More recently, the concept of moving species beyond their current range to reach future suitable climate space or enhance their ability to reach such space by overcoming dispersal barriers, has been debated as a potential conservation management tool (e.g., Brooker et al. 2011; Hewitt et al. 2011). This process is known as assisted colonisation, amongst other names (see IUCN/SSC 2013; National Species Reintroduction Forum 2014a,b). While the main benefits are obviously the protection of biodiversity and prevention of extinction, concerns include species becoming invasive out of their known range, the impact on donor populations and the use of assisted colonisation as a substitute for other conservation efforts (Hewitt et al. 2011; IUCN/SSC 2013). There is clearly a need for research in this area, for example there is a lack of practical trials of transplant methods, specifically for species most likely to be impacted by climate change (Brooker et al. 2011). Some bryophytes (mosses, liverworts and hornworts) are vulnerable to environmental changes, e.g. pollution (Bates and Preston 2011) as they often occupy patchy habitats, and consist of comparably small populations with restricted dispersal abilities (Söderström and Herben 1997).

Oceanic-montane liverwort-rich heath (hereafter 'liverwort heath' or 'the community') is a plant community containing liverwort species likely to be impacted by environmental change (Flagmeier et al. 2014). The community only occurs in the British Isles and Norway, with Scotland being home to the most species-rich stands (Averis 1992; Paton 1999). Within the National Vegetation Classification (NVC; Rodwell 1991), liverwort heath is classified as *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath, *Mastigophora woodsii-Herbertus aduncus* subsp. *hutchinsiae* sub-community (H21b) and the *Vaccinium myrtillus-Racomitrium lanuginosum* heath, *Bazzania tricrenata-Mylia taylorii* sub-community (H20c). It is characterised by a leafy liverwort-rich understore. Some of the liverworts also occur outside Europe, and show remarkable disjunct distributions between north-western Europe and north-western North America and/ or the Himalayas and western China (Hill et al. 1991). The narrow geographic distribution of the component leafy liverwort species, and their restriction to oceanic-montane areas, may make them particularly sensitive to climate change. They are also severely impacted by habitat changes, mainly those involving loss of shelter, like removal of dwarf shrubs or those of trampling by herbivores, which promote grass overgrowth. All of these threats have been linked to observed liverwort declines in Scotland (Flagmeier et al. 2014) and in Ireland (Holyoak 2006).

The distribution of liverwort heath is limited to areas with an oceanic climate with high rainfall (at least 220 rain days a year with > 1 mm rain per day) and even temperatures, which is amplified by topography such as north- to east-facing mountain slopes and glacial corries (Ratcliffe, 1968). However, the community seems to be much less widespread in Scotland than would be expected from these climatic requirements. Distribution modelling, based on climatic and topographic variables, has demonstrated that even in areas in Scotland and Ireland which have apparently suitable conditions, fewer of the component liverwort species than predicted occur (Averis 1992; Hodd et al. 2014). Several reasons for this were suggested. First, the species could be under-recorded, especially in remote areas; in the last decade, more records have been added (Hill et al. 2008), but these liverworts have still not been observed at some sites, despite their apparent suitability in terms of climate and/or habitat requirements. Second, the liverworts have never been outside their present ranges, which actually represent their climatic range limits. Finally, the community has once been more widespread, but has since declined due to multiple and interactive drivers of environmental change including the practice of burning as well as sheep and deer grazing, both of which result in a loss of dwarf shrubs as shelter for the liverworts (Averis 1992;

Averis 1994; Flagmeier et al. 2014). It has long been suggested that overgrazing and burning may be responsible for the restricted distribution of these specialist liverwort species (McVean and Ratcliffe 1962; Ratcliffe 1968; Birks 1973; Hobbs 1988; Rodwell 1991; Averis 1992), and some sites have been lost and/or damaged in Scotland (Hobbs 1988) as well as in Ireland (Holyoak 2006).

The ability of these liverworts to re-colonise lost habitat or establish new populations is unpredictable as they have not been observed to produce spores in the British Isles (Hill et al. 1991), and most of them do not develop specialised propagules (Paton 1999). They are able to regenerate from vegetative fragments (Flagmeier et al. 2013), but it is unclear how far these can travel; it seems unlikely that they travel far in mountain terrain (Averis 1994). In summary, it is possible that additional suitable sites in terms of habitat and climatic conditions exist, but these have not been colonised by the liverworts due to their restricted dispersal ability. Furthermore, some sites where the liverwort heath has existed in the past have been environmentally degraded. It remains unclear whether these sites could sustain populations, should liverwort propagules arrive there.

Transplantation of bryophytes as whole plants or fragments has been successfully tested for habitat restoration and other conservation purposes, including population maintenance. Gunnarsson and Söderström (2007) demonstrated the potential of transplanting *Sphagnum angermanicum* to new sites in Sweden with highest establishment rate from whole shoots. Kooijman et al (1994) re-introduced *Scorpidium scorpioides* from Ireland to sites in the Netherlands where the species had disappeared, and Rothero et al (2006) augmented the only British population of *Bryum schleicheri* var. *latifolium* with material derived from *ex situ* cultivation. Establishment of transplants from moss fragments has been successful in restoration experiments (Graf and Rochefort 2010; Aradottir 2012; Jeschke 2012). Overall however, there have been fewer transplant studies for bryophytes than for higher plants (Brooker et al. 2011).

To evaluate whether transplantation is a possible conservation tool for the liverworts of the liverwort heath, *Herbertus hutchinsiae* (Gottsche) A. Evans (Evans 1917), was chosen for a transplantation experiment and transplanted to areas within its current distribution where it has declined ('reinforcement'), and to suitable habitat within the current distribution, but where the species is not present e.g. due to dispersal limitation ('empty' localities cf.

Söderström and Herben, 1997). At the same time, the potential for assisted colonisation was tested by transplanting the species outside its current distribution range. Dispersal limitation of this species was also investigated by species distribution modelling, to enable comparison of climatically suitable land with current species occurrence. The following questions were addressed: (1) How do transplants of *H. hutchinsiae* grow (a) in suitable habitat within its current distribution, (b) in suitable habitat outside its current distribution, and (c) at degraded sites where it was once more widespread but has declined? (2) Which environmental factors influence *H. hutchinsiae* growth from transplants?

Materials and methods

The species

Herbertus hutchinsiae is an uncommon species in the British Isles (nationally scarce: occurring in fewer than 100 hectads (10 km squares)), and a European endemic. Outside the British Isles, it only occurs in Norway. Neither male plants nor sporophytes have ever been observed, and it is assumed that it does not reproduce sexually. The species occurs on shaded mountain slopes in north- or east-facing corries, cliffs and boulder fields and can also be found in montane woods and ravines. *H. hutchinsiae* is a representative and relatively frequent species of the liverwort heath community and was chosen in order to test the transplantation method without affecting the source populations of the rarer species. However, despite being locally abundant, its distribution is 'curiously patchy' (Hill et al. 1991), and it is absent from apparently suitable hills (Hill et al. 1991; Averis 1992).

Study area

The study was carried out in the Highlands of Scotland. Nine transplant sites were selected, each belonging to one of three categories: (1) sites within the current distribution of *H. hutchinsiae*, where populations are close-by, but where the species is not present (category 1); (2) sites outside the current distribution of *H. hutchinsiae* (category 2); and (3) sites where *H. hutchinsiae* is present but was once more widespread and has apparently declined due to habitat degradation (category 3). The sites in categories 1 and 2 were chosen by examination of distribution data in the National Biodiversity Network Gateway (https://data.nbn.org.uk/), to select those hectads which had records for *H. hutchinsiae* (category 1), and hectads adjacent to category 1 hectads without *H. hutchinsiae* records (category 2). Possible transplant sites within these areas were then chosen by consulting topography maps to select north-facing slopes between 200 and 600 m altitude. The two degraded sites within the currently known distribution of *H. hutchinsiae* (category 3) were selected on the basis of expert advice (G. Rothero pers. comm.) and reports (Averis 1991a; Horsfield 2006). All sites were visited prior to the experiment to confirm the suitability of the habitat for transplantation, i.e. presence of dwarf shrubs and/or large boulders for shelter. The selection process resulted in nine transplant sites (Figure 1), with four sites in category 1, three in category 2, and two in category 3 (Table 1).

Transplant growth assessment

Herbertus hutchinsiae was collected in June 2010 from one site where the species is abundant, the north-facing slopes of Liathach, a mountain in the north-west of Scotland (OS grid reference NG 948 588). Each transplant comprised of a bundle of shoots of ca. 5 cm diameter and 10 cm length. The transplants were taken off the hill, weighed, and kept in plastic bags (stored cool) until being transplanted up to one week after collection. Reference samples were also collected (see below).

Before weighing, transplant and reference samples were left to air-dry and equilibrate with ambient humidity at ~ 20 °C in the laboratory for 12 h. This amount of time was deemed appropriate for air-drying without killing the samples. Even though leafy liverworts are thought to be sensitive to drying out, experiments on *H. hutchinsiae* and several other leafy liverworts of the community showed that they can survive some drought as measured by percentage of cells alive post-treatment (Clausen, 1964), and also recover from drought (measured by carbon dioxide exchange), even after several days of air-drying (Averis 1994). The air-dried samples were weighed, and the reference samples were then oven dried at 60 °C for 24 h and weighed again. Transplant growth was assessed as change in oven-dried biomass after estimating the initial oven-dry weight using an air-dried:oven-dried weight ratio obtained from the reference samples as e.g. in McCune et al (1996) and Muir et al (2006). At the end of the experiment, stems that had grown through the garden netting in which the transplants were wrapped, were counted (see below), as an additional indicator of growth.

Transplantation in the field

Each bundle of *H. hutchinsiae* was wrapped in garden netting and then pegged into the vegetation with plastic-coated wire. At each transplant site, 30 transplants were placed within a marked out area of about 40 m x 40 m on a mountain slope with dwarf-shrub cover. Each transplant was pegged into the vegetation within an individual 25 cm x 25 cm plot, with four corners marked with garden pegs to aid re-location. The transplants were placed out in June 2010 and left an average of 424 days on site. Control transplants were established at the donor site in the context of a parallel study investigating suitable microhabitats, and they all grew.

Environmental variables

At each plot, information on the (micro-)environment was recorded by assessing the vegetation cover of dwarf-shrubs, graminoids (grasses, sedges and rushes) and bryophytes (mainly mosses). From this information each plot was later attributed to one of three microhabitat categories dominated by dwarf-shrubs, grasses or mosses. Mean vegetation height (cm) at eight localities surrounding the transplant plot was measured as a proxy for shelter. Presence of other liverworts of the community in the plots was also noted. At the end of the experiment any factors that could influence the growth of the transplants were recorded, e.g. the presence of algae on the liverworts and whether the transplant was partly overgrown by other plants or covered by plant litter.

For each site, climate (weather) information was collected. Rainfall data (average daily rainfall and number of rain days) for the duration of the experiment from the closest weather station for each site was obtained from the UK Met Office MIDAS dataset (UK Meteorological Office, 2012). Furthermore, three temperature data loggers were placed at each site to obtain a local measurement of temperature every 4 h as spot measurements. The data were used to calculate maximum, minimum and average temperature over the experimental period as well as the average temperature for February and July representing the winter and summer temperatures. A measure of relative oceanicity was calculated (Averis 1991b), as the number of rain days (> 0.1 mm precipitation) during the experimental period divided by the difference between the highest and lowest monthly mean daily temperatures in °C.

Data analysis

Data were analysed using the software package SPSS version 19 (SPSS 2010). The data on biomass change of the transplants were normally distributed with equal variances. Transplants with negative growth rates were kept in the analyses, ensuring that estimates of growth were conservative and also more realistic as they included losses of material from transplants. We used a two-tailed, paired t-test to test the null hypothesis that transplant biomass had not changed over the experimental period.

To test the differences in biomass change (hereafter also 'growth') between site categories, a general linear model (ANCOVA) was applied. The initial biomass of the transplants was included as a covariate to account for any influence of the starting weight on growth. This seemed to have an influence, therefore the relationship between the starting weight of a transplant and the growth response was investigated. The initial ANCOVA model included an interaction term (site category x initial biomass), but this was not significant, i.e. the relationship between final and initial weight did not differ between the three site categories, and so the interaction term was removed. The residuals of the model were checked for normality and equality of variance, and also for differences between sites. There was no effect of site on the residuals, therefore site was not used as a block in the model. A Sidak correction post-hoc test, suitable for investigating ANCOVA results (Field 2013), was applied to compare the differences in growth between site categories. To investigate the growth of transplants relating to their microhabitats the same model construction was used, with microhabitat category instead of site category. The number of branches (count data) between site categories was analysed using a generalised linear model (GLM) with a Poisson log-link function and subsequently compared with a Sidak post-hoc test.

Environmental variables (see above) were also compared between site categories. As the variables did not fulfil ANOVA assumptions, a non-parametric Kruskal-Wallis test was used followed by Mann-Whitney test with Bonferroni correction where effects were detected. The presence-absence variables 'presence of other liverworts', 'algae', 'overgrowth' and 'plant litter' were analysed by calculating the proportions of plots at each site with presence of the respective variable. From this, the mean value of each variable was compared between site categories as for the other environmental variables.

To assess the influence of environmental variables on transplant growth, the relationships between the environmental variables were first investigated with Pearson's correlation tests. Many variables were correlated (e.g. average temperature and maximum temperature, average rainfall and number of rain days) and thereafter only one representative of each group of correlated variables was retained in further analysis. This left four explanatory environmental variables, two describing the climate (oceanicity and mean temperature in July), and two representing the vegetation (cover of grasses and mean vegetation height). These variables were used in multiple linear regression, with a forward selection and backwards elimination stepwise regression to identify the best model. The optimal model was identified with the highest R^2 in which all independent variables with $P > 0.25$ were removed. The influence of the presence-absence environmental variables (see above) on growth were investigated using a Mann Whitney test.

Species distribution modelling using occurrence and bioclimatic variables

Modelling suitable niches enables identification of mismatches between the model and the actual current distribution, which reflect dispersal limitation. It is also a powerful tool in conservation activities for identifying suitable areas of habitat for a species. We investigated whether or not there are climatic limitations to the occurrence of *H. hutchinsiae* in large, currently unoccupied areas in Ireland and Scotland, by generating species distribution models. Presence data with resolution of 1-km or higher were used, and as predictors a set of uncorrelated bioclimatic variables were obtained from www.worldclim.org: annual mean temperature (bio1), mean diurnal range (bio2), temperature annual range (bio7), annual precipitation (bio12), and precipitation seasonality (bio15). Niche models were constructed setting several parameters to default ('auto features', convergence = 10^{-5}, maximum number of iterations = 500), while varying the prevalence (0.5, 0.6 and 0.7) and regularisation value (1, 2 and 3) to determine which combination of settings generated the best outcomes while minimizing the number of model parameters, as well as producing 'closed', bell-shaped response curves guaranteeing model transferability. As geographic background, we fitted a third-degree Trend Surface Analysis (TSA), and extracted 5000 points from the area with TSA values equal or higher than the lowest TSA value observed in a presence; this area additionally represents a well-recorded territory for bryophytes, and thus we combined recommendations by Acevedo et al (2012) and Anderson and Raza (2010). Performance of the model was assessed by means of the AUC in a ROC statistic through 10-fold cross-validation.

Results

Of the 270 transplanted bundles, 268 (99 %) were re-located at the end of the experiment. The primary question driving this study was to determine whether bundles of *H. hutchinsiae* transplanted to other sites could survive and grow there. There was, indeed, significant growth at each site in all site categories (Table 2; Figure 2). The mean transplant biomass across all sites increased significantly over the duration of the experiment by 22 % (t=-15.32, df=267, P < 0.001), from a mean oven-dry mass of 4.28 ± 0.07 to 5.24 ± 0.06 g dry mass, with individual site mean biomass increases ranging from 8% to 45%. Of the 268 transplants over the nine sites, 39 samples (15%) had negative biomass change, the greatest loss being 2.6 g (45%). On average, 10 shoots were counted growing through the netting of each transplant, the number of shoots growing though varied from 0 to 95 in a single transplant.

There was a significant negative relationship between the initial transplant weight and the absolute growth response (Figure 3), indicating that small transplants grew better than big ones. Controlling for this effect by using initial weight as a covariable in ANCOVA, growth differed significantly between site categories ($F_{2,264}$=4.90, P = 0.008; Figure 2), but not between microhabitats (data not shown). The Sidak-corrected post-hoc comparison showed that there was significant difference in growth between sites within the current range and both the sites outside the range (P = 0.030) and the sites at which the species has declined (P = 0.027). The sites outside the current range and the sites at which the species has declined did not differ significantly in growth (P = 0.978). The number of new branches also differed significantly between site categories (P <0.001), but in contrast to the biomass results, transplants at sites within the current range of *H. hutchinsiae* had fewer branches (8.55 ± 0.27; P <0.05) than those at sites outside the range (10.89 ± 0.35) or at damaged sites (9.93 ± 0.41).

Some environmental variables differed between site categories (Table 3), namely the cover of dwarf shrubs was highest at sites within the current range of *H. hutchinsiae*, whilst the cover of grasses was highest at degraded sites. Only vegetation height differed among all site categories (Table 3), with mean vegetation height highest at the sites outside the current range (category 2; 22.8 ± 0.8 cm), followed by sites within the current range (category 1) and damaged sites (category 3).

Transplant growth showed weak linear relationships with three continuous environmental variables; a positive relationship with oceanicity ($y = -0.890 + 0.141x$; $P = 0.022$; $r^2 = 0.036$), and negative relationships with mean July temperature ($y = 2.580 - 0.148x$; $P = 0.021$; $r^2 = 0.02$) and cover of grasses ($y = 1.135 - 0.008x$; $P = 0.030$; $r^2 = 0.02$), but no relationship with vegetation height. However, when all these variables and initial weight were used as predictors of growth in a stepwise multiple linear regression, the best model ($F_{2,265} = 66.15$, $P < 0.005$) included only initial weight and mean July temperature, which explained 33 % ($R^2 = 0.333$) of the variation in growth (biomass change = 4.21 - 0.492 initial weight - 0.104 mean July temperature). None of the variables measured as presence-absence (other liverworts, algae, overgrowth or plant litter) influenced growth significantly.

The best and least complex distribution model obtained with TSA background (Figure 4; beta multiplier = 2, prevalence = 0.5) had a test AUC value of 0.948 ± 0.008. The current distribution of *H. hutchinsiae* is narrower than the climatically suitable land estimated by the model in Scotland, suggesting that the liverwort could occur in several locations where it is apparently absent.

Discussion

Is the distribution of Herbertus hutchinsiae *limited by habitat availability?*

This study has shown that it is possible to successfully transplant bundles of the liverwort *H. hutchinsiae* to new sites, where it can continue to grow. There was no indigenous *H. hutchinsiae* present at most of these transplant sites; neither does the species occur in large areas of the British Isles and Scandinavia predicted to be suitable (Figure 4). Such mismatch could be the consequence of generating models without variables that would be important at finer scales, such as microtopography, due to the problems of obtaining such data. Despite this, the overall current range of H. *hutchinsiae* matches the distribution of the most suitable areas as predicted by the model quite well, but its occurrence at the local scale within that range is very limited. Thus observations from both the field transplants and the model suggest that *H. hutchinsiae* is dispersal limited rather than habitat limited, a conclusion which is supported by the fact that this species has not been observed to produce spores in Scotland and can only reproduce vegetatively. Spores tend to travel further than asexual propagules or vegetative fragments (Laaka-Lindberg et al. 2003). Vegetative reproduction is thought to help maintain local populations where sexual reproduction is rare or absent (e.g., Eckert 2001). Therefore, dispersal limitation arising from the failure to produce sporophytes could be the cause of the patchy distribution of *H. hutchinsiae*. Successful, yet rare, dispersal events followed by its 'phalanx' strategy of clonal growth would explain why the species does not fill the geographic area predicted suitable, and yet does cover relatively extensive areas in the glacial corries where it does occur. In a meta-analysis of life-history characteristics, population dynamics and habitat attributes of British bryophytes, Söderström and During (2005) found that population characteristics linked to limited dispersal rather than habitat limitations are often the cause for restricted distributions. This is indicated by the occurrence of 'empty' localities or unoccupied habitat and can only be proven through transplantation experiments (Söderström and During 2005), as in this study.

Transplanting Herbertus hutchinsiae *to overcome dispersal limitation – site selection and practical considerations*

The transplants grew at all sites, but growth was higher at sites within the current range of *H. hutchinsiae* than at sites either outside of the current range, or where the species has declined due to some form of disturbance. This suggests that even though there were no strong links with environmental variables, the environmental conditions at unoccupied habitat close to extant populations are the most suitable. *H. hutchinsiae* also grew at sites outside its current range and these sites may be at the climatic range limits of the species yet are able to support its growth. This indicates that the species is limited in its dispersal ability, preventing colonisation of these localities. Together with the sites within the current distribution this represents a wide range of sites which are available for potential increase of the number of populations. In contrast to the biomass results, transplants at sites within the current distribution of *H. hutchinsiae* had fewer branches than those at sites outside the distribution or at damaged sites, indicating that regardless of differences in overall biomass increase, growth responses such as expansion by branching is possible in all site categories.

When selecting sites for transplants it is important to consider not only broad-scale climatic conditions (e.g. in a 10-km square), but also local climate and habitat conditions, as these determine the survival and establishment of the transplants (Gunnarsson and Söderström 2007; Graf and Rochefort 2010). In this study, transplanted bundles of shoots grew independent of microhabitat type, only a very small negative influence of cover of grasses on growth was indicated. However, transplanted fragments of *H. hutchinsiae* have been shown to grow better between other bryophytes than in other microhabitats (Flagmeier et al. 2013). Graf and Rochefort (2010) similarly reported an effect of microhabitat on transplants of *Sphagnum* with fragments regenerating better under a dense canopy of herbaceous plants. Hence, even if vegetation type were not critical for population persistence, the success of fragment establishment and growth, and therefore population expansion, may be influenced by the surrounding vegetation. In the absence of long-term transplantation studies, during which more effects of microhabitat may become apparent, the most promising approach for establishing transplants is to select and imitate the environmental conditions in which the liverworts currently occur as closely as possible. This includes transplanting individuals together, e.g. in single-species bundles.

Transplant bundle weight may also be important to transplantation success, as an unexpected effect of initial transplant weight on growth was observed in this study, suggesting that smaller transplants grew better than bigger transplants. Where *H. hutchinsiae* occurs it does so abundantly, building big orange cushions (Hill et al. 1991; Averis 1994). In fact, this species seems to fit the 'phalanx' strategy of clonal growth by which acrocarpous bryophytes form dense cushions as a 'physiologically integrated front', thereby preventing interspecific competition (Cronberg et al. 2006). These bryophytes also tend to carry resources from the mother plant as they expand by branching, and indeed *H. hutchinsiae* has a relatively high branch production (Flagmeier et al. 2013). Perhaps smaller transplants show greater growth because the species strategy is to initiate a higher growth response when less dense, to eventually build dense cushions e.g. to prevent water losses. Bigger transplants on the other hand may experience more self-shading, leading to shoot etiolation and consequently less biomass increase (Rydin 2009). The latter may also be exacerbated if shoots within large transplant bundles were packed at higher densities than would occur naturally. Although generally, negative effects (decreased growth or increased mortality) with increasing shoot density is common in vascular plants ('self-thinning rule', see Begon et al. 2006), this also applies to some bryophytes. Negative effects of density were also observed on growth of three mosses from fragments (Scandrett and Gimingham 1989), and on shoot recruitment in *Sphagnum*, although in this case the phenotypic plasticity of the species allowed it to form slender but tall (etiolated) shoots to escape burial by keeping their apex at the surface (Rydin 1995). This may have been the case for our bigger transplants, where shoots in the middle of the transplants might have become more etiolated.

Generally, the use of relative growth rate or biomass increase rather than absolute biomass is not seen as critical in bryophytes as shoot growth is independent of initial size (Rydin 2009), but our observations show that it is worth double-checking for effects of initial size or mass when transplanting bundles of shoots, as there could be growth responses related to shoot density for species which show preference for growing in cushions, such as *H. hutchinsiae*.

Transplanting Herbertus hutchinsiae *– potential for restoration*

Both of the sites at which *H. hutchinsiae* has declined were within the current range of the species, but the transplants at those sites grew less well than the ones within the current range and close to extant, healthy populations. This indicates that the lower growth rate at sites of historical decline is due to habitat conditions rather than wider climatic factors. One of these sites, Ben More Coigach, has been subjected to burning and high deer numbers in the past (Averis 1991a; Horsfield 2006), and the resulting habitat is of patchy dwarf-shrub heath, with remnants of liverworts. Grazing also opens up the dwarf-shrub cover, and allows the invasion of grasses (e.g., Hartley and Mitchell 2005). The damaged sites had overall more grass cover than other sites (Table 3). Also, there are patches of bare ground covered by lichens (e.g. *Trapeliopsis pseudogranulosa*) and algae (authors' pers. obs.). In fact, of all sites, Ben More Coigach had most algae covered transplants (17 out of 36), suggesting that the algae from the bare patches can spread onto transplants. Despite no statistical evidence that this affected their growth (Mann Whitney test P = 0.14), this is worth mentioning as it could affect transplant growth over a longer period of time. The other site where liverwort heath has declined, Glenfinnan, had *H. hutchinsiae* only as remnants on crags, supposedly also a result of historical overgrazing of the surrounding vegetation leading to loss of *Calluna vulgaris* and subsequent decline in *H. hutchinsiae*. The site was fenced for woodland regeneration, and there is presently abundant tree regeneration and rank *Calluna* and grasses. The vegetation is however now so tall that competition, especially with grasses, may become a problem if permanent transplants of *H. hutchinsiae* were to be attempted to enhance the existing population. At a transplant site of *Bryum schleicheri* var *latifolium* in Scotland (Rothero et al. 2006), 40% of transplants survived 2 years, but the site has since been invaded by the rush *Juncus acutiflorus*, threatening the continued establishment of the moss (G. Rothero pers. comm.). Competition from higher plants for resources (light, space) can therefore be problematic. Former dwarf-shrub heaths that have been degraded by grazing or burning should recover to a certain standard (e.g. with a minimum area of dwarf-shrub cover and without obvious signs of trampling, but not under total absence of grazing), before attempting the restoration or enhancement of liverwort populations (IUCN/SSC, 2013). Based on these results, although transplanted *H. hutchinsiae* can grow at degraded sites, transplanting it to these sites for restoration is less promising than protecting the current populations from future damage.

Assisted colonisation of Herbertus hutchinsiae

Enhancing the current populations of *H. hutchinsiae* and/or creating new ones by moving the species only within its range would negate the concerns raised by some (e.g., Hewitt et al. 2011) associated with moving a species outside of its current range. However, this study has shown that *H. hutchinsiae* is a suitable species for assisted colonisation because it does not give rise to the common concerns associated with that method (IUCN/SSC 2013; National Species Reintroduction Forum 2014). *H. hutchinsiae* is locally frequent and can be grown *ex situ* (Flagmeier et al. 2013), so that material for translocations does not need to affect source populations (as done e.g., by Rothero et al. 2006). Furthermore, it is unlikely to become invasive; the few reported bryophytes that have become invasive in Europe (reviewed in Brooker et al. 2011) are mosses characterised by high spore and/or vegetative propagule production. These features do not apply to *H. hutchinsiae*, and as shown here, its distribution is restricted due to dispersal limitation in the first place. These conclusions may be applied to the other liverworts of the liverwort heath as they are closely coexisting species with similar characteristics and life history.

However, before assisted colonisation is undertaken, one first needs to know if climate is the main threat for the future persistence of this species. The liverworts that occur in liverwort heath need a constant humid environment and frequent rainfall (Ratcliffe, 1968; Averis, 1994), which suggests that they are highly vulnerable to climate change (Hodd et al., 2014). In the north-west Highlands of Scotland, liverwort heath flourishes in an oceanic climate with a low annual temperature range (mean January temperature 3 – 4 ºC, mean July temperature < 14 ºC) and high annual rainfall of > 1500 mm (Hill et al. 1991). This study found a negative effect of an increase in average temperature in July on growth of the transplants and this may manifest itself under future climate scenarios, as temperatures, particularly in summer and autumn, are predicted to rise by up to 4.5 ºC over parts of north-west Scotland by 2080 (medium emissions scenario, IPCC A1B) (UK Climate Projections 2009). In fact, average spring, summer and winter temperatures have already risen by more than 1 ºC since 1961, along with an average increase in winter precipitation of 60% for northern and western Scotland, and drier summers (Barnett et al. 2006). Changes in seasonality and pattern of rainfall are likely to be problematic for these species. Clearly, climate change is one of the main threats for this oceanic-montane community, and has been implicated in changes in the community over the last 50 years (Flagmeier et al. 2014).

The absence of sexual reproduction in the liverwort heath species may reduce genetic variation and therefore evolutionary potential, resulting in less ability to adapt to environmental change (Laaka-Lindberg et al. 2000), while their low dispersal ability means that they will not be able to track any suitable climate space, whether along an elevation or latitude gradient, and essentially become 'stranded'. Species distribution modeling for lichens in the UK (Ellis et al. 2007) and oceanic-montane species including liverworts of the liverwort heath in Ireland (Hodd et al. 2014), predict losses in southern ranges counteracted by range expansion northwards. Given the dispersal limitation of the liverworts, they are unlikely to reach this future climate space. Therefore, if conditions become unsuitable at current sites under climate change, assisted colonisation to overcome dispersal limitation provides a promising option to safeguard this internationally important community. However, climate change is only potential threat to the liverworts today; they have declined due to changes in habitat in Scotland (Ratcliffe 1968; Averis 1992; Flagmeier et al. 2014) as well as Ireland (Holyoak 2006), linked amongst other factors, to overgrazing and burning. These 'manageable' threats should also be addressed and controlled *in situ* and complemented with assisted colonisation to give the species a chance to persist as suitable climate space moves.

Conclusions

Using suitable transplant methods, this study has shown that there are unoccupied sites available for possible colonisation by *H. hutchinsiae*, and that transplanting this species can help to overcome the barriers of dispersal limitation, given that climate and habitat requirements are taken into account. The distribution modelling illustrated that habitat limitation is unlikely to be the cause of the scarce distribution of this liverwort in Scotland. Monitoring transplants over a longer period of time is essential to ensure that not only growth, but also long-term establishment can take place. The new growth observed in the form of shoots that had grown through the netting around the *H. hutchinsiae* bundles may be an initial indication that there is potential for transplants to spread.

Transplantation of bryophytes for conservation purposes has mainly involved mosses (e.g., Kooijman et al. 1994; Rothero et al. 2006; Gunnarsson and Söderström 2007). Transplantation of the leafy liverwort *Marchesinia mackaii* to establish new populations resulted in low survival of the plants (Geissler 1995). Dynesius (2012) successfully transplanted three leafy liverworts not directly for conservation purposes, but in an experiment on effects of ash on growth and survival of bryophytes. Therefore, this study provides, to our knowledge, the first evidence for successful transplant of a leafy liverwort for conservation purposes. It is likely that the other leafy liverworts of the liverwort heath could also be transplanted by this method, although it should be tested individually on a small scale to confirm this. This study demonstrated that *H. hutchinsiae* can grow in the field from transplants of whole shoots, and of fragments (Flagmeier et al. 2013), and this, together with the ability to select suitable habitat based on the known habitat requirements of the species, provides an opportunity for practical conservation applications. These could include enhancing extant populations and increasing the number of populations within the current range to increase the resilience of the species, restoring populations that have declined over the last half century (Flagmeier et al. 2014) and transplanting material to future suitable climate space as an active conservation strategy to mitigate against liverwort heath species becoming stranded without an effective mode of dispersal in future climate scenarios.

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Table 1. Parameters of sites selected for transplantation of *Herbertus hutchinsiae* at … sites in north-west Scotland. Category 1, sites within species' current range; category 2, sites outside current range; category 3, sites where species has declined. Relative oceanicity was calculated after Averis (1991b), as the number of rain days (> 0.1 mm precipitation) during the experimental period divided by the difference between the highest and lowest monthly mean daily temperatures in °C. Associate liverworts: Ao, *Anastrepta orcadensis*; Bt, *Bazzania tricrenata*; Bp, *Bazzania pearsonii*; Hh, *Herbertus hutchinsiae*; Mt, *Mylia taylorii*; Mw, *Mastigophora woodsii*; Pc, *Plagiochila carringtonii*; Pp, *Pleurozia purpurea*; Sg, *Scapania gracilis*.

Site name	OS grid reference	Site category	Elevation (m)	Slope (°)	Annual mean temperature (°C)	Oceanicity index	Associate liverworts present
Cul Beag	NC163088	1	240	28	6.3	13.7	*Ao, Bt, Mt, Pp, Sg*
Creag Dubh	NH124615	1	460	33	5.3	12.6	*Ao, Bt, Mt, Sg*
Creag Meagaidh	NN451885	1	600	23	4.0	15.5	*Ao*
Coire Ardair	NN438878	1	700	25	3.7	14.2	*Ao, Bt, Mt, Mw, Pc*
Alladale	NH409882	2	300	20	5.8	14.0	*Bt, Mt*
Geal Charn	NN575982	2	600	20	4.7	12.5	*Ao, Bt, Pp*
Corserine	NX515868	2	450	24	5.3	10.9	*Sg*
Ben More Coigach	NC105050	3	300	25	5.9	14.8	*Bt, Bp, Hh, Mt*
Glenfinnan	NM904845	3	200	26	6.8	12.0	*Ao, Bt, Mt, Sg*

Table 2. Mean growth (g dry mass as absolute increase over the experimental period) at sites where *Herbertus hutchinsiae* was transplanted, north-west Scotland. Category 1, sites within species' current range; category 2, sites outside current range; category 3, sites where species has declined. *P*-value for growth indicates significance of difference from initial biomass (paired t-test).

Site name	Site category	Mean growth (g)	*P*-value
Cul Beag	1	1.19 ± 0.24	<0.001
Creag Dubh	1	1.49 ± 0.14	<0.001
Creag Meagaidh	1	1.20 ± 0.20	<0.001
Coire Ardair	1	1.10 ± 0.19	<0.001
Alladale	2	1.45 ± 0.11	<0.001
Geal Charn	2	0.58 ± 0.16	<0.01
Corserine	2	0.41 ± 0.19	<0.05
Ben More Coigach	3	0.65 ± 0.20	<0.01
Glenfinnan	3	0.62 ± 0.13	<0.001

Table 3. Environmental variables (mean ± SE) for each site category in a transplantation experiment of *Herbertus hutchinsiae*, north-west Scotland. Category 1, sites within species' current range; category 2, sites outside current range; category 3, degraded sites where species has declined. Letters indicate significant differences between site categories (P <0.05), assessed by Mann Whitney test.

Site category	Dwarf shrub cover (%)	Bryophyte cover (%)	Graminoid cover (%)	Vegetation height (cm)	Temperature July (°C)	Oceanicity index	Proportion of occurrence			
							Liverworts	Algae	Overgrown	Plant litter
1	48.9±1.9*a*	38.3±1.7	13.0±1.5*a*	19.1±1.0*a*	10.1±0.6	14.0±0.6	0.32±0.12	0.09±0.02	0.36±0.06	0.04±0.02
2	39.6±2.0*b*	42.6±2.2	17.8±2.2*a*	22.8±0.8*b*	11.0±0.4	12.5±0.9	0.35±0.18	0.04±0.04	0.31±0.13	0.14±0.07
3	35.2±2.3*b*	38.3±2.1	26.3±1.8*b*	14.1±0.9*c*	11.7±0.5	13.4±1.4	0.30±0.10	0.35±0.18	0.33±0.30	0.13±0.10

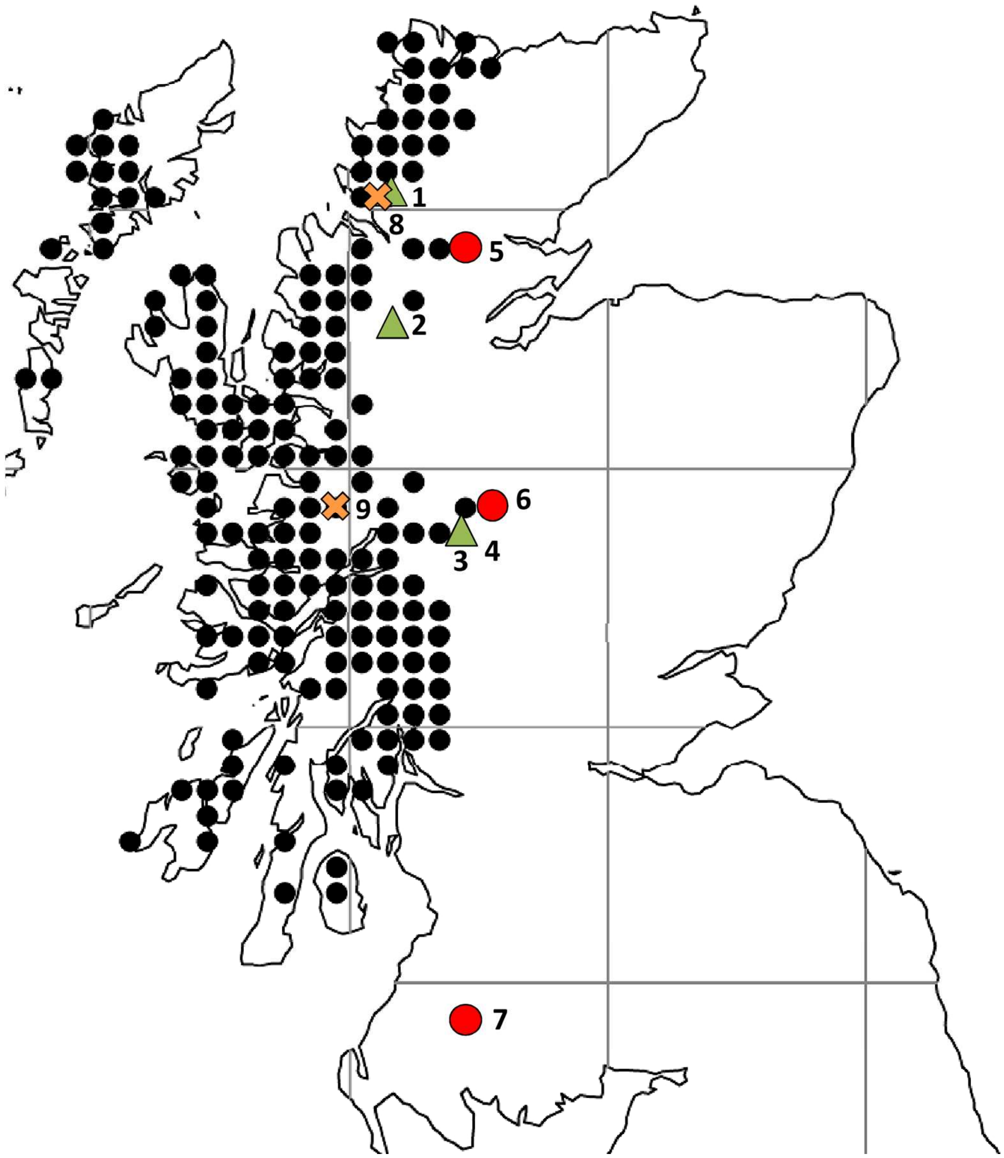
Figure captions

Figure 1. Distribution map (10x10 km squares; small circles) of *Herbertus hutchinsiae* records in Scotland (Shetland Islands not shown), with the experimental sites for transplantation of *H. hutchinsiae* marked. Triangles: sites within the current range (1 Cul Beag; 2 Creag Dubh; 3 Creag Meagaidh; 4 Coire Ardair). Circles: sites outside the current range (5 Alladale; 6 Geal Charn; 7 Corserine) and crosses: sites where *H. hutchinsiae*has declined (8 Ben More Coigach; 9 Glenfinnan).

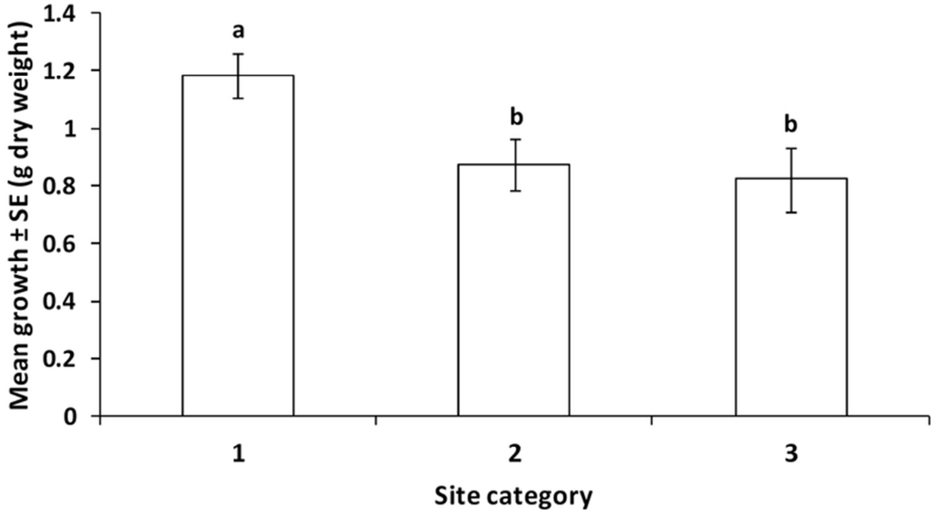
Figure 2. Increase in biomass of transplanted *Herbertus hutchinsiae* bundles after 14 months, in different site categories in north-west Scotland: Category 1, sites within species' current range; category 2, sites outside current range; category 3, sites where species has declined. Mean growth (g dry mass) ± SE. Letters indicate significant differences (P <0.03).

Figure 3. Scatter plot diagram showing the relationship between initial biomass and change in biomass (g) of transplanted *Herbertus hutchinsiae* bundles. ***, P <0.001.

Figure 4. Species distribution model of *Herbertus hutchinsiae* in the British Isles. 'TSA-background' continuous model, showing presences used to generate the model (white dots), as well as the transplant localities. Habitat suitability increases from pale blue to green to red. Black dots: sites within the current range of the species; green triangles: sites outside current range; red squares: sites where the species has declined.



Distribution map (10x10 km squares; small circles) of Herbertus hutchinsiae records in Scotland (Shetland Islands not shown), with the experimental sites for transplantation of H. hutchinsiae marked. Triangles: sites within the current range (1 Cul Beag; 2 Creag Dubh; 3 Creag Meagaidh; 4 Coire Ardair). Circles: sites outside the current range (5 Alladale; 6 Geal Charn; 7 Corserine) and crosses: sites where H. hutchinsiaehas declined (8 Ben More Coigach; 9 Glenfinnan).
160x189mm (300 x 300 DPI)



Increase in biomass of transplanted Herbertus hutchinsiae bundles after 14 months, in different site categories in north-west Scotland: Category 1, sites within species' current range; category 2, sites outside current range; category 3, sites where species has declined. Mean growth (g dry mass) ± SE. Letters indicate significant differences (P <0.03).
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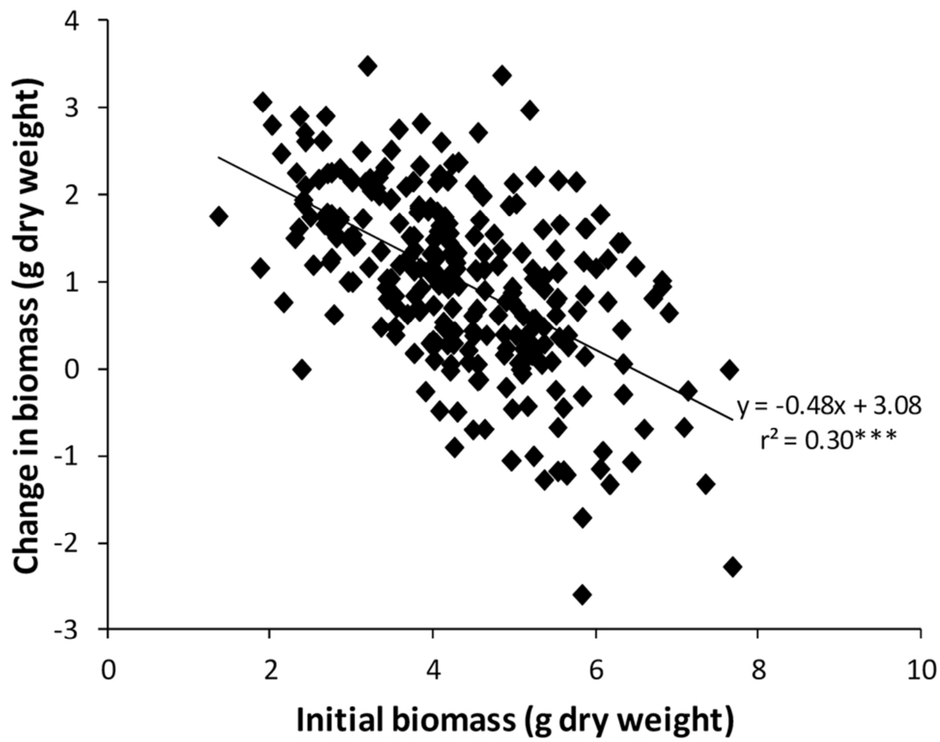

Scatter plot diagram showing the relationship between initial biomass and change in biomass (g) of transplanted Herbertus hutchinsiae bundles. ***, P <0.001.
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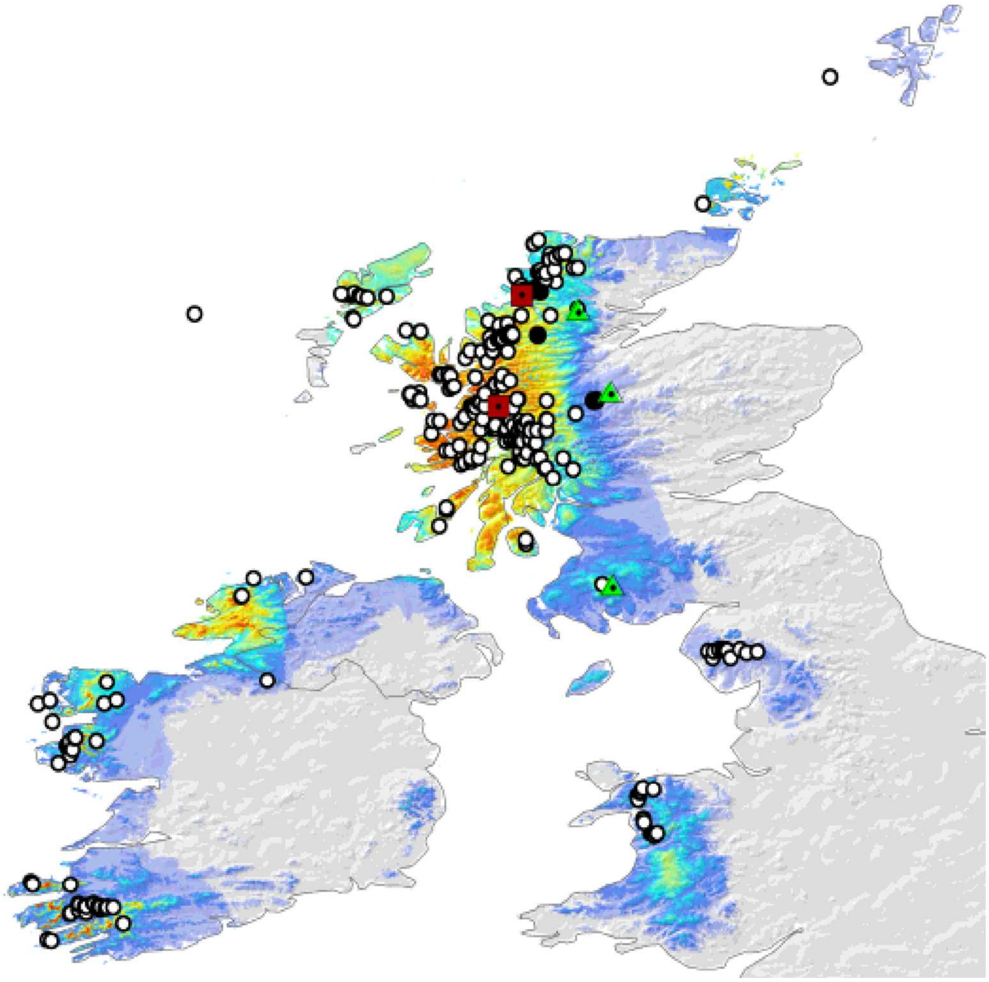

Species distribution model of Herbertus hutchinsiae in the British Isles. 'TSA-background' continuous model, showing presences used to generate the model (white dots), as well as the transplant localities. Habitat suitability increases from pale blue to green to red. Black dots: sites within the current range of the species; green triangles: sites outside current range; red squares: sites where the species has declined.
156x154mm (300 x 300 DPI)