Making inroads into the drivers behind Rhododendron ponticum invasion

Mapping Rhododendron ponticum's distribution and pathways of invasive spread in temperate rainforest zone

Rhododendron ponticum in temperate rainforest oak tree. Image credit: Louis Mielke

Mapping *Rhododendron ponticum's* distribution and pathways of invasive spread in temperate rainforest zone

William Brown

Student ID: 3124759

Supervisors: Zarah Pattison and Ana Novoa

Table of contents

1 Abstract

Invasive *Rhododendron ponticum* poses a significant threat to the temperate rainforests of the Loch Lomond basin, disrupting native ecosystems through the formation of dense monocultures. This study examines the influence of human-mediated disturbances, particularly roads and footpaths, on the distribution and spread of *R. ponticum*. By integrating environmental and human disturbance variables, the species' presence was mapped, and dispersal pathways were assessed using generalised linear models (GLMs) and boosted regression trees (BRTs). The results indicate that vehicle movement, rather than habitat fragmentation alone, is a key driver of *R. ponticum* spread along roadways, with traffic intensity significantly increasing the likelihood of its presence. Despite the importance of footpaths in predicting *R. ponticum* presence, footpath usage, however, showed no conclusive correlation. Based on these findings, recommendations and risk maps were developed to assist land managers in prioritising control efforts. Targeting areas along high-traffic roads and footpaths in semi-open woodlands, particularly near high-conservation-value sites should be prioritised. Further research is suggested to refine estimates of footfall and assess the role of watercourses in *R. ponticum* dispersal. The study provides essential insights for long-term, landscape-scale management strategies to combat the spread of one of the UK's most impactful invasive species.

2 Introduction

Plant invasions around the world are increasing with little sign of slowing down (Clements et al. 2022). This is as a result of deliberate and accidental introductions: deliberately through importing plants for their ornamentation, food and medicinal value; and accidentally due to increasing globalised trade and travel where seeds hitchhike on vehicles, animals and people (Kowarik and von der Lippe 2007). However, this increase may also be due to an increased susceptibility of ecosystems to invasion due to degradation as a result of human activities, namely pollution, land use change and habitat fragmentation (Richardson and Pyšek 2006). These plant invasions cause a variety of negative impacts to biodiversity and the provision of ecosystem services. They disrupt natural processes and outcompete native species, putting endemic and rare species at risk of extinction (D'Antonio and Flory 2017; Downey and Richardson 2016). Many invasive plants also reduce the benefits that healthy and resilient ecosystems provide to human society in provisioning, regulating and cultural value (Lázaro-Lobo et al. 2023). It is clear that plant invasions should be managed to reduce these ongoing risks to native ecosystems and ecosystem services. Interventions to manage invasive species should be framed by what stage of invasion they are at, from transportation, to colonisation, establishment and landscape spread (Theoharides and Dukes 2007; Vermeij 1996), where the cost of intervention increases the more established an invasion becomes (Epanchin-Niell 2017). This makes prevention and control prioritisation important considerations for land managers.

Rhododendron ponticum is a well studied species that through further study can provide an instructive example of dealing with highly established invasive species threatening a rare habitat. Native to the Iberian peninsula and the black sea, *R. ponticum* is recorded as invasive in Scotland, Ireland and the rest of the UK (Cross 1975). Introduced in the 1700s for its ornamental flowers and as cover for game birds (Elton 1958), this invasive shade tolerant evergreen shrub has become established across Scotland's west coast where it presents a significant threat to native ecosystems (Cross 1981). In particular, it threatens restoration efforts of temperate rainforest, a globally scarce habitat that less than 1% of the planet's land surface has the climatic conditions suitable for it (Alliance for Scotland's Rainforests 2019). Temperate rainforest is found in hyper-ocean climatic bioclimes—such as North America's Pacific Northwest, southwest coast of Chile, New Zealand and the Atlantic coast of Europe (Mackey et al. 2017) —that have low temperature fluctuation and high rainfall essential to the bryophyte community that defines this rare woodland (Aubrey et al. 2013). The British Isle's oceanic bioclimatic conditions represent 40% of Europe's suitable land for temperate rainforest, with this land focused on the west coast from Cornwall, to Wales, Atlantic coast of Ireland and Scotland's west coast (DellaSala 2011). The woodland community is typically defined by oak, ash and hazel with indicator lichen species such as *Gomphillus calycioides*, *Pseudocyphellaria intricata*, and *Leptogium brebissonii* (Ellis 2016). It is species such as these that are at threat from *R. ponticum* invasion. The dense evergreen understory cover that *R. ponticum* creates as it laterally grows prevents almost any understory plants from growing, reducing biodiversity even 30 years after removal of the *R. ponticum* (Maclean et al. 2018), however bryophytes are better able to recover post-control (Maclean et al. 2017). This effect also applies to tree regeneration, with a study on *R. ponticum* in its native Black Sea region finding that it significantly reduced natural regeneration by approximately 99.7% (Vacek et al. 2020). This threat is amplified by the recent arrival of *Phytophthora ramorum*, a pathogen hosted by *R. ponticum* that may pose a future risk to native oak species (Forest Research 2024). Long term and uncontrolled *R. ponticum* spread is not just a threat to the species that rely upon temperate rainforest but threatens the trees that form the very structure of this rare ecosystem. Controlling *R. ponticum* invasion is therefore an essential element of any temperate rainforest restoration initiative.

Land managers aiming to control *R. ponticum* and restore temperate rainforest face challenges due to the scale of invasion and a lack of guidance in how to deal with a highly established invasive species. Guidance from Forestry and Land Scotland on how to prioritise *R. ponticum* control recommends mature stands and regenerating bushes from recent control as highest priority based on the seed production potential (Edwards 2006). However, this advice feels relevant to an invasive species in the colonisation and establishment stages of invasion rather than a widely spread species such as *R. ponticum* – there is such abundance of mature stands that the guidance falls short in informing where land managers and national park authorities should prioritise control. This presents a dilemma for land managers due to the cost and time of removal. Eradication of *R. ponticum* is a time-intensive exercise involving mechanical or chemical treatment with necessary follow-ups over multiple years to check for regrowth (Tyler et al. 2006). A study from a 2001 survey with land managers found that costs ranged from £416 to £10,000 per hectare depending on site access and terrain challenges (Dehnen-Schmutz et al. 2004), costs which are likely to have increased further since its publication. These costs are in danger of multiplying over the long term if spread is not kept in check. Control of approximately 10 square kilometres led by Loch Lomond and Trossachs National Park Authority (LLTNPA) around Inversnaid was described as a ten year effort (pers. comms. LLTNPA). On a landscape scale of hundreds of square kilometres, control of *R. ponticum* is likely a multi-decadal initiative. The long time frame of eradication presents the risk of increasing *R. ponticum* spread in yet-to-be-controlled areas and even reinvasion (Lookingbill et al. 2014). It would make sense then, to understand where an invasive species has the greatest potential to spread farthest and fastest to reach areas that are intact and of important ecological value. This way, resources may be directed to reduce *R. ponticum* spread in the long term and thus increase control efficiency.

Identifying which areas are at greater risk of *R. ponticum* invasion and therefore of higher priority for management is increasingly requiring consideration of human drivers of spread. A review of progress in invasion science has found that the role of human interactions are historically overlooked, with 92.4% of publications being concerned with ecological issues and only 7.6% involving a social element (Vaz et al. 2017). Indeed, this reflects the literature on *R. ponticum* which has good coverage of its physiology (Cross 1975; Erfmeier and Bruelheide 2004) and habitat requirements (Erfmeier and Bruelheide 2010; Harris et al. 2011) but information regarding human dynamics on its invasiveness is still far from complete. This knowledge gap is more apparent when comparing what is known about invasive plant species generally in the literature. Invasion science has highlighted the role of various means of human-mediated dispersal on plant invasiveness; namely that of vehicles (Closset-Kopp et al. 2019), roads (Deeley and Petrovskaya 2022), traffic (Lemke et al. 2019), footwear (Wichmann et al. 2009), and settlements (Seboko et al. 2024). When formulating strategies for invasive plant species management, these examples make clear the importance of accounting for human factors. However, none of these human-disturbance variables have been applied to *R. ponticum* and as a result can not be accounted for in the management of this invasive plant species. In order for land managers to make science-informed decisions to enable long-term management of *R. ponticum*, these human-disturbance variables should be quantified for their impact on creating optimal growth conditions and assisted dispersal.

2.1 Aims and objectives

Rhododendron ponticum, due to its invasiveness and abundance in the oceanic West Scotland bioregion, is a threat to globally scarce temperate rainforest habitat (Alliance for Scotland's Rainforests 2019). However, the high cost of *R. ponticum* removal presents a challenge for control or eradication. Therefore, an alternative approach is needed to protect temperate rainforest from further *R. ponticum* invasion, namely better understanding pathways of spread and assessing the extent and risk of invasion to prioritise management action. The aim of this research was to quantify the role of human-mediated dispersal in *R. ponticum* invasion, and develop a management strategy to prioritise its control. Specifically, the following objectives were addressed:

1. Assess the importance of human factors as drivers of *R. ponticum* dispersal in relation to environmental variables.
2. Assess whether the frequency in use of roads and footpaths impacts the abundance of *R. ponticum*, i.e. to determine whether human movement or habitat fragmentation is driving spread.
3. Identify future areas at risk of *R. ponticum* invasion in Loch Lomond and Trossachs National Park temperate rainforest zone.
4. Propose management recommendations that protects temperate rainforest habitat from *R. ponticum* invasion.

By investing resources into tackling areas at highest risk of *R. ponticum* invasion, spread may be controlled in a cost and time effective manner whilst protecting key habitats from subsequent invasion. Such a management strategy is of direct use to the Loch Lomond and Trossachs National Park Authority (LLTNPA) and land managers across the west coast of Scotland dealing with *R. ponticum*.

3 Methods

3.1 Methodological approach

The aims and objectives of this project were designed in collaboration with LLTNPA with the intention of providing applied outcomes relevant to ongoing projects at the national park authority. Stakeholders at LLTNPA were consulted multiple times during the process—project scoping, research and results—in a participatory approach. Their needs and perspectives were incorporated into the project framing to direct the research towards usable outcomes in the intention to improve decision making (Barreteau et al. 2010; Reed 2008).

3.2 Study area

The study area is located within the Loch Lomond Rainforest project area, situated within Loch Lomond and Trossachs National Park (LLTNP) on the west coast of Scotland. With an extent of 222772E 683282N to 244849E 733677N, Loch Lomond Rainforest has an area of approximately 64,200 hectares and contains temperate rainforest habitat under threat by *R. ponticum* invasion. The landscape is a river basin characterised by Loch Lomond—the largest loch (lake) in Scotland by surface area—flanked by mountains north of the highland boundary fault and flatter fertile farmland to the south. Loch Lomond was formed by glacial erosion during the Loch Lomond Stadial, where the British-Irish Glacial Sheet emptied out of the hard granite mountains into the flat sandstone landscape south of Conic Hill marking the highland boundary fault (Pierce 2008).

The study area has a diverse range of ecosystems and resulting land uses. There are 11,372 hectares of woodland in the study area of which 2,689 hectares (approximately 24%) is classified as ancient (Nature Scot 2022). These woodlands fall within the Scottish west coast oceanic zone for temperate rainforest suitability, making them a likely candidate for hosting this rare ecosystem type (Alliance for Scotland's Rainforests 2019; Ellis 2016). Loch Lomond National Nature Reserve, Inchcailloch Island and woodlands surrounding Inversnaid have been identified by the Alliance for Scotland's Rainforests as exemplary of temperate rainforest (Alliance for Scotland's Rainforests 2024). The range in altitude to 800m creates a gradient change in vegetation to upland heath, characterised by heather and blanket bog formation, and upland birchwood (Dickinson 1994). These ecosystems are recognised for their importance, with 36 protected areas across five protected designations (NNR, RAMSAR, SAC, SPA, and SSSI) covering a total of 22,750 hectares. This natural capital attracts mixed land uses: from farming to tourism, conservation, shooting, and outdoor recreations such as hiking.

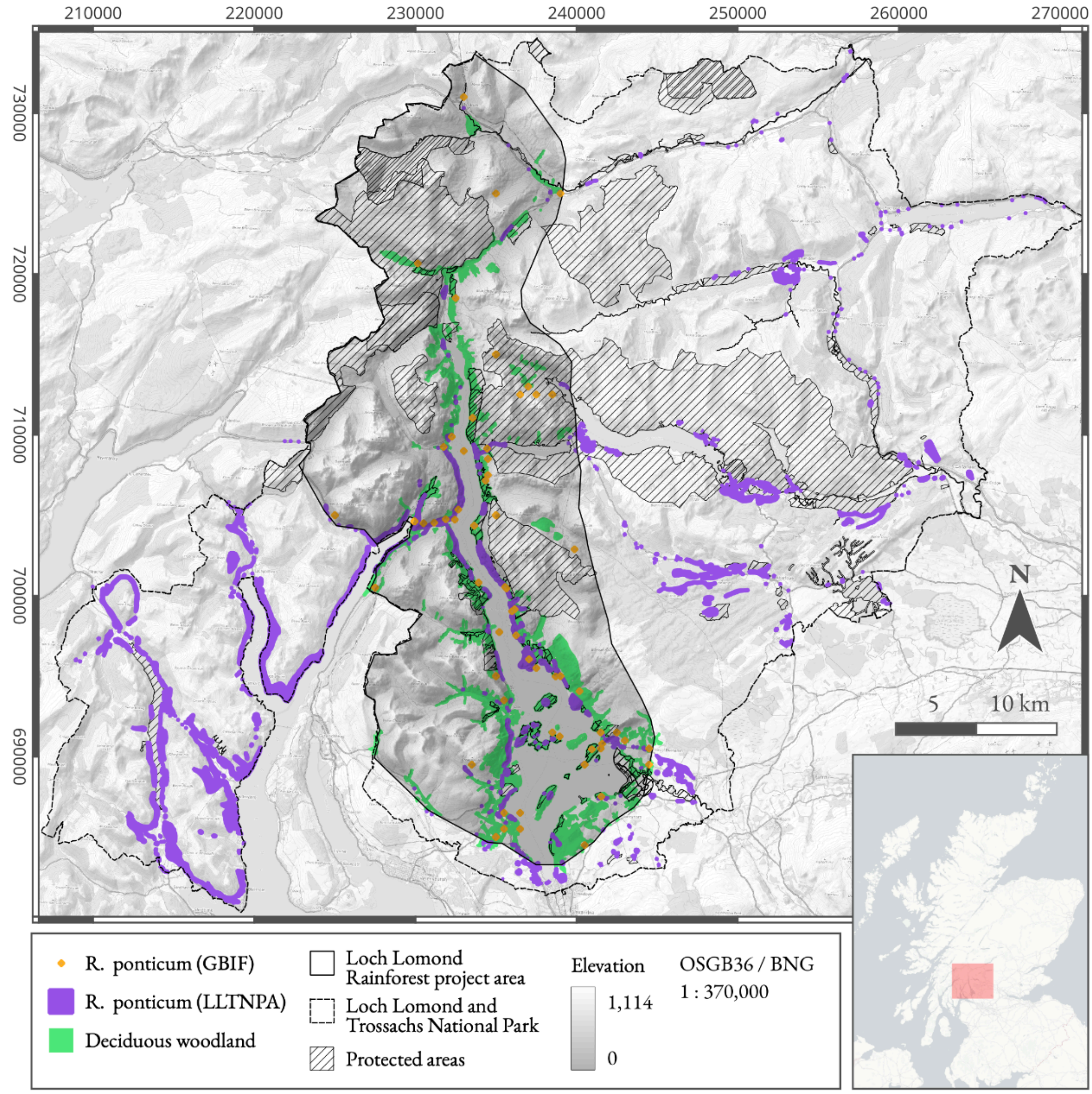

Figure 1: The Loch Lomond Rainforest project area—the study area for this research—situated within the Loch Lomond and Trossachs National Park on the west coast of Scotland.

3.3 Study species

Rhododendron ponticum L. is an evergreen, shade-tolerant shrub introduced to the British Isles in the 1700s for its ornamental value and as cover for game animals (Cross 1981). Native to the Iberian Peninsula *(R. ponticum* subsp. *baeticum*) and the coastal areas around the Black Sea (*R. ponticum* subsp. *ponticum*), it was once widespread across Europe, including the British Isles, as evidenced by fossil pollen predating the last ice age (Cross 1975). Its historical presence in the British Isles suggests that its current invasiveness may be due to a "genetic memory" of the region's bioclimatic conditions, especially as it is now endangered in its native range (Erfmeier and Bruelheide 2004).

R. ponticum spreads rapidly through seeds and lateral branching. Each flower head produces thousands of wind-dispersed seeds, capable of travelling up to 200 metres (Stephenson et al. 2007), though with low germination success - particularly in undisturbed soil (Daly et al. 2014). Optimal germination occurs in moist, light-exposed environments like moss-covered tree stumps near streams or under semi-open canopies (Harris et al. 2011; Stephenson et al. 2006). It also propagates through lateral branching, allowing it to form extensive monocultures (Cross 1975). These dense thickets inhibit other plant growth through allelopathy and shading (Davis 2013). This prevents tree regeneration, leading to forest degradation and biodiversity loss (Vacek et al. 2020). As a result, *R. ponticum* is one of the UK's most impactful and expensive invasive species (Dehnen-Schmutz and Williamson 2006).

3.4 Site selection

Within the Loch Lomond basin a stratified random sampling method was used to select sample sites that have been confirmed not to contain *R. ponticum* based on abundance data supplied by LLTNPA (Baker et al. 2024) and publicly available records (GBIF.org 2024a). The site map was made up of a 200m resolution grid focused on the deciduous woodland in the study area as this was most likely to contain the temperate rainforest. Sample sites were selected along roads and footpaths of varying busyness, in addition to control sites that included undisturbed areas and along gradients from human disturbance pathways to undisturbed areas. Traffic was quantified as daily vehicle counts (DfT 2023) and footfall was quantified as a proxy measure via the density of iNaturalist observations along footpaths (GBIF.org 2024b). To identify these sites, a map of the study area was made using QGIS version 3.28 that included environmental variables and human disturbance factors (Table 1, appendix).

The amount of overlap of human disturbance and environmental variables within each grid square was captured in a dataframe for the area of vector polygons, length of vector lines and count of point data. Zonal statistics was used to find the average of raster data. Each of these were captured in numerical format. From this, the 'random points in polygons' tool in QGIS was used to randomly assign grid squares as sample points. From each sample point a line of up to five grid squares was made to compose a single sample box transect of 1 km in length and 200 m in width. There were 46 box transects created in total; more than required in anticipation of some sites being later removed due to having restricted or dangerous access. The overlap analysis of predictor variables was repeated at coarser spatial scales of 600m and 1000m to account for the increasing influence of landscape and human-disturbance variables, and a diminished importance of biotic variables (Kotowska et al. 2024). The coarser spatial scale squares were created using the buffer tool in QGIS around each 200m grid square.

Table 2. Stratifications used in the random selection of transect sites with their definitions and total number generated for site selection.

Stratification	Definition	n

Road	Starting at a grid square containing a road of varying traffic with no known *R. ponticum* presence in a transect in line with the road.	12
Footpath	Starting at a grid square containing a footpath of varying use with no known *R. ponticum* presence in a transect in line with the path.	12
Undisturbed	Starting at a grid square within undisturbed deciduous woodland containing no known *R. ponticum* presence.	12
Adjacent	Starting at a grid square containing road or footpath with no known *R. ponticum* presence in a transect line perpendicular into undisturbed deciduous woodland.	7
Known presence	Starting at a grid square containing road or footpath with known *R. ponticum* presence in a transect line with the road or footpath.	7

3.5 *R. ponticum* data collection

Grid squares within each box transect were sampled to cover the 200 x 200m area within visible sight – i.e. in open areas less walking was required due to greater range of view whereas the opposite was true for dense understory canopy or obscuring landscape features. For each transect grid square, the following sampling procedure was carried out estimating occurrence, density, and tree canopy species composition.

Along each box transect the occurrence of *R. ponticum* was recorded. The DOMIN scale was used to make visual estimates of *R. ponticum* density. To aid in accuracy and mitigate against the bias to overestimate, the number of *R. ponticum* individuals and their area of ground cover was noted and compared to the DOMIN 2.6 scale mid-range value (Currall 1987). In total, 162 grid squares were sampled.

3.6 Data analysis

All analysis was carried out using R Statistical Software v4.4.1 (R Core Team 2024) unless stated otherwise. During all of the following analysis using generalised linear models and linear models, diagnostic plots using the performance and ggally R packages (Lüdecke et al. 2021; Wickham, Hadley 2016) were used to check model assumptions and variables transformed using boxcox function of the MASS R package (Venables and Ripley 2002) to improve homoscedasticity and normality. Multicollinearity was assessed using the car R package (Fox and Weisberg 2019) with highly scoring predictors removed.

3.6.1 Variable importance in R. ponticum distribution

Generalised linear models (GLM) were selected as the most suitable to assess the relative importance of human-disturbance (length of roads, footpaths, railway lines, powerlines; and number of buildings and listed buildings) versus environmental variables (length of watercourses; area of waterbodies, woodland, pine, deciduous and plantation woodland; mean value of elevation, aspect, and slope) as predictors of *R. ponticum* occurrence as a binomial response variable (Guisan and Zimmermann 2000) using the lme4 R package (Bates et al. 2015). Stepwise regression was used to backward eliminate predictors from the model, using an F-test of overall significance and pseudo R-squared to assess model suitability (McFadden 1972). A GLM using standardised coefficients was fitted to assess variable importance for the final model. The stepwise regression and standardisation of variables was repeated at the two subsequent spatial scales of 600m and 1000m. The resulting standardised coefficients were joined into a single dataframe using the dplyr R package (Wickham, H. et al. 2023) for comparison on a single plot using the ggplot2 R package (Wickham, Hadley 2016).

The data at each spatial scale was used to fit boosted regression trees (BRT) as an alternative modelling approach to assess variable importance in predicting *R. ponticum* probability of occurrence (Elith, Jane and Leathwick 2018). BRTs can fit non-linear relationships and automatically consider interactions to produce a decision tree that can be more easily interpreted for an applied audience (Elith, J. et al. 2008). The BRTs were fitted and assessed for variable importance (Therneau and Atkinson 2023) the decision tree (Milborrow 2024) and variable importance visualised (Sjoberg 2024).

3.6.2 Role of human movement in R. ponticum spread

Statistical modelling was used to determine whether the importance of roads and footpaths in predicting *R. ponticum* invasion could be explained by fragmentation of habitat due to their physical presence creating conditions more suitable for germination and growth; or the movement of vehicles or people assisting the dispersal of seed propagules along those pathways. The occurrence and cover of *R. ponticum* response variables were individually fitted to the traffic and footfall predictor variables. Occurrence as a binomial response was fitted as a logit GLM (lme4 package) drawing from the full sample size (n = 363 for traffic and n = 509 for footfall) and cover as a continuous numerical response was fitted as a linear model (core stats package) using a reduced sample size (n = 32 for traffic and n = 64 for footfall). A rejection of the null hypothesis would indicate that the hypothesis of vehicles and human movement assisting *R. ponticum* seed dispersal is more likely.

3.6.3 Risk map of R. ponticum invasion

To predict the risk of *R. ponticum* spread across the study area in unsampled grid squares, two distribution maps were created.

The first was the probability of *R. ponticum* occurrence that was extrapolated from the best performing model, the 600m spatial scale GLM. The model was fitted from a dataframe containing all the *R. ponticum* occurrence data: LUC, GBIF and data collection and therefore would best predict areas where *R. ponticum* is most likely to be. The performance of the model was assessed using the sensitivity score from the confusion matrix (Kuhn 2008) to reduce the number of false positives (Fielding and Bell 1997). This is useful for reducing the probability of missing *R. ponticum* occurrences in the field, essential for invasive plant management. The data frame of predicted *R. ponticum* occurrence was then exported to QGIS for visualisation.

The second risk map of future invasion risk was fitted as a GLM using stepwise regression based on the data collected in this study only as it focused on areas where *R. ponticum* was previously not known to be present in. This data set was smaller but was ground truthed with both presence and absence observations and therefore would best predict where the frontiers of *R. ponticum* invasion are. The 600m spatial scale model was also chosen for this risk map and the following predictors were used: road, railway, building, watercourse and deciduous woodland type.

4 Results

Within LLTNP, 3172 grid squares intersected with deciduous forest. Of these, *R. ponticum* was present in 800—approximately 25% of the forest area—based on data collection and data from LLTNPA and GBIF. Ground truthing data collection showed approximately 33% occupancy of *R. ponticum* presence in 54 of 162 grid squares. Generally, *R. ponticum* was present at low elevations along main roads and footpaths.

Table 3: Summary of human disturbance and environmental variable ranges and means (in parentheses) for absence and presence of *Rhododendron ponticum*.

Type	Variable	Absent	Present
Human disturbance	road	0 - 3186 (399.8)	0 - 3174.3 (920.1)
	footpath	0 - 2835.9 (202.7)	0 - 3502.7 (614.5)
	railway	0 - 1225.6 (40.6)	0 - 1171.8 (108.5)
	powerline	0 - 1876.6 (162.1)	0 - 1238.9 (230.3)
	building	0 - 183 (2.2)	0 - 145 (8.3)
	listed	0 - 40 (0.3)	0 - 43 (0.9)
Environmental	watercourse	0 - 5692.3 (1659.7)	0 - 5001.1 (1159.1)
	waterbody	0 - 319137.4 (34399.7)	0 - 271531.8 (66987.8)
	woodland.area	561.9 - 323662.8 (131701.2)	7379 - 323662.3 (170448.5)
	elevation	6.1 - 466.2 (126.9)	6.7 - 246.6 (50.4)
	aspect	42.5 - 318.8 (177.9)	51.9 - 328.7 (180.9)
	slope	0.6 - 36.2 (14.6)	0.9 - 31.7 (13.4)
	woodland.type.pine	0 - 28126.7 (34.1)	0 - 13131.9 (30.1)
	woodland.type.plant	0 - 280977.8 (12325.7)	0 - 263768.8 (23783.9)
	woodland.type.decid	561.9 - 323662.8 (119311)	7379 - 323662.3 (146621.7)
	woodland.cover	0.1 - 0.9 (0.6)	0.1 - 0.9 (0.7)

In fitting the reduced GLM, the predictors removed from the model at each spatial scale were deciduous woodland type, waterbody and aspect; whilst pine woodland type and building were also removed at 200m and 1000m spatial scale, and listed was removed at 600m. This was due to high collinearity in the case of deciduous woodland type and waterbody, and low p-values for pine, building and listed. In the resulting models the best performing was at 600m spatial scale, with a McFadden's R-squared of 0.356, compared to 0.308 and 0.322 for 200m and 1000m spatial scales respectively. This GLM used *R. ponticum* occurrence as a binomial response with the following predictor variables: elevation, footpath, railway, woodland area, road, watercourse, canopy cover, slope, plantation woodland area, powerline, building, and pine woodland area.

4.1 Variable importance in R. ponticum distribution

Standardised variable coefficients from the final GLMs showed that at all spatial scales elevation was most influential in predicting probability of *R. ponticum* occurrence (β_1 = -1.00 to -0.88, $p < 0.001$), at least three times higher than other variable coefficients. This was followed by footpath (β_1 = 0.22 to 0.37; $p<0.001$), road (β_1 = 0.23 to 0.29; $p<0.001$) and woodland.area (β_1 = 0.21 to 0.28; $p<0.001$). At a 200m spatial scale, roads were more important, whereas at coarser spatial scales footpaths were more important.

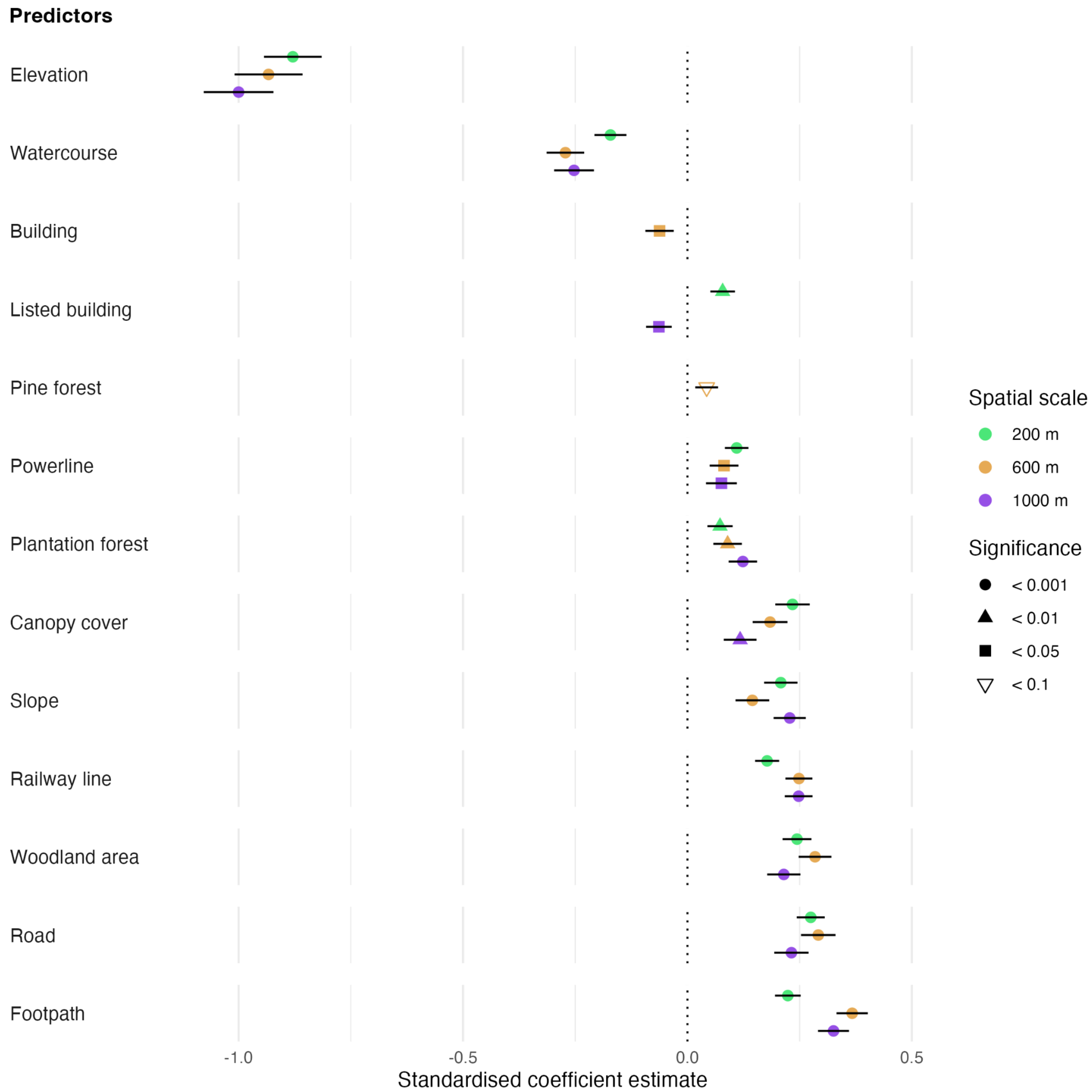

Figure 2: Relative importance of variables in predicting *Rhododendron ponticum* occurrence across various spatial scales within the Loch Lomond and the Trossachs National park.

The BRT showed similar results when compared to the GLM output. Elevation, footpath and road had high variable importance in the fitting of the classification trees. The most notable differences were the decreasing importance of elevation at coarser spatial scales, and the increased importance of footpaths and waterbodies at coarser spatial scales.

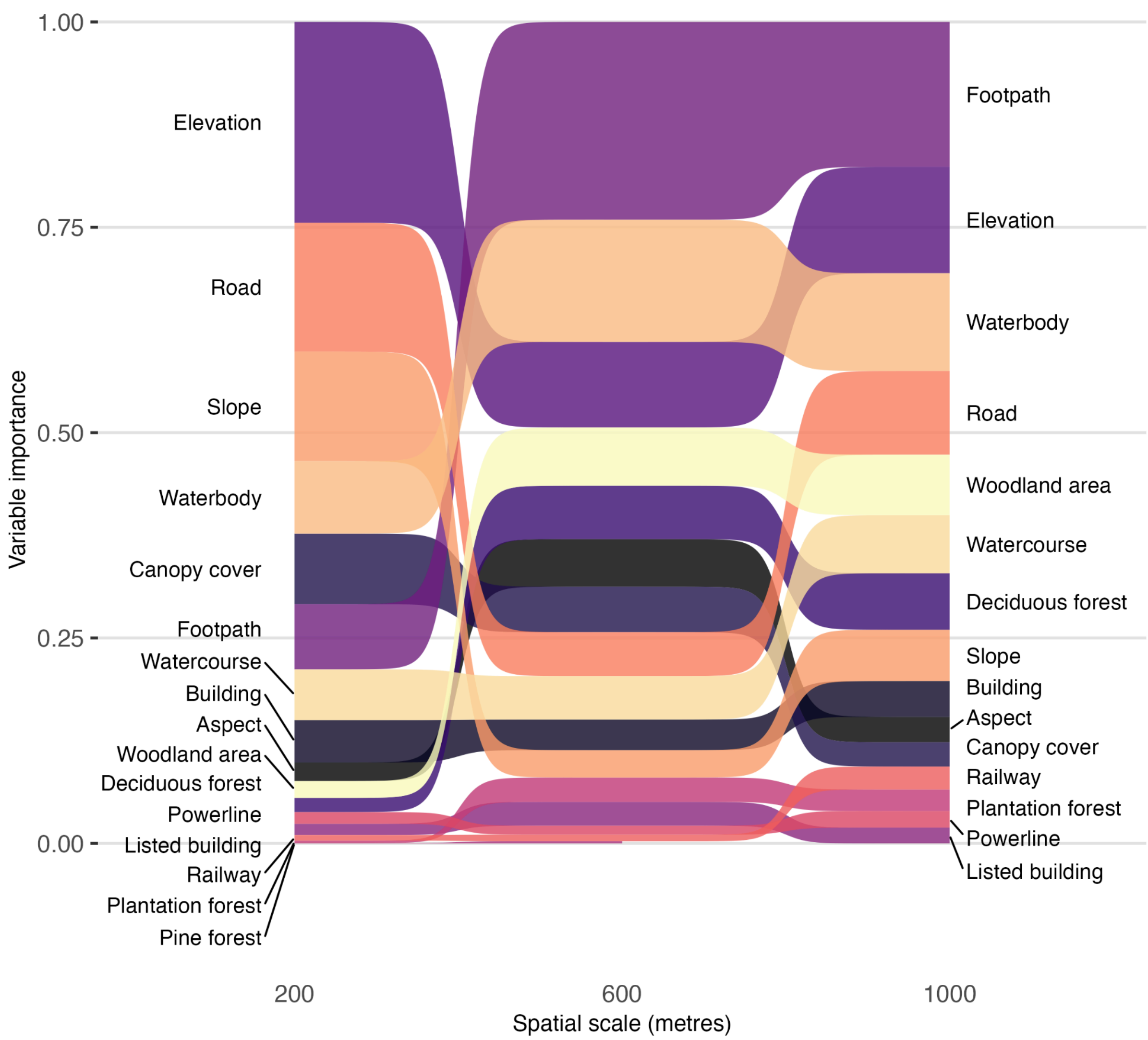

Figure 3: Variable importance of boosted regression tree models predicting the probability of *Rhododendron ponticum* occurrence at increasing spatial scales of 200m, 600m and 1000m.

4.2 Role of human movement in R. ponticum spread

The fitted binomial GLMs predicting the probability of *R. ponticum* occurrence based on road traffic and footfall intensity found that traffic increased the probability of *R. ponticum* occurrence ($p < 0.001$), whilst for footfall there was no statistically significant relationship ($p = 0.233$). Likewise for the linear models predicting cover of *R. ponticum* based on road traffic and footfall intensity again found that traffic increased the density of *R. ponticum* density ($p = 0.007$) whilst for footfall there was no relationship ($p = 0.224$).

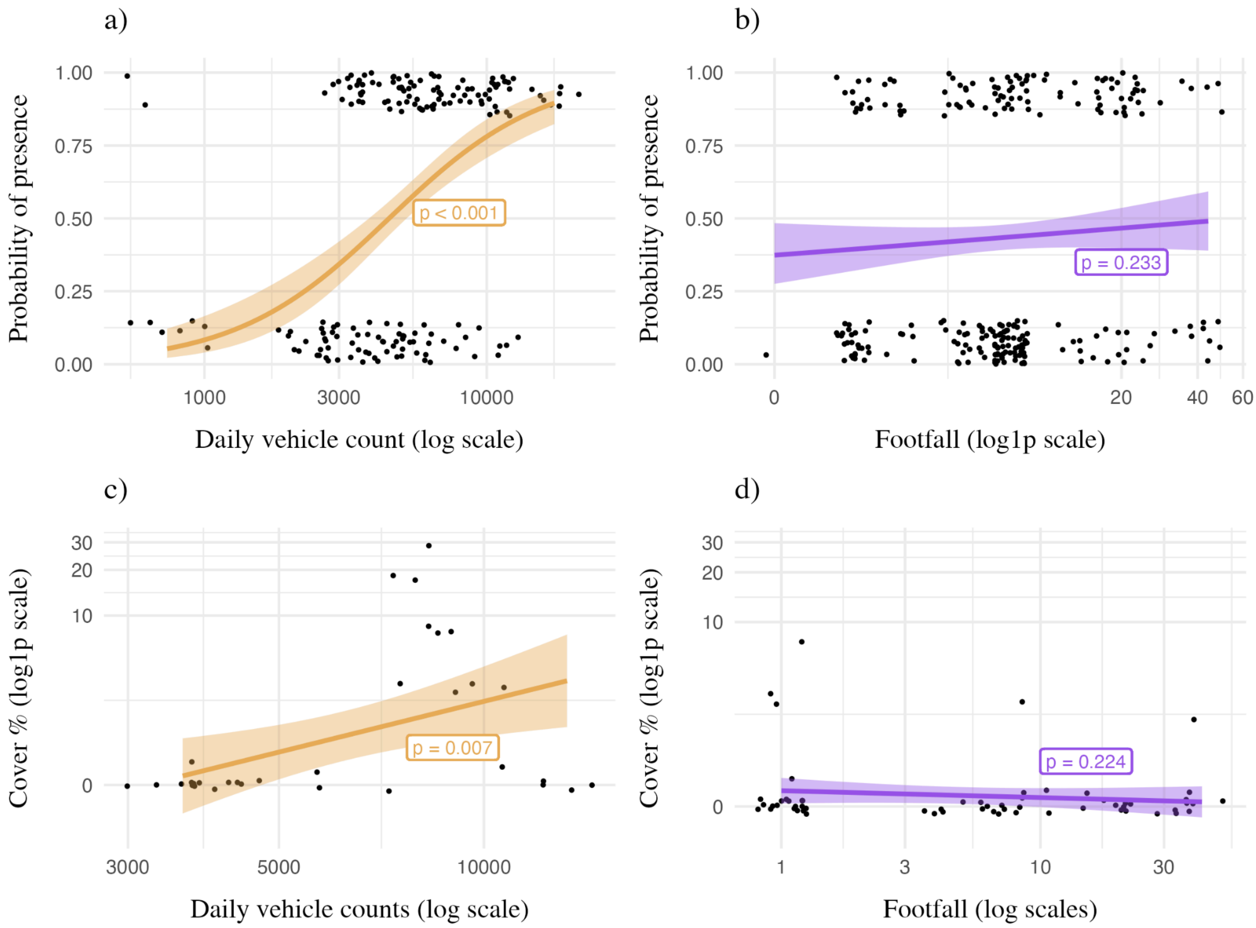

Figure 4: Scatterplots of the probability of *Rhododendron ponticum* presence (a. and b.) or density (c. and d.) predicted by traffic (blue) or footfall (purple) intensity. Presence measured as binomial presence/absence, and density measured using DOMIN2.6 scale. R-squared of a) = 0.129; c) = 0.218. Sample sizes: a) n = 363, b) n = 509, c) n = 32 and d) n = 64.

4.3 Risk map of R. ponticum invasion

The 600m spatial scale model was chosen to visualise the probability of *R. ponticum* presence as it explained the most variance (McFadden's R^2 of 0.356) and had highest detection of true positives (sensitivity of 0.855). The highest probability of *R. ponticum* presence was focused on the main roads and shoreline around Loch Lomond with very little predicted elsewhere.

The 600m spatial scale model was also chosen to visualise the probability of *R. ponticum* invasion to new areas as it had the McFadden's R^2 of 0.393 and sensitivity of 0.826. The highest probability of *R. ponticum* presence was predicted along roads, railways and areas of human habitation.

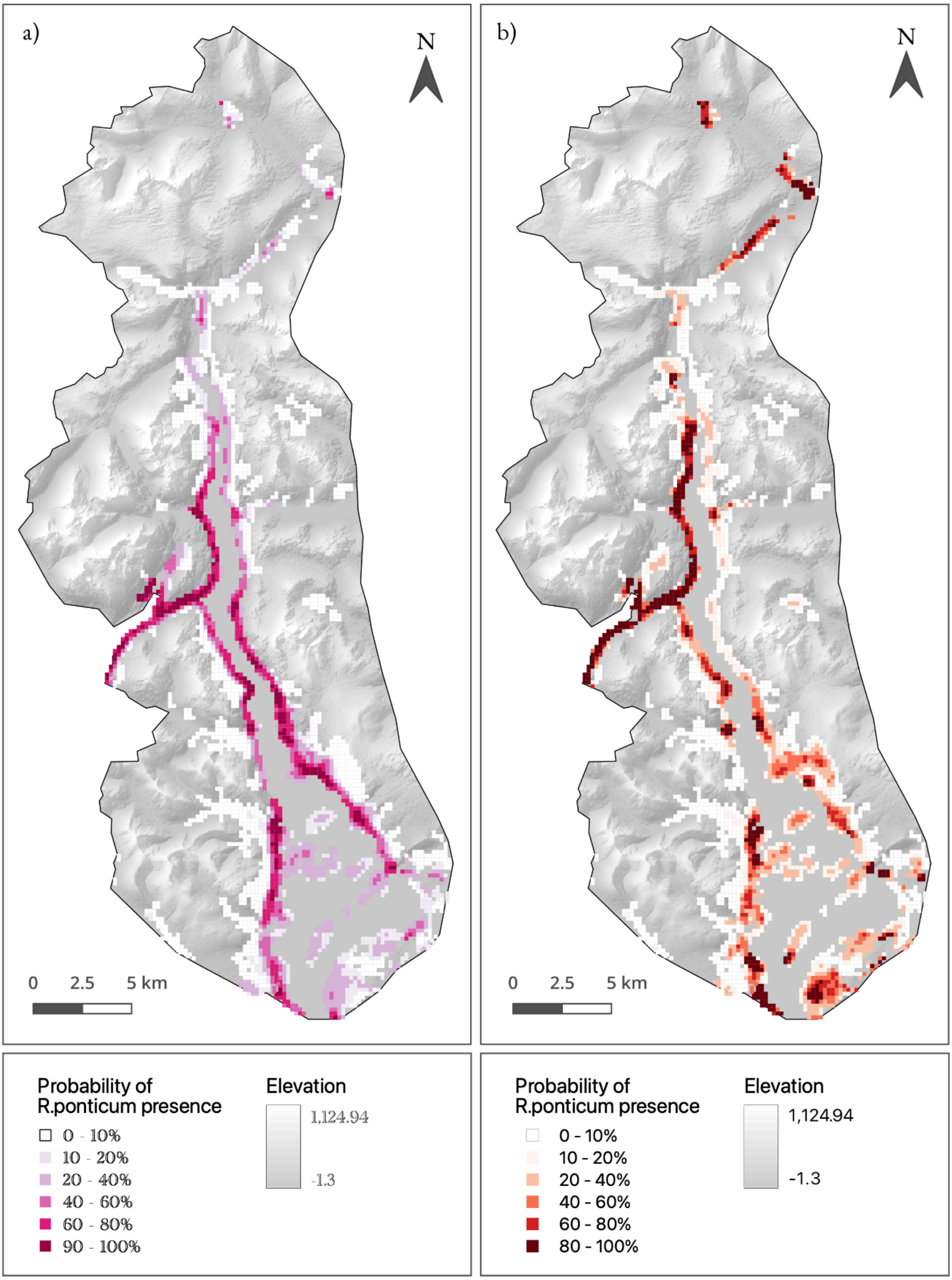

Figure 5: Maps of modelled Rhododendron ponticum distribution in the Loch Lomond Rainforest project area based on data from a) LLTNPA and GBIF that indicates probable current distribution and b) data collected by random stratified sampling in this project that indicates areas of future invasion risk.

Table 4: Comparison of confusion matrix results across multiple spatial scales for optimal *Rhododendron ponticum* distribution and risk map generalised linear model selection.

Model outcome	Probability of presence			Invasion risk		
Spatial scale	200m	600m	1000m	200m	600m	1000m
McFadden's R^2	0.308	0.356	0.322	0.296	0.393	0.371
Accuracy	0.827	0.821	0.812	0.773	0.769	0.761
Kappa	0.459	0.473	0.472	0.305	0.343	0.305
Sensitivity	0.853	0.855	0.835	0.809	0.826	0.815
Specificity	0.684	0.672	0.713	0.575	0.545	0.529
Detection rate	0.716	0.694	0.678	0.685	0.657	0.662

5 Discussion

Given the extent of *R. ponticum* invasion across Scotland, the current guidance on how to prioritise its management is in need of an update. This is especially pertinent to the strategy required by LLTNP for landscape-scale management of *R. ponticum* across the national park. To ensure investment in finite resources to adequately manage *R. ponticum* are used effectively, the importance of various environmental and human disturbance variables in predicting *R. ponticum* occurrence across the Loch Lomond basin was quantified at various spatial scales. Elevation was the most significant predictor of *R. ponticum* occurrence, particularly at finer spatial scales; while human disturbance via roads and footpaths also ranked highly across multiple spatial scales. This quantification of variables that contribute to spread informs national park stakeholders to prioritise management efforts where *R. ponticum* has the greatest invasive potential. To further disentangle the role of roads and footpaths—whether they contribute to *R. ponticum* invasion through habitat fragmentation or human assisted dispersal—traffic and footfall predicting *R. ponticum* occurrence and density was modelled. Whilst there was no correlation between *R. ponticum* occurrence or density with footfall, there was a positive relationship with traffic. This informs the type of interventions that may be implemented by land managers to mitigate the impact of road traffic on *R. ponticum* assisted dispersal, such as car and footwear washing (Rew and Fleming 2011). These results have been summarised in two maps: a distribution map of where *R. ponticum* is likely to be based on data gathered by LLTNPA partners; and an invasion risk map of where the frontiers of expansion are most likely to be based on ground truthed data collected during this study. These maps inform national park stakeholders where to look for *R. ponticum* when implementing monitoring and control actions.

5.1 Human disturbance facilitates the spread of *R. ponticum*

Roads and footpaths were more important than most environmental variables in predicting the occurrence of *R. ponticum*. Notably, these variables rank higher in importance than environmental factors like watercourses and woodland cover, which are typically linked to optimal growing conditions for *R. ponticum* (Cross 1975). This is especially apparent for roads, which performed well even at fine spatial scales, where biotic variables would be expected to take precedence (Kotowska et al. 2024).

Understanding the role of human disturbance variables is important when trying to identify occurrence and spread of invasive plants for management. However, accounting for human disturbance is missing from the guidance on *R. ponticum* management (Edwards 2006; Maguire et al. 2008) despite the importance of anthropogenic pressures in invasive species management (Meyer et al. 2021). Habitat suitability and species distribution models may likewise not account for this, with less than 10% of models including human disturbance variables (Mod et al. 2016). Indeed, this omission may result in bold claims that should be re-examined with consideration of human disturbance. An example of this includes the finding that future climate scenarios predict a decrease of *R. ponticum* occurrence in Eryri (Snowdonia) National Park (Manzoor et al. 2018) despite it being the most frequented national parks in Wales (National Parks 2020) and highly popular across the UK with increasing visitor numbers (James 2023). An inclusion of human disturbance variables in future models would aid their accuracy and usefulness to land managers in managing invasive species.

The low variable importance of buildings and listed buildings was surprising—even at coarse spatial scales—given their status as the likely origins of *R. ponticum* to the park. This contradicts the hypothesis that since these places would have higher probability of presence due to them being the likely sources of *R. ponticum* from gardens and estate grounds (Dehnen-Schmutz et al. 2004). Two possible explanations would account for these contradictory results. First, while seed dispersal may begin in these areas, the plants may establish more successfully in optimal habitats elsewhere, aided by invasion pathways. Second, buildings and listed buildings, often associated with human habitation, might be areas where control efforts have been prioritised (Lenda et al. 2023). In any case, the low importance of buildings and listed buildings suggests that *R. ponticum* invasion has reached stage 4—landscape spread—of plant invasion (Theoharides and Dukes 2007). This underscores the importance of controlling *R. ponticum* in areas of high dispersal over focusing solely on its original sources. However, with most gardens being in proximity to roads that act as pathways for dispersal, management of *R. ponticum* may still be necessary in these areas. The laissez-faire dynamics of low cost to the individual for invasive plants on private land (Epanchin-Niell and Wilen 2015) means that wider incentives will be required to manage *R. ponticum* near buildings.

5.2 Environmental variables align with *R. ponticum*'s known ecology and invasive behaviour

The high importance environmental variables align with the known ecology of *R. ponticum* and the behaviour of invasive plant species. Whilst elevation scored the highest across all spatial scales it may be argued that this variable is not fully independent of other variables and may not represent a full distribution of occurrence due to its status as an invading species (Hui 2023). It may not be fully independent of where *R. ponticum* is likely to have originated in the Loch Lomond basin: in gardens and built-up areas at lower elevations (Dehnen-Schmutz and Williamson 2006). It has also not yet achieved full range expansion. It is known from *R. ponticum*'s native and other invasion habitats to grow at higher elevations—980m in Banis Khevi, Georgia (Erfmeier and Bruelheide 2004) and 520m in Torc, Ireland (Cross 1975) —than that recorded in this study (247m). Therefore, the decrease in *R. ponticum* presence at higher elevations is indicative that it has plenty of headroom to expand upslope and is not at full range expansion yet. On the other hand, the relatively high importance of woodland cover is in alignment with previous findings by Harris et al. (2011) that *R. ponticum* thrives best in woodland edges and half cover than full cover and open habitats due to the optimum balance of light and moisture growth conditions. This may be a priority area to focus *ponticum* control in areas where it is more likely to germinate and spread: half cover woodlands over closed woodlands and—to a lesser extent—open areas.

The negative correlation between watercourses and *R. ponticum* presence was surprising due to knowledge in the literature that suggests otherwise. *R. ponticum* is typically found in gorge habitats in its native range (Mejías et al. 2007) and watercourses are known to be effective corridors for plant spread generally (Calçada et al. 2013). This may be explained by the differences in climate between *R. ponticum*'s dry native range of the Iberian peninsula and around the Black Sea in comparison to its temperate invasion range. The temperate, wet climate of the Loch Lomond basin and surrounding west coast of Scotland is ideal for *R. ponticum* (Cross 1975), likely reducing its reliance on watercourses for humidity during the summer months. However, this lack of importance may be attributed to the spatial scale not accurately capturing a relationship between watercourses and *R. ponticum*. The topography and climate of the Loch Lomond basin results in a landscape of abundant watercourses that may not be captured at even the finest spatial resolution (200m) grid square used for this analysis. To further explore the role of watercourses, further analysis should use a smaller spatial resolution to capture heterogeneity in proximity to watercourses.

5.3 Traffic assists *R. ponticum* dispersal, but how?

The positive correlation of high traffic roads with an increased probability of *R. ponticum* occurrence and density validates the hypothesis of human movement assisting seed dispersal (Taylor et al. 2012). Yet, an understanding of what is the mechanistic cause of this relationship is important to defining recommendations for mitigating its effect. There are three possible ways that human movement may assist seed dispersal—road verge maintenance equipment, airflow of passing vehicles and attachment to car bodies—with management implications for each. Firstly, road verge maintenance equipment, such as hedge trimmers and lawn mowers used along the main roads may spread *R. ponticum* seeds that stick to equipment. This has been observed in road maintenance vehicles spreading Japanese stiltgrass (*Microstegium vimineum*) in Pennsylvania, USA (Rauschert et al. 2017). For LLTNP, road verge maintenance may further spread *R. ponticum* during the eradication phase of management, and pose a risk of reinvasion after eradication. This is mitigated through simple requirements of road verge equipment to be cleaned between use on different sites, especially when bringing in equipment from outwith the national park. Secondly, passing the drag of vehicles creates a strong airflow that carries airborne seeds longer distances than natural dispersal alone. A study by von der Lippe et al. (2013) into the effects of vehicle airflow on seed dispersal distance found that they were equal to or greater than wind dispersal. In addition to wind, this has the potential to double the dispersal distance of *R. ponticum*. However, the effects may be even greater due to the smaller seed size of *R. ponticum* compared to those used in the study, and the typical speeds of 60 mph on busy roads through Loch Lomond basin, such as the A82, compared to 30 mph in the study. Mitigating this effect of airflow would require removing *R. ponticum* from within typical wind dispersal distance from the road where it may be picked up and carried further. Removing *R. ponticum* from within 50m of high traffic roads would reduce the percentage of seeds reaching the road by 99.98% according to experimental trials by Stephenson et al. (2007). Thirdly, seed dispersal may be assisted by sticking to car bodies. Trials by Taylor et al. (2012) found that 0.3–80% of seeds were still stuck to car bodies after 256 km during wet conditions and 86–99% retained during dry conditions. A scenario where seeds stuck to a car during dry conditions to be much later released during dry conditions could feasibly mean that seeds from hundreds of kilometres be carried into the Loch Lomond basin. Prioritising removal of *R. ponticum* from within proximity to roads would also help reduce dispersal within the national park, however would not prevent reinvasion from outwith the national park. Monitoring high traffic roads for reinvasion would be required during and after control of *R. ponticum*. Preventing invasion or reinvasion into sites of conservation importance would require a means of washing vehicles of accumulated mud that may contain seeds (Ansong and Pickering 2013; Rew and Fleming 2011). However, the inconvenience and cost of intervention should be proportional to the cost of *R. ponticum* management. This demonstrates the need for a national-scale coordination of management to adequately deal with *R. ponticum* in the long term.

5.4 A lack (or not?) of footfall assisting *R. ponticum* dispersal

The lack of correlation between footfall intensity and *R. ponticum* occurrence or density may indicate a lack of relationship or a measurement error in how footfall was estimated. Measurement error is indeed possible, as evident in Cashel Forest being estimated as the path with highest footfall. From the author's observations, Cashel is not as popular a walking destination as Ben Lomond, Conic Hill or Luss conservation village. The high estimate for Cashel is more likely attributed to the number of iNaturalist bioblitzes—community science organised events to increase iNaturalist observations—organised by the Cashel Forest ranger known to the author. This will have introduced error into the metric of footfall. A better measure would be manual counts of car park occupation and headcounts of people using the paths, however this data is not currently available.

Further consideration of footfall may be necessary despite the lack of correlation between this variable and *R. ponticum* spread. There is strong evidence that seed propagules are transported by humans hiking, running and on horseback via their clothing and footwear (Michael Ansong and Catherine Pickering 2014; Pickering and Mount 2010; Smith and Kraaij 2020) over 5km before falling off (Wichmann et al. 2009) – with seeds even being introduced over long distances in this way to remotes places like the Arctic (Ware et al. 2011). Despite the lack of correlation between footfall intensity and *R. ponticum* spread the precautionary principle should be applied in this instance to introduce mitigation measures until this can be more robustly verified (Kriebel et al. 2001). This is especially so in light of the high importance of footpaths in predicting *R. ponticum* presence. Awareness and facilities are potential mitigation solutions. Surveys in national parks elsewhere in the world reveal a lack of awareness among hikers of plant invasion risks as a result of their activities and appropriate biocontrol measures (Dolman and Marion 2022). However, there may be support from the general public in Scotland for such measures if introduced (Bremner and Park 2007). Likewise, boot washing is effective in reducing human assisted seed dispersal (Lukács and Valkó 2021), whilst also reducing—but not eliminating—the risk of key tree diseases such as *Phytophthora sp (Liew et al. 2023).*Therefore, increasing public awareness of checking clothing and washing boots—and providing the facilities for boot washing—would help change visitor behaviour. However, methods for effectively removing *R. ponticum* seeds specifically have not yet been explored in the literature and may benefit from focused investigation.

Should further analysis demonstrate more robustly a lack of correlation between footfall and *R. ponticum* spread then at the very least the high importance of footpaths as a variable in the predictive models indicates that habitat fragmentation is driving the spread in proximity to footpaths.

5.5 Using risk maps to address plant invasion on a landscape scale

The distribution and invasion risk maps inform where to prioritise looking for *R. ponticum* where it is likely to be present. Whilst initial data received from LLTNPA estimated approximately 2,800 hectares where *R. ponticum* is present, the risk map demonstrates that this may be even higher due to the number of false negatives discovered during the ground truthing data collection. Yet at the same time, woodland with known *R. ponticum* may not be as densely invaded as previously thought. Being able to focus time and resources will be important so the modelling suggests places to prioritise looking for *R. ponticum* within the temperate rainforest zone. In temperate rainforest of high conservation importance the maps indicate that sites of half cover canopies with roads, footpaths and watercourses (especially where all of these intersect) should be prioritised due to the high likelihood of *R. ponticum* presence and the likely speed of spread along those vectors (Perry et al. 2017). The amount of time it will take to remove *R. ponticum* on a landscape scale requires a careful balance of focusing on protecting high value sites against where the *R. ponticum* is spreading most quickly—therefore incurring future costs—as has been prioritised by land managers in Galapagos National Park based on invasion speed (Trueman et al. 2014). By focusing on these local areas within temperate rainforest containing the variables listed above, this has the potential benefit to direct resources most efficiently to target a larger area over the long term.

A long term and landscape-scale view of invasive plant management also highlights the invasion risk of previously cleared sites whilst continuing control elsewhere in the national park. Reducing the risk of reinvasion is more effective for the long term control of invasive plant species (Lookingbill et al. 2014). Human disturbance pathways identified as high probability of *R. ponticum* occurrence—such as the A82, A83, A814 roads, the West Highland Railway Line and the West Highland Way—pose a threat to areas previously cleared. Prioritising removal of *R. ponticum* from pathways such as these after the control of high conservation importance areas will reduce the risk of reinvasion. However, removal may not always be possible, due to *R. ponticum* often growing as an ornamental plant in private gardens near roads (Dehnen-Schmutz et al. 2004). The Wildlife and Natural Environment (Scotland) Act 2011 and associated Code of Practice stipulates that it is an offence to allow an invasive non-native species to escape into the wild (Scottish Government 2012). However, it may be challenging to prove escape due to the potential for long-distance spread due to human-assisted dispersal highlighted in this paper. For *R. ponticum* at least, this legislation should be updated to provide greater restrictions of the purchase and growing of *R. ponticum*. In the absence of enforcement, voluntary removal may be encouraged through a grant, as has been implemented by the National Trust for Scotland's 'Community Garden Scheme' as part of their *R. ponticum* removal project in Torridon (NTS 2024). Without complete eradication, especially along human disturbance pathways, then the risk of reinvasion threatens control efforts.

5.6 Recommendations for *R. ponticum* management

The learnings from this project's mapping and modelling of *R. ponticum* have been summarised in recommendations in the table below. They have been reviewed and iterated by LLTNPA as part of stakeholder engagement to increase their relevance to land managers in encouraging an approach to *R. ponticum* control with long term benefits. These recommendations are reliant on public bodies to enact new schemes, campaigns and policy that act on the learnings in this project to reduce risk of reinvasion and invasion to undisturbed areas of importance. This multi-stakeholder approach is necessary to deal with the landscape-scale challenge of *R. ponticum* management.

Box 1: Recommendations for land managers, public bodies and policy makers to increase efficiency of Rhododendron ponticum management and reduce risk of invasion on a landscape-scale.

1. **Target removal of *R. ponticum* within areas of high conservation value.**
   Human disturbance creates optimal pathways for *R. ponticum* spread. Coupled with specific environmental conditions, disturbed areas also have the highest probability of *R. ponticum* presence if its distribution is unknown. These areas should be prioritised for management within areas of high conservation value:
   a. **Network connection points**: Where human disturbance pathways (roads, footpaths and railways) intersect.
   b. **Pathways of high spread**: Along human disturbance pathways within areas of high conservation value — particularly where they penetrate into undisturbed areas.
   c. **Highly suitable habitat:** Prioritise areas of habitat that offer more suitable conditions for *R. ponticum* invasions. Suitable habitats are areas of low elevation, steep slope, and semi-open woodland canopy cover.

2. **Prioritise *R. ponticum* management along human disturbance pathways to reduce reinvasion risk and establish geographically defensible areas.**
   Outwith areas of high conservation value, prioritise removal along 'invasion corridors' (roads, footpaths and railways), especially those that connect high conservation value areas to corridors or high human movement. This can support the establishment of geographically defensible areas of high conservation value.
3. **Raise awareness of human-assisted seed dispersal.**
   Educate visitors to the national park about the ways in which they may inadvertently assist seed dispersal of invasive plant species such as *R. ponticum*. This may be achieved via campaigns and signage at entry points into the park, major car parks and tourist hubs. Further research may be required to understand the methods most effective for reducing assisted *R. ponticum* spread in particular.
4. **Offer boot and car washing facilities to visitors.**
   Strategic placement of free-to-use boot and car washing facilities may reduce the human assisted spread of *R. ponticum*. Further research may be required to understand which methods of washing and placement of facilities is most effective.
5. **Offer replacement planting for residents to replace *R. ponticum* in gardens with non-invasive species.**
   Incentivise removal of R. ponticum via a grant scheme that offers free, non-invasive replacement plants that offer similar functional benefits – such as windbreak, visual shielding or aesthetic appeal.
6. **Lobby for policy intervention to deal with *R. ponticum* on private land.**
   Propose updates to the Wildlife and Natural Environment (Scotland) Act 2011 that would enforce deadheading of *R. ponticum* after flowering or (grant supported) replacement with a non-invasive species.

6 Conclusion

In summary, this study has underlined the significance of human disturbance variables—roads and footpaths in particular—on the distribution and spread of *Rhododendron ponticum* throughout the temperate rainforest zone of the Loch Lomond Rainforest project area. Indeed, this study has gone further to demonstrate that it is the movement of vehicles that underlies the role of roads in assisting the dispersal of this invasive shrub to new sites. These conclusions have been reached by mapping, modelling and quantifying the relative importance of environmental and human disturbance variables in predicting the probability of *R. ponticum* presence. The role of assisted dispersal via vehicles was realised through fitting models of road traffic to *R. ponticum* presence and density.

The implications of this research for landscape-scale management have been outlined in recommendations and risk maps designed for land managers, national park authorities and policymakers. Notably, this study recommends prioritising *R. ponticum* removal in areas of rapid spread along roads, footpaths and railway sidings, especially in semi-open woodland habitat types that are particularly susceptible to further establishment. Priority should be given to these conditions within areas of high conservation importance alongside invasion pathways that directly connect to them in order to minimise reinvasion risk and establish geographically defensible areas.

Further research may be required to more accurately quantify a measure of footfall as this study's findings in that area were inconclusive, and similarly to measure the relationship between *R. ponticum* abundance and watercourse proximity at a finer spatial scale. To support the implementation of these recommendations, further research and development will be required to determine the most effective interventions to reduce seed propagule pressure via invasion pathways.

Ultimately, this study provides essential insights for developing long-term, landscape-scale strategies to combat one of the UK's most impactful invasive species, with important implications for the conservation of temperate rainforests and the biodiversity they support.

7 Appendix

A folder with the appendix items can be accessed at:

https://drive.google.com/drive/folders/1cC47U45A3nh4nondK-UydIYyk3WXuS5e?usp=sharing

Appendix items

- Table 1: Variables used in the selection of sample sites and subsequent data modelling.
- Figure 6: Environmental and human-disturbance variables used in prediction of R. ponticum risk to the temperate rainforest zone of the Loch Lomond Rainforest project area.
- Figure 7: Road traffic and path footfall variables used to test hypotheses of human movement versus habitat augmentation on R. ponticum presence.
- Figure 8: Decision trees that can be used to classify whether a 200m square area may have presence or absence of Rhododendron ponticum based on environmental and human disturbance variables within range at different spatial scales.

8 References

Alliance for Scotland's Rainforests (2019) *The State of Scotland's Rainforests.* The Woodland Trust. Available: https://www.woodlandtrust.org.uk/publications/2019/05/state-of-scotlands-rainforest/ [Accessed: 1st August 2024].

Alliance for Scotland's Rainforests (2024) *Top places to visit in Scotland's rainforest.* Available: https://savingscotlandsrainforest.org.uk/map [Accessed: 1st August 2024].

Aubrey, D.A., Nadkarni, N.M. and Broderick, C.P. (2013) Patterns of moisture and temperature in canopy and terrestrial soils in a temperate rainforest, Washington. *Botany,* 91 (11), pp. 739–744.

Baker, J., M. Andrew, L. Hutchison and S. Underwood (2024) Loch Lomond Rainforest Project Report. , March. Available: .

Barreteau, O., Bots, P.W.G. and Daniell, K.A. (2010) A Framework for Clarifying "Participation" in Participatory Research to Prevent its Rejection for the Wrong Reasons. *Ecology and Society,* 15 (2), pp. 1.

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015) Fitting Linear Mixed-Effects Models Using {lme4}. *Journal of Statistical Software,* 67 (1), pp. 1–48.

Calçada, E.A., Closset-Kopp, D., Gallet-Moron, E., Lenoir, J., Rêve, M., Hermy, M. and Decocq, G. (2013) Streams are efficient corridors for plant species in forest metacommunities. *Journal of Applied Ecology,* 50 (5), pp. 1152–1160.

Clements, D.R., Upadhyaya, M.K., Joshi, S. and Shrestha, A. (2022) Global Plant Invasions on the Rise. *Global Plant Invasions,* , pp. 1–28.

Closset-Kopp, D., Hattab, T., Decocq, G. and Edwards, D. (2019) Do drivers of forestry vehicles also drive herb layer changes (1970–2015) in a temperate forest with contrasting habitat and management conditions? *Journal of Ecology,* 107 (3), pp. 1439–1456.

Cross, J.R. (1975) Rhododendron Ponticum L. *The Journal of Ecology,* 63 (1), pp. 345–364.

Cross, J.R. (1981) The Establishment of Rhododendron Ponticum in the Killarney Oakwoods, S. W. Ireland. *The Journal of Ecology,* 69 (3), pp. 807–824.

Currall, J.E.P. (1987) A transformation of the Domin scale. *Vegetatio,* 72 (2), pp. 81–87.

Daly, E., McCarthy, &., Nick, O'Halloran, &., John, Irwin, &., Sandra, Ó Rathaille, &. and Milo. (2014) Effect of forest litter depth on seed germination efficacy of Rhododendron ponticum. *Irish Forestry,* 71 (1).

D'Antonio, C. and Flory, S.L. (2017) Long-term dynamics and impacts of plant invasions. *Journal of Ecology,* 105 (6), pp. 1459–1461.

Davis, B. (2013) *The mechanisms used by the invasive shrub Rhododendron ponticum to inhibit the growth of surrounding vegetation.* University of Southampton.

Deeley, B. and Petrovskaya, N. (2022) Propagation of invasive plant species in the presence of a road. *Journal of Theoretical Biology,* 548, pp. 111196.

Dehnen-Schmutz, K., Perrings, C. and Williamson, M. (2004) Controlling Rhododendron ponticum in the British Isles: an economic analysis. *Journal of Environmental Management,* 70 (4), pp. 323–332.

Dehnen-Schmutz, K. and Williamson, M. (2006) Rhododendron ponticum in Britain and Ireland: Social, Economic and Ecological Factors in its Successful Invasion. *Environment and History,* 12 (3), pp. 325–350.

DellaSala, D.A. (2011) *Temperate and Boreal Rainforests of the World: Ecology and Conservation.* Washington, DC: Island Press/Center for Resource Economics. Available: https://library.biblioboard.com/viewer/89e694ba-17c5-4f22-94b4-8ac3765f998a .

DfT (2023) Abstract only. Available: https://roadtraffic.dft.gov.uk/downloads.

Downey, P.O. and Richardson, D.M. (2016) Alien plant invasions and native plant extinctions: a six-threshold framework. *AoB Plants,* 8.

Edwards, C. (2006) *Practice Guide: Managing and controlling* *invasive rhododendron.* Edinburgh: Forestry Commission. Available: https://www.forestry.gov.scot/publications/93-managing-and-controlling-invasive-rhododendron/viewdocument/93 [Accessed: 29th August 2024].

Elith, J., Leathwick, J.R. and Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology,* 77 (4), pp. 802–813.

Elith, J. and Leathwick, J. (2018) *R Documentation,* Abstract only. Available: http://download.nust.na/pub3/cran/web/packages/dismo/vignettes/brt.pdf.

Ellis, C. (2016) Oceanic and temperate rainforest climates and their epiphyte indicators in Britain. *Ecological Indicators,* 70, pp. 125–133.

Elton, C.S.&. (1958) *The Ecology of Invasions by Animals and Plants.* Dordrecht: Chapman & Hall. Available: https://doi.org/10.1007/978-94-009-5851-7 .

Epanchin-Niell, R.S. (2017) Economics of invasive species policy and management. *Biological Invasions,* 19 (11), pp. 3333–3354.

Epanchin-Niell, R.S. and Wilen, J.E. (2015) Individual and Cooperative Management of Invasive Species in Human-mediated Landscapes. *American Journal of Agricultural Economics,* 97 (1), pp. 180–198.

Erfmeier, A. and Bruelheide, H. (2004) Comparison of native and invasive Rhododendron ponticum populations: Growth, reproduction and morphology under field conditions. *Flora. Morphologie, Geobotanik, Oekophysiologie,* 199 (2), pp. 120–133.

Erfmeier, A. and Bruelheide, H. (2010) Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive Rhododendron ponticum populations. *Biological Invasions,* 12 (3), pp. 657–676.

Fielding, A.H. and Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* 24 (1), pp. 38–49.

Forest Research (2024) *Ramorum disease (Phytophthora ramorum).* Available: https://www.forestresearch.gov.uk/tools-and-resources/fthr/pest-and-disease-resources/ramorum-disease-phytophthora-ramorum/ [Accessed: 11th September 2024].

Fox, J. and Weisberg, S. (2019) *An {R} Companion to Applied Regression.* Third ed. Thousand Oaks, CA: Sage.

GBIF.org (2024a) Abstract only. doi: 10.15468/dl.vm5md2 Available: https://doi.org/10.15468/dl.vm5md2.

GBIF.org (2024b) Abstract only. doi: 10.15468/dl.js5kd4 Available: https://doi.org/10.15468/dl.js5kd4.

Guisan, A. and Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling,* 135 (2), pp. 147–186.

Harris, C.M., Stanford, H.L., Edwards, C., Travis, J.M.J. and Park, K.J. (2011) Integrating demographic data and a mechanistic dispersal model to predict invasion spread of Rhododendron ponticum in different habitats. *Ecological Informatics,* 6 (3), pp. 187–195.

Hui, C. (2023) The dos and don'ts for predicting invasion dynamics with species distribution models. *Biological Invasions,* 25 (4), pp. 947–953.

James, C. (2023) *STEAM 2018-2022 Gwynedd Regeneration Areas PDF.* Snowdonia National Park. Available: https://www.visitsnowdonia.info/research [Accessed: 3rd September 2024].

Kotowska, D., Skórka, P., Pärt, T., Auffret, A.G. and Żmihorski, M. (2024) Spatial scale matters for predicting plant invasions along roads. *Journal of Ecology,* 112 (2), pp. 305–318.

Kowarik, I. and von der Lippe, M. (2007) Pathways in Plant Invasions. In: M.M. Caldwell et al., ed. *Biological Invasions.* Berlin, Germany: Springer, pp. 29–44.

Kuhn, M. (2008) Building Predictive Models in R Using the caret Package. *Journal of Statistical Software,* 28 (5), pp. 1–26.

Lázaro-Lobo, A., Alonso, Á, Fernández, R.D., Granda, E., Romero-Blanco, A., Saldaña-López, A. and Castro-Díez, P. (2023) Impacts of Plant Invasions on Ecosystem Functionality: A Perspective for Ecosystem Health and

Ecosystem Services . In: S. Tripathi et al., ed. *Plant Invasions and Global Climate Change.* SpringerJan 1, pp. 31–56.

Lemke, A., Kowarik, I., Lippe, M. and Pauchard, A. (2019) How traffic facilitates population expansion of invasive species along roads: The case of common ragweed in Germany. *Journal of Applied Ecology,* 56 (2), pp. 413–422.

Lenda, M., Skórka, P., Possingham, H.P. and Knops, J.M.H. (2023) Abandoned land: Linked to biological invasions. *Science (American Association for the Advancement of Science),* 381 (6655), 277. doi: 10.1126/science.adi7833.

Lookingbill, T.R., Minor, E.S., Bukach, N., Ferrari, J.R.&. and Wainger, L.A.&. (2014) Incorporating Risk of Reinvasion to Prioritize Sites for Invasive Species Management. *Natural Areas Journal,* 34 (3), pp. 268–281.

Lüdecke, D., Ben-Shachar, M.S.&., Patil, I., , Waggoner, P. and Makowski, D. (2021) {performance}: An {R} Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software,* 6 (60), pp. 3139.

Mackey, B., Cadman, S., Rogers, N. and Hugh, S. (2017) Assessing the risk to the conservation status of temperate rainforest from exposure to mining, commercial logging, and climate change: A Tasmanian case study. *Biological Conservation,* 215, pp. 19–29.

Maclean, J.E., Mitchell, R.J., Burslem, D.F.R.P., Genney, D., Hall, J. and Pakeman, R.J. (2017) The epiphytic bryophyte community of Atlantic oak woodlands shows clear signs of recovery following the removal of invasive Rhododendron ponticum. *Biological Conservation,* 212, pp. 96–104.

Maclean, J.E., Mitchell, R.J., Burslem, D.F.R.P., Genney, D., Hall, J. and Pakeman, R.J. (2018) Understorey plant community composition reflects invasion history decades after invasive Rhododendron has been removed. *Journal of Applied Ecology,* 55 (2), pp. 874–884.

Maguire, C.M., Kelly, J. and Cosgrove, P.J. (2008) *Best Practice Management Guidelines Rhododendron Rhododendron ponticum and Cherry Laurel Prunus laurocerasus.* Available: https://invasivespeciesireland.com/wp-content/uploads/2012/01/Rhododendron-BPM.pdf [Accessed: 3rd September].

Manzoor, S.A., Griffiths, G., Iizuka, K. and Lukac, M. (2018) Land Cover and Climate Change May Limit Invasiveness of Rhododendron ponticum in Wales. *Frontiers in Plant Science,* 9, pp. 664.

McFadden, D. (1972) Conditional logit analysis of qualitative choice behavior. *Frontiers in Econometrics,* .

Meyer, S., Callaham Jr, M., Stewart, J. and Warren, S. (2021) Invasive Species Response to Natural and Anthropogenic Disturbance. In: *Invasive Species in Forests and Rangelands of the United States : A Comprehensive Science Synthesis for the United States Forest Sector.* 1 ed. , pp. 85–86.

Milborrow, S. (2024) Abstract only. Available: https://CRAN.R-project.org/package=rpart.plot.

Mod, H.K.&., Scherrer, D., Luoto, M. and Guisan, A. (2016) What we use is not what we know: environmental predictors in plant distribution models. *Journal of Vegetation Science,* 27 (6), pp. 1308–1322.

National Parks, U.K. (2020) *Key Facts and Figures for all 15 UK National Parks.* Available: https://www.nationalparks.uk/app/uploads/2020/10/Key-Facts-and-Figures-for-the-15-UK-National-Parks.pdf [Accessed: 3rd September 2024].

Nature Scot (2022) *Ancient Woodland Inventory.* Available: https://opendata.nature.scot/datasets/snh::ancient-woodland-inventory/about [Accessed: 29th April 2024].

Ordnance Survey (2024a) Abstract only. Available: https://osdatahub.os.uk/downloads/open/OpenUPRN.

Ordnance Survey (2024b) Abstract only. Available: https://osdatahub.os.uk/downloads/open/OpenZoomstack.

Pierce, L. (2008) Loch Lomond: An example of quaternary megageomorphology. *Scottish Geographical Journal,* 115 (1), pp. 71–80.

R Core Team (2024) Abstract only. Available: https://www.R-project.org.

Reed, M.S. (2008) Stakeholder participation for environmental management: A literature review. *Biological Conservation,* 141 (10), pp. 2417–2431.

Rew, L.J. and Fleming, J. (2011) *Developing Functional Parameters for a Science-Based Vehicle Cleaning Program to*

Reduce Transport of Non-Indigenous Invasive Plant Species. Available: https://apps.dtic.mil/sti/citations/ADA553532.

Richardson, D.M. and Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography,* 30 (3), pp. 409–431.

Seboko, T.C., Ruwanza, S. and Shackleton, C. (2024) The distribution and abundance of woody invasive alien plants in small towns in Eastern Cape Province, South Africa. *Urban Ecosystems,* .

Sjoberg, D. (2024) Abstract only. Available: https://github.com/davidsjoberg/ggsankey.

Stephenson, C.M., MacKenzie, M.L., Edwards, C. and Travis, J.M.J. (2006) Modelling establishment probabilities of an exotic plant, Rhododendron ponticum, invading a heterogeneous, woodland landscape using logistic regression with spatial autocorrelation. *Ecological Modelling,* 193 (3), pp. 747–758.

Stephenson, C.M., Kohn, D.D., Park, K.J., Atkinson, R., Edwards, C. and Travis, J.M. (2007) Testing mechanistic models of seed dispersal for the invasive Rhododendron ponticum (L.). *Perspectives in Plant Ecology, Evolution and Systematics,* 9 (1), pp. 15–28.

Taylor, K., Brummer, T., Taper, M.L., Wing, A. and Rew, L.J. (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Diversity & Distributions,* 18 (9), pp. 942–951.

Theoharides, K.A. and Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist,* 176 (2), pp. 256–273.

Therneau, T. and Atkinson, B. (2023) Abstract only. Available: https://CRAN.R-project.org/package=rpart.

Tyler, C., Pullin, A.S. and Stewart, G.B. (2006) Effectiveness of Management Interventions to Control Invasion by Rhododendron ponticum. *Environmental Management (New York),* 37 (4), pp. 513–522.

Vacek, Z., Vacek, S., Eşen, D., Yildiz, O., Král, J. and Gallo, J. (2020) Effect of Invasive Rhododendron ponticum L. on Natural Regeneration and Structure of Fagus orientalis Lipsky Forests in the Black Sea Region. *Forests,* 11 (5), pp. 603.

Vaz, A.S.&., Kueffer, C., Kull, C.A.&., Richardson, D.M.&., Schindler, S., Muñoz-Pajares, A.J., Vicente, J.R.&., Martins, J., Hui, C., Kühn, I. and Honrado, J.P.&. (2017) The progress of interdisciplinarity in invasion science. *Ambio,* 46 (4), pp. 428–442.

Venables, W.N.&. and Ripley, B.D.&. (2002) *Modern Applied Statistics with S.* Fourth ed. New York: Springer.

Vermeij, G.J. (1996) An agenda for invasion biology. *Biological Conservation,* 78 (1), pp. 3–9.

Walkhighlands (2024) Abstract only. Available: https://www.walkhighlands.co.uk/lochlomond/.

Wichmann, M.C., Alexander, M.J., Soons, M.B., Galsworthy, S., Dunne, L., Gould, R., Fairfax, C., Niggemann, M., Hails, R.S. and Bullock, J.M. (2009) Human-mediated dispersal of seeds over long distances. *Proceedings - Royal Society. Biological Sciences/Proceedings - Royal Society. Biological Sciences,* 276 (1656), pp. 523–532.

Wickham, H., François, &., R, Henry, L., Müller, &., K and Vaughan, D. (2023) dplyr: A Grammar of Data Manipulation.

Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis.* New York: Springer-Verlag.

Wildlife and Natural Environment (Scotland) Act 2011 2011 Part 2 Section 14. Available: https://www.legislation.gov.uk/asp/2011/6/part/2/crossheading/nonnative-species-etc/enacted.