Developing a Habitat Suitability Model for Welsh Lesser Horseshoe Bats

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Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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Abstract

Lesser horseshoe bats (*Rhinolophus hipposideros*) are protected in the UK under the Wildlife and Countryside Act 1981, having a threatened status. Habitat Suitability Models (HSM) offer a practical way to determine species-specific predictions on potential roost sites for bats, aiding in the protection and conservation of threatened species. Fuller, Shewring & Caryl (2018) present a novel HSM method for identifying roost sites for *R. hipposideros* in Wales, UK. This study aims to test the hypothesis that national-scale models are not appropriate for use in making accurate predictions at local levels, by recreating their HSM within Gower AONB, a region of Wales ~1% the size of the whole of Wales. The difference in environmental variables for two pseudo-absence methods (random and building) across Wales and Gower AONB were assessed, and the accuracy of both was investigated using known bat roost presences, provided by the Bat Conservation Trust. Additionally, a third ensemble model was assembled from both pseudo-absence methods and assessed. Sites within Gower AONB with high bat roost presence probability were then identified. This studies' assessments generally supported the stated hypothesis, with Gower AONB having significantly different environmental structure to the whole of Wales, and despite predictive performance being 'fair' for both pseudo-absence methods (0.782 for building pseudo-absences and 0.787 for random pseudo-absences) and the ensemble model (0.700), accuracy was low throughout (known bat presences that should have probabilities of 1.00 instead had probabilities of 0.548 [building pseudo-absences, 0.57 [random pseudo-absences], and 0.571 [ensemble model]). Although Fuller, Shewring & Caryl's HSM have practical use in determining likely roost sites of *R. hipposideros* across Wales, their use across Gower AONB is diminished by the variable environment of the regions being investigated. These findings suggest that applying large-scale HSM's to smaller-scale regions is not effective for identifying potential roost sites for *R. hipposideros* and may potentially serve as a cautionary case study for other species-specific HSM's. However, given that the random pseudo-absence model had 'fair' predictive performance, and was able to correctly predict bat roost presences more than half the time, it was used to provide three sites within Gower AONB of highest probability. These three sites would be used to feed into *R. hipposideros* conservation by providing them to the Bat Conservation Trust for observation. Should these sites prove to include roost sites for *R. hipposideros*, it would suggest the uses of such HSM's across smaller-scale regions still have some merit for other species with large-scale HSM's available.

Contents

1.0 Introduction

1.1 Background

Species-specific distribution models are a reliable method for conservation of many species (Villero, Pla, Camps, Ruiz-Olmo, & Brotons. 2016), such as in predicting potential bat roosts (Razgour, Rebelo, Di Febbraro, & Russo. 2016). Bats, being typically nocturnal animals, are difficult to monitor in the wild, relying instead on known roost locations, and night-time observation surveys, which could include bat detectors that are sensitive enough to detect and record bat echolocation calls, or harmless traps such as mist and harp traps. Species distribution models make for an easier method of determining possible roost locations, providing sites for which observation surveys can be carried out, contributing to known-presence data. Species distribution modelling also doesn't require expensive equipment, long hours during nights for observations, or handling of bats that can stress the animals or risk spread of disease to humans. Lesser Horseshoe Bats have seen intense declines in the UK, being protected under the Wildlife and Countryside Act, 1981, as well as considered a priority species under the UK Post-2010 Biodiversity Framework, and a European Protected Species under Annex IV of the European Habitats Directive (European Commision. 2020). The Bat Conservation Trust, a registered charity in England, Wales, and Scotland, collaborate with local bat groups and its members to monitor and protect bat populations, whilst educating and engaging with the community on matters concerning bats. All bats in the UK are protected, meaning it is illegal to injure or kill any, disturb or destroy a roost or a roost site, sell or trade bats, or obstruct a bats access to its roost. This protected status applies to buildings, meaning they need to be surveyed prior to destruction or renovation (Conservation of Habitats and Species Regulations. 2017). Furthermore, bats economic value includes pest control, seed dispersal, and pollination, to name a few (Kasso & Balakrishnan. 2013). This highlights the need for UK conservation efforts of bats, including *R. hipposideros*.

1.2 Lesser Horseshoe Bat Biology

The Lesser Horseshoe Bat, *Rhinolophus hipposideros* (henceforth *R. hipposideros*), is a small Microchiroptera, insectivorous species found throughout Europe and the United Kingdom, with an estimated population size of 159 roost sites across Wales, Southwest and West Midlands of England (Bat Conservation Trust. 2020). Their unselective diet consists of several commercially important pest orders, where moths of Lepidoptera make up 18.7% of their diet, and mosquitoes and biting midges of Nematocera made up 13.4% of their diet (McAney & Fairley. 1989). Bats are prominent moth predators, the evolutionary arms race between the two being well documented (ter Hofstede & Ratcliffe. 2016), highlighting the commercial and agricultural importance of *R. hipposideros* worldwide, given the diversity in their diet and propensity for feeding on numerous moth pest species (Baroja *et al*. 2019). They spend the day roosting in building roofs, but also have night roosts that individuals use during their night-time feeding for rest and digestion, upwards of five night roosts per individual (Knight, & Jones. 2009). Foraging would tend to occur 2-3 km from these maternity roosts within woodlands, hedgerows, and tree lines (Schofield. 1996), with preference for broadleaf forests (Bontadina, Schofield, & Naef-Daenzer. 2002). Diet is determined by examining faeces, or in more modern studies, performing DNA metabarcoding (Aldasoro *et al*. 2019), but this does not provide diet by sex. On average, *R. hipposideros* was found to travel roughly 14.2 km per night (Downs et al. 2016). *R. hipposideros* mating occurs in the Autumn each year, and in the following Spring, females arrive at mixed-sex maternity roosts in buildings in May, with most females giving birth to a single pup in June/July. The young are then raised in these maternity roosts for four to five weeks until they're able to fly. Throughout the winter months, *R. hipposideros* hibernate in caves and cellars, and typically live for twenty years (Bat Conservation Trust, 2010).

R. hipposideros are listed as "near threatened" across Europe by the IUCN, and due to their dwindling population size are protected under the UK Habitats and Species Regulations 2017, specifically the Council Directive 92/43/EEC. Suggested causes for population decline have been attributed to habitat loss and fragmentation, climate change, and pesticide contamination (Conservation of Habitats and Species Regulations, 2017). It has also been suggested that competition with Pipistrelle bats (*Pipistrellus pipistrellus*) could also negatively affect population sizes (Arlettaz, Godat, & Meyer. 2000). However, early monitoring of *R. hipposideros* suggests populations are slowly increasing (Wright, Kitching, Hanniffy, Palacios, McAney, & Schofield, 2022), providing a trend for which to compare to with modern monitoring.

1.3 Monitoring methods

Typically, surveys of known foraging areas or summer roost counts are used to monitor the trends in bat populations (Jan et al. 2017, Warren & Witter. 2002). This relies on detecting bats at periods of very low visibility during dusk and night, as well as contending with changes as roosts come and go as the maternities change. Whilst visual counts are cost effective and can be done by many observers, be they volunteers or trained experts, this recording method suffers from the same disadvantages of any observation-based count data. Namely, it relies on observers counting every present individual, which is made more difficult given the low-light environments, as well as simply being in the right place to observe bats, a disadvantage that has needed to be considered during such studies for decades (Marshall & William. 1982).

However, a novel model-based strategy was presented by Fuller, Shewring, & Caryl (2018) that could make monitoring this bat species considerably more cost and time efficient. By ascertaining environmental factors ideal for *R. hipposideros* based on known roosts, potential roost sites could be estimated using geological survey data, thus indicating potential sites for monitoring. This includes the use of pseudo-absence data, which is background data with known environmental variables but no known bat presence. Fuller, Shewring, & Caryl's (2018) work was conducted across the whole of Wales, UK, using 116 locations as presence data and 21 measurable environmental variables across 8 spatial scales to quantitatively determine favourable roost conditions. The study identified 19 potentially suitable buildings to contain roosts with a >0.5% probability, roughly 1% of suitable buildings present across all of Wales. 21 measurable environmental variables across 8 spatial scales were selected and quantitatively assessed against known bat roost locations to determine favourable environmental conditions for *R. hipposideros*. This research has the potential to be appliable across smaller study area scales, maintaining its resolution and accuracy in pinpointing possible bat roost sites. However, resolution of a HSM is only so fine, and when considering the ~21,000 km^2 area of Wales's environment being investigated, an "average environment" made of the averages of all variables will have a large standard deviation. Small-scale regions of Wales at local levels may have significantly different environmental variability, skewing the ability of the HSM to accurately predict bat roosts. Although it is an appealing application of HSM's to be used when assessing a local scale environment within the model's study area, it bears investigating as to whether this is a reliable technique or not.

1.4 Aims and Objectives

The overall aim of this study is to test the hypothesis that national-scale models are not appropriate for use in making accurate predictions at local levels. The change in scale is not something accounted for in the model's creation, and local environments can vary considerably from an "average environment" model prediction, as investigated in modelling in studies such as that done by Hirzel & Arlettaz (2003).

1. Reproduce Habitat Suitability Model (HSM) across Wales, as produced by Fuller, Shewring, & Caryl (2018). This will generate a HSM for use in this study.

To investigate the HSM produced by Fuller, Shewring, & Caryl (2018) across Gower AONB, its code was used to generate an identical HSM for use in this study, provided by the aforementioned. This HSM would form the basis of this studies' investigation within ArcGIS Pro, and all further analyses. Once the HSM is recreated, it can be manipulated to only Gower AONB and have Pixel Intensity Values mapped over it to deduce predictive performance.

2. Assess environmental variables used in Wales HSM across only the Gower AONB, derived from pseudo-absence points from Fuller, Shewring, & Caryl's (2018) study that were generated in the Gower AONB. These will be compared to visualise difference in environment structure between Wales and Gower AONB.

To ensure reliability, the environmental variables used by Fuller, Shewring, & Caryl (2018) were also used when investigating only Gower AONB. The HSM used the environmental variables with the highest predictive probability when generating its pseudo-absence points, but Gower AONB, being only a tiny portion of the whole of Wales, would generate a different HSM due to the natural environmental variability. This can be best visualised by overlaying histograms of each environmental variable, and statistically scrutinised using Kolmogorov-Smirnov tests to fully investigate the differences.

3. Assess the accuracy of Wales HSM when applied to Gower AONB, using known bat presence data (supplied by the Bat Conservation Trust) to make comments on said accuracy.

To test the true effectiveness of the HSM, the Pixel Intensity Values of known bat presences within Gower AONB can be generated from the model. This presence data should ideally have been predicted by the model, with Pixel Intensity Values indicating high probability. This will give a predictive performance indicator of the HSM as a result.

4. Using the HSM within the Gower AONB, deduce possible Lesser Horseshoe Bat roost sites to inform conservation efforts with the Bat Conservation Trust.

A truly effective HSM will be able to positively inform conservation efforts by predicting roost sites to a high predictive probability that have not yet been identified. This studies' hypothesis is contradictory to this aim, however, the HSM may still have application, given Gower AONB was an area included in Fuller, Shewring, & Caryl's (2018) original HSM. In a scenario where this hypothesis is rejected, or not fully accepted, the HSM's use in providing reliable predicted roosts to the Bat Conservation Trust is an opportunity not to be missed. This will be determined by the predictive performance of the HSM across Gower AONB as stated by the third aim mentioned above.

It is known by the Bat Conservation Trust that Lesser Horseshoe Bats are present in Gower, Wales. Using a Species Distribution Model produced specifically for Lesser Horseshoe Bats across Wales to determine the accuracy of using such models across smaller geographical scales will highlight the application of species distribution models used in this way, whilst potentially highlighting further roost sites not currently observed.

2.0 Methodology

2.1 Study Area

The study area covered the Gower, a peninsula off the coast of southwest Wales, specifically the area designated as an Area of Outstanding Natural Beauty (AONB) (OS grid reference: SS465904). The polygon used as a boundary for this area was produced in ArcGIS Pro v2.8.0 (ArcGIS Development Team, 2021), using the Lle database (Lle; http://lle.gov.wales/catalogue/item/ProtectedSitesAreasOfOutstandingNaturalBeauty/?lang=en) and refined to land area only using OS Vector Map District (OS Data Hub, 2019) (Figure1). This AONB accounts for <1% of the area of Wales, at 149 km^2. As a peninsula, most of the Gower AONB's border is coastland, with its landmass consisting mainly of heather grasslands and deciduous woodlands, with predominantly arable land, and saltmarshes to the north. Less than 2 km^2 of Gower AONB is covered by buildings, housing a human population of ~10,000 (https://landscapesforlife.org.uk/about-aonbs/aonbs/gower).

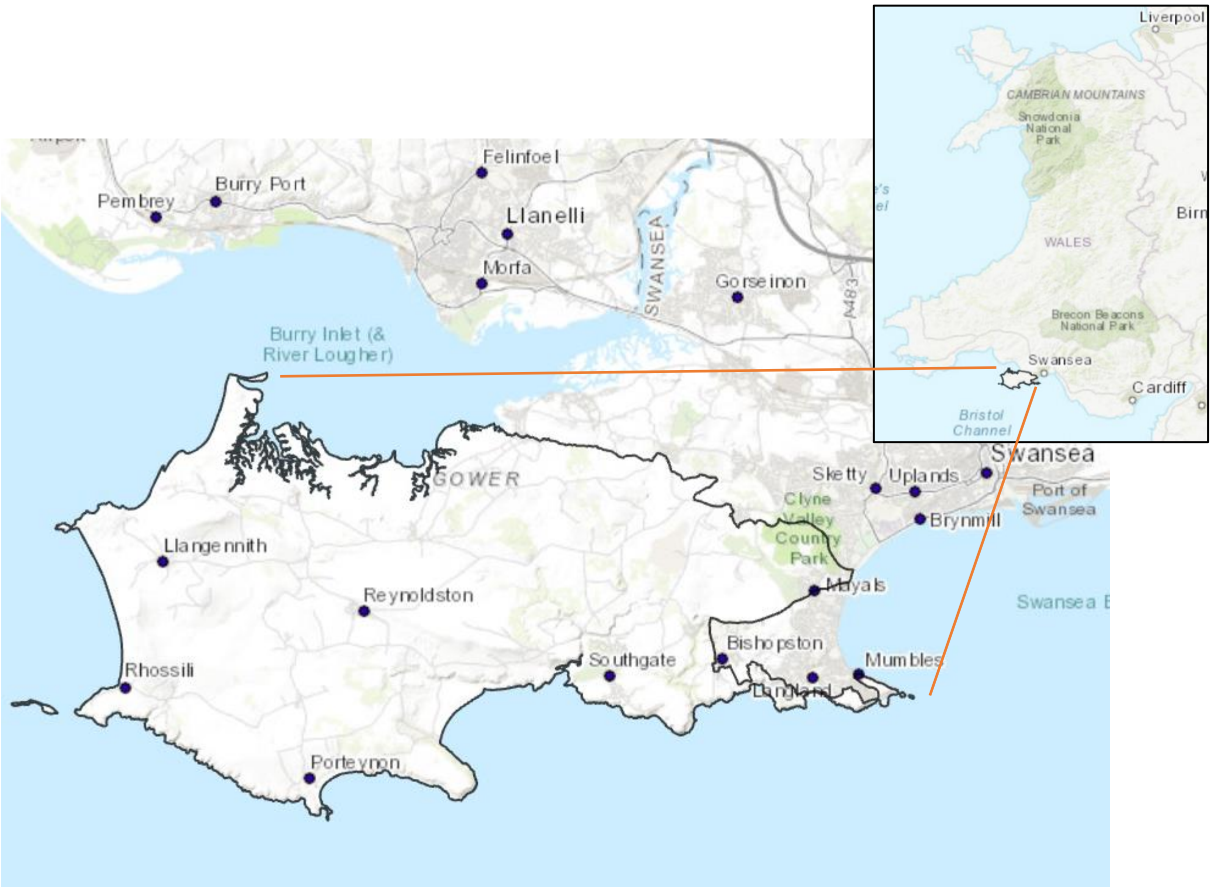


Figure 1. Designated boundry for study area of the Gower AONB within Wales, UK, not accounting for surface area of sea. Dark blue points are aspects of the base map layer, and are reference points for towns and villages. Produced in ArcGIS Pro v2.8.0.

2.2 Bat Roost Recordings

Bat maternity roost observations across the Gower AONB were carried out by volunteers of the Bat Conservation Trust using visual observation at reported bat roosts in conjunction with bat echolocation recorders to determine the species being observed (BCT; https://www.bats.org.uk/). *R. hipposideros* are known to have populations in the Gower AONB, with several cave and building roosts being documented. It was these roosts that were observed to obtain bat count data, providing this studies' "Presence" data (Figure 2). Given these are observation surveys conducted by amateur volunteers and experts, the accuracy of such data has its limitations, as discussed previously.

2.3 Pseudo-absence Selection

Fuller, Shewring, & Caryl (2018) produced several pseudo-absence datasets in their research, to account for the lack of true absence locations. For this study, "random selection of 10,000 buildings from non-urban areas" (PseudoAbsBuild) was decided upon and sampled to only points found within

GowerAONB+0.5BUFFER, totalling 104 points (see Appendix). PseudoAbsBuild was selected due to the bat presence data for the Gower AONB being all buildings, and to provide a larger data set for the purpose of reliable findings.

Additionally, "random selection of 10,000 locations from the background of the study area" (PseudoAbsRand) was included for comparison to building pseudo-absences and was sampled to only points found within GowerAONB+0.5BUFFER, totalling 76 points (see Appendix).

Furthermore, Fuller, Shewring, & Caryl (2018) implemented "non-chiropteran mammal record centre data" in their study to indicate areas mammal surveys had been conducted, but no bats species were recorded. However, this was not considered for Gower AONB due to a lack of data points; only six.

2.4 Bat Presence Data within Gower AONB

There were 17 locations observed to generate this data (see Appendix), provided by the Bat Conservation Trust. Three points were within a 0.5 mile range outside of the designated AONB boundary. It was decided that the study would benefit from using all locations, given the sample size was already quite small, so a 0.5 mile boundary was added to the AONB boundary (Figure. 2), and all analysis were done including this extension. The polygon produced by combining Gower AONB with the 0.5 mile buffer zone will henceforth be called GowerAONB+0.5BUFFER.

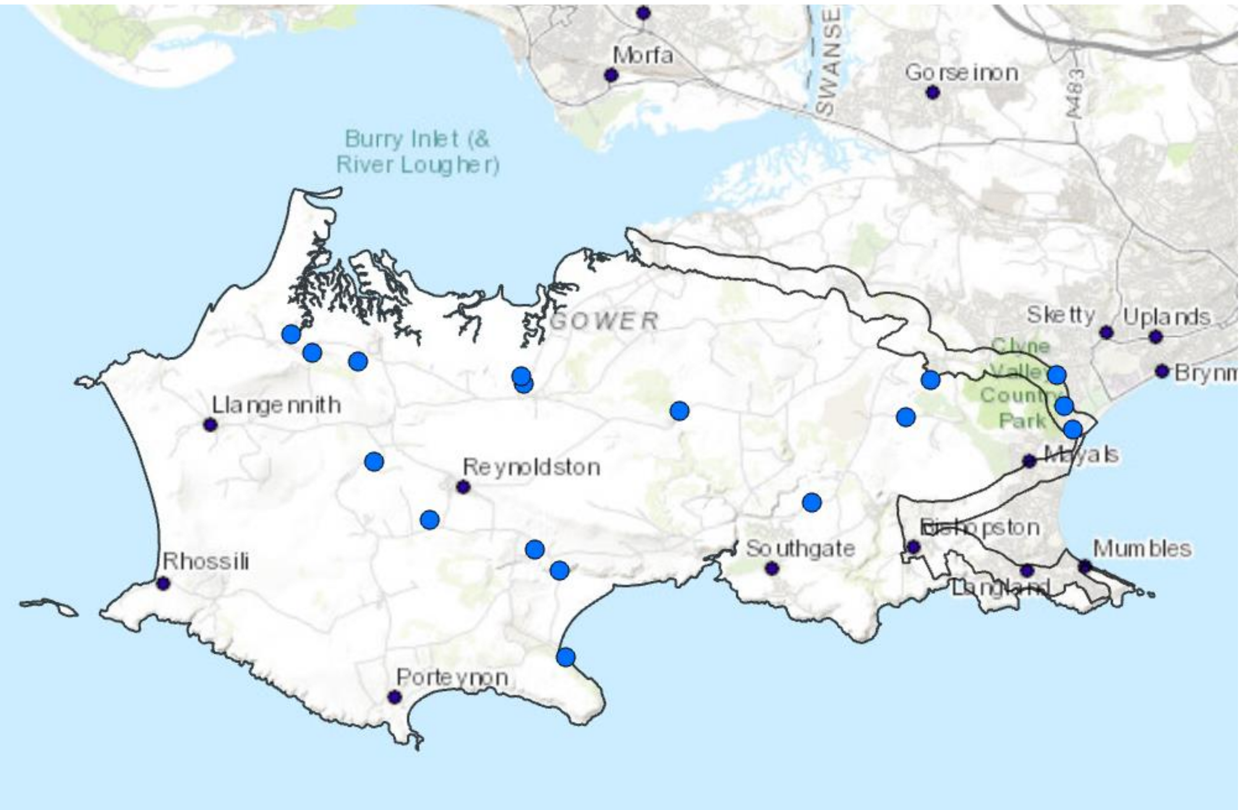


Figure 2. Gower AONB boundary with 0.5 mile boundary extension, not accounting for sea water, and all 17 Presence location data points (in sky blue). Dark blue points are aspects of the base map layer, and are reference points for towns and villages. Produced in ArcGIS Pro v2.8.0.

2.5 Pseudo-absence data within Gower AONB

Using the polygon GowerAONB+0.5BUFFER described in Figure1 to screen environmental variable data, PseudoAbsRand and PseudoAbsBuild were sampled to only within Gower, producing PseudoAbsRandAONB and PseudoAbsBuildAONB (Figure3), respectively. Bat Presence data was also added to the map (Figure2), providing both presence and pseudo-absence data for the analysis.

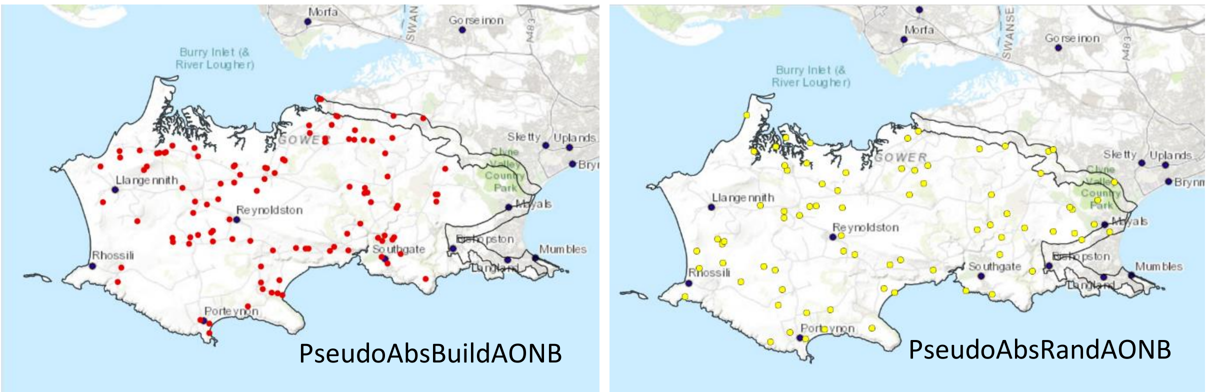


Figure 3. GowerAONB+0.5BUFFER including PseudoAbsBuildAONB (104 total points in RED) and PseudoAbsRandAONB (76 total points in YELLOW) pseudo-absence data points. Dark blue points are aspects of the base map layer, and are reference points for towns and villages.

Secondary layers of TIF files were added and clipped to just within GowerAONB+0.5BUFFER. These layers, reproduced from data provided by Fuller, Shewring, & Caryl (2018), had Pixel Intensity Values (PIV's) on a grey scale included for visualisation. Each pixel and the associated PIV, determined by the Habitat Suitability Model produced by Fuller, Shewring, & Caryl (2018), indicate bat probability in that region by pseudo-absence selection. The PIV for pseudo-absence and presence points were then derived from each respective layer for PseudoAbsRand, PseudoAbsRandAONB, PseudoAbsBuild, PseudoAbsBuildAONB and Bat Presence for the purpose of addressing Aims & Objectives 2. Further, Area Under Curve (AUC) statistics were calculated in R Studios from Receiver Operating Characteristics (ROC) curves to determine sensitivity and specificity of both random and building pseudo-absence HSM's for Gower AONB for full-model performance comparison. The ROC curves here would indicate the performance of the models' ability to predict bat roosts from the pseudo-absences and true presence data used across Gower AONB. To make comments on ensemble performance, random pseudo-absence and building pseudo-absence data was combined to produce BuildRandAONB. This included combining TIF files of PseudoAbsBuildAONB and PseudoAbsRandAONB to generate a new TIF file that averaged the PIV's and collated all pseudo-absences for PseudoAbsBuildAONB and PseudoAbsRandAONB. An AUC value was also calculated for the ensemble model. Lastly, for visual comparison, statistics for the most important environment variables for random pseudo-absence and building pseudo-absence were extracted for PseudoAbsBuild and PseudoAbsBuildAONB, and PseudoAbsRand and PseudoAbsRandAONB. These statistics were compiled and presented in two-way histograms with Wales-wide data scaled against

GowerAONB+0.5BUFFER data at a ratio of 1:100. This was done to compare the histogram shape and pattern, and not lose the GowerAONB+0.5BUFFER data against the Wales-wide data of considerably greater volume. Kolmogorov-Smirnov tests were then done for each environmental variable to compare the distributions between Wales and Gower AONB. This acted as a quantitative investigation of whether the AONB data was significantly different from the Wales data it was a subset of.

2.6 Environmental Variable Selection

Fuller, Shewring, & Caryl (2018) used twenty-one environmental variables, each across eight spatial scales (100 m, 500 m, 1000 m, 1500 m, 2000 m, 3000 m, 4000 m, and 5000 m), in producing their species distribution models. These scales were applied to the tested environmental variables (see their Supplemental Material S3). Fuller, Shewring, & Caryl (2018) derived variables most important for bat presence probability from their HSM, which did not include all variables, and those it did, only at the single spatial scale most important. These important variables were different between PseudoAbsBuild and PseudoAbsRand. Given these variables have already been found to be most important for bat presence probability by Fuller, Shewring, & Caryl (2018), this study uses those most important variables at the described spatial scales, providing fourteen environmental variables for PseudoAbsRandAONB, and sixteen for PseudoAbsBuildAONB (Figure4).

Figure 4. Environmental variables for each model considered in this study, from a possible twenty-one variables, each at eight spatial scales. These variables were chosen due to their being most important for bat presence probability, as determined by Fuller, Shewring, & Caryl (2018)

Environmental Variables most important for Bat Presence Probability	
PseudoAbsBuild	**PseudoAbsRand**
Building Proportional Cover (100m)	Building Proportional Cover (100m)
Broadleaf Proportional Cover (4000m)	Distance to Nearest Woodland (100m)
Distance to Nearest Woodland (100m)	Broadleaf Woodland Proportional Cover (400m)
Broadleaf Woodland Maximum Patch Size (5000m)	Woodland Edge Density (5000m)
North-South Aspect (3000m)	Woodland Proportional Cover (5000m)
Woodland Maximum Patch Size (3000m)	Broadleaf Woodland Maximum Patch Size (5000m)
Elevation (3000m)	Elevation (3000m)
East-West Aspect (500m)	Slope (5000m)
Woodland Proportional Cover (5000m)	North-South Aspect (1000m)
Surface Water Proportional Cover (5000m)	Distance to Nearest Conifer Forest (100m)
Roughness (3000m)	East-West Aspect (1000m)
Slope (5000m)	Road Density (5000m)
Distance to Nearest Conifer Forest (100m)	Surface Water Proportional Cover (5000m)
Woodland Edge Density (5000m)	Distance to Nearest Surface Water (100m)
Distance to Nearest Surface Water (100m)	
Road Density (1000m)	

2.7 Determining possible Lesser Horseshoe Bat roost sites within Gower AONB

PseudoAbsBuildAONB, PseudoAbsRandAONB, and BuildRandAONB will be examined to determine potential roost sites. The ensemble model will attempt to take both pseudo-absences into account, making for a more complete HSM for GowerAONB, though any inaccuracies in PseudoAbsBuildAONB or PseudoAbsRandAONB would only be compounded. Of the three (PseudoAbsBuildAONB, PseudoAbsRandAONB, BuildRandAONB), the PIV's for the Bat Presence will be determined and averaged, with the highest average HSM being used to determine potential bat roost sites. The chosen HSM will then have buildings within Gower AONB that have a PIV of 1.00 determined, and their map coordinates listed as potential bat roost sites. A PIV of 1.00 was decided upon to keep the initial number of possible sites low, and to offset low reliability if the chosen HSM does not accurately predict bat roost sites, determined by the average PIV of Bat Presence.

3.0 Results

3.1 Recreating the Welsh lesser horseshoe bat HSM

TIF files were generated from data provided by Fuller, Shewring, & Caryl (2018) in R Studios, and layered over Wales as rasters in ArcGIS Pro. These TIF files, PseudoAbsBuild and PseudoAbsRand, display the Pixel Intensity Value (PIV) for "building pseudo-absences" (Figure 5,panel A) and "random pseudo-absences" (Figure 5,panel B).

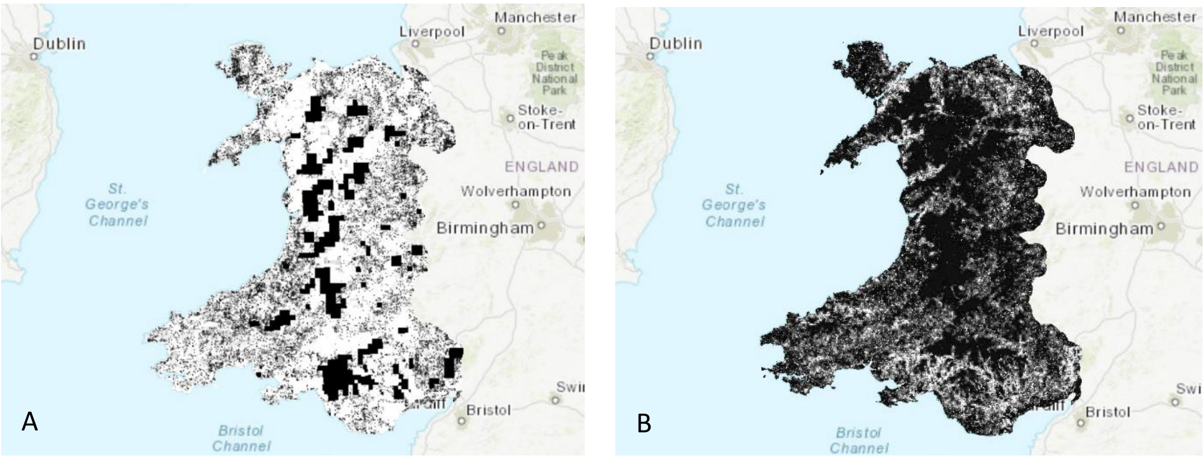


Figure 5. Pixel Intensity map for Wales, UK, produced using data provided by Fuller, Shewring, & Caryl (2018). Greyscale pixel intensity values denote predicted habitat suitability, with black (low pixel intensity) showing probability = 0.00, and white (high pixel intensity) showing probability = 1.00. Panel A: Pseudo-absences restricted to buildings. Panel B: Pseudo-absences without spacial restrictions.

3.2 Focusing the Welsh lesser horseshoe bat HSM on Gower Area of Outstanding Natural Beauty

For both Random Pseudo-Absences and Building Pseudo-Absences, bat predictions from Fuller, Shewring, & Caryl (2018) were mapped across Gower as high resolution, greyscale Pixel Intensity Maps. The darker areas have low bat predictions, whilst whiter areas have high bat predictions (Figure 5).

As in Fuller, Shewring & Caryl (2018) (see their Supplementary Figure S4), the Building Pseudo-Absence model predicts generally high probability coverage (Figure 6, panel A vs. B), with buildings being the focal point for darker areas of low probability (for example, see Figure6, panels C and D). In contrast, the Random Pseudo-Absence model predicted much lower probability coverage, with buildings being the focal point for ligher areas of high probability.

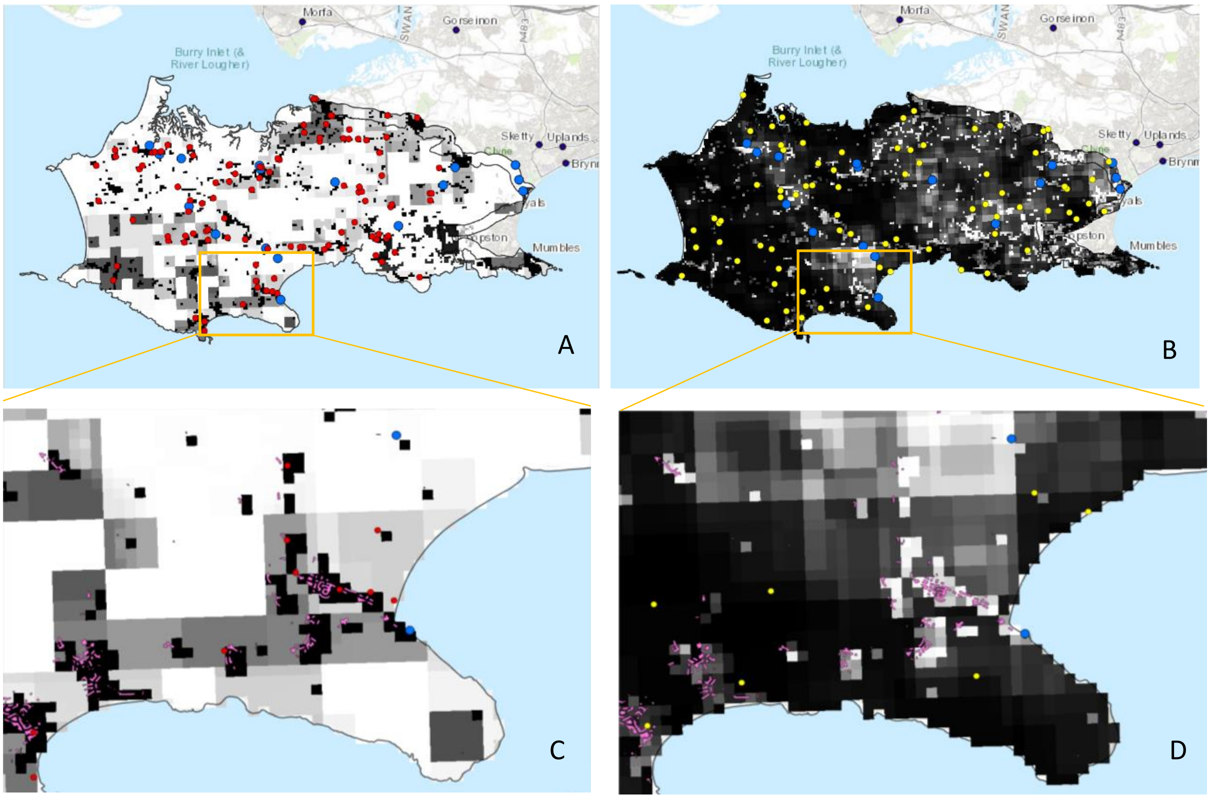


Figure 6. Pixel Intensity Map for Gower Area of Outstanding Natural Beauty (AONB) with additional 0.5 km buffer. Greyscale pixel intensity values denote predicted habitat suitability, with black (low pixel intensity) showing probability = 0.00, and white (high pixel intensity) showing probability = 1.00. Blue points show bat presence observed data. Panel A: Red points show pseudo-absences from Fuller, Shewring, & Caryl (2018) restricted to buildings. Panel B: Yellow points show pseudo-absences without spatial restriction. Panels C and D show zoomed-in (5x zoom of panels A and B respectively) areas chosen randomly for purpose of providing an example. Pink areas denote buildings.

To test the effectiveness of the HSM at the spatial scale of Gower AONB, pseudo-absences and empirical data on bat presence were used to construct Receiver Operating Characteristics (ROC) plots and calculate the Area Under Curve (AUC) values. This assesses the balance between ‘sensitivity’ (true positive rate, tpr) and ‘specificity’ (1 – false positive rate, 1-fpr) for a given model.

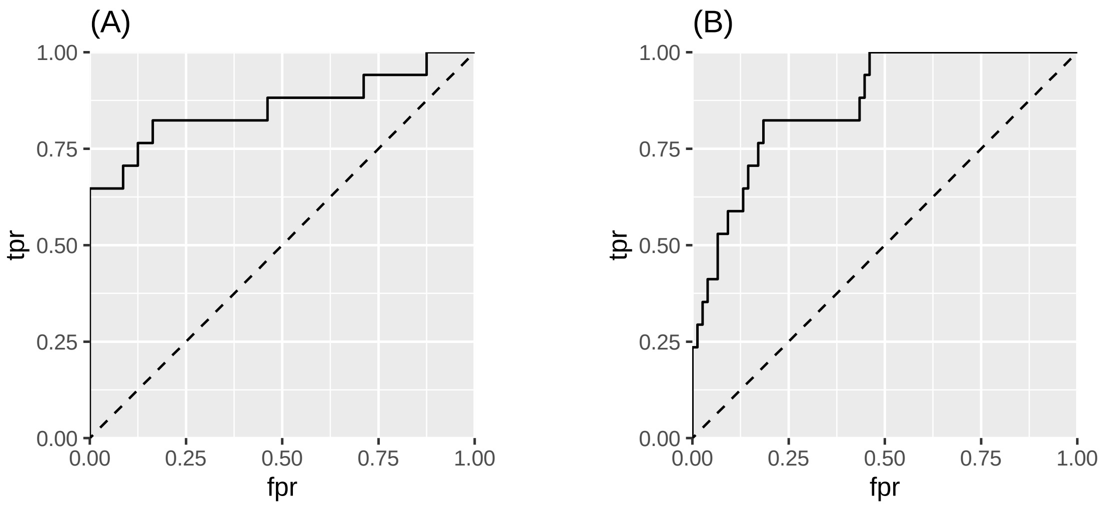


Figure 7. ROC 'curves' (solid line) for the building pseudo-absence HSM (panel A) and random pseudo-absence HSM (panel B) for Gower AONB. The diagonal line represents random prediction (AUC = 0.5), with tpr = 'true positive rate' (sensativity), and fpr = 'false positive rate' (1-specificity).

The AUC value was 0.782 for the building pseudo-absence HSM, and 0.787 for the random pseudo-absence HSM. Despite the substantial difference in average PIV, these AUC values suggest both models have very similar performance, representing 'fair' (Araújo, Pearson, Thuiller, & Erhard. 2005) discriminative ability. In fact, prediction is based on variation and pattern around average values, so further critical analysis is needed to fully assess model performance. These AUC values indicate both pseudo-absence models are returning 'true positives' more than 'false positives'; the pseudo-absence points are actual bat absences more often than they are bat presences.

<u>3.3 Assessing environmental biases within Gower AONB compared to Wales</u>

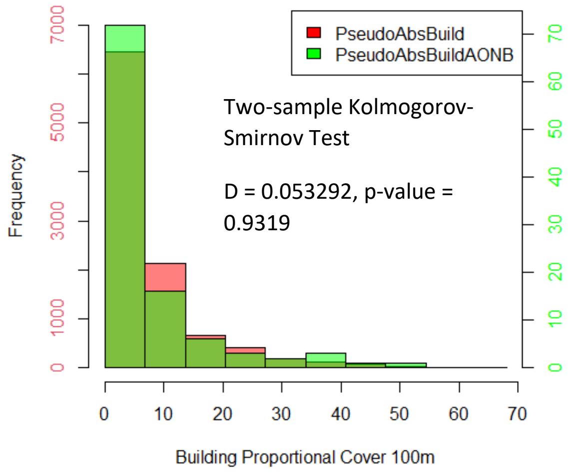
Given the importance of the environmental variables chosen, the more dissimilar their frequency in GowerAONB to that across the whole of Wales, the more likely we can expect a HSM for GowerAONB to be different to one for the whole of Wales.

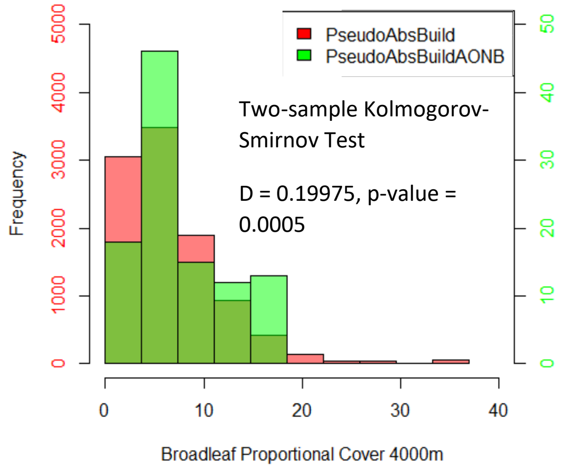
For building pseudo-absence, of the sixteen variables, only three variables showed similar patterns of distribution across GowerAONB as they did for the whole of Wales: Building Proportional Cover (100m) (D=0.053292, p=0.9319), Distance to Nearest Woodland (100m) (D=0.056513, p=0.8975), and East-West Aspect (500m) (D=0.093002, p=0.3354). Broadleaf Proportional Cover (4000m), Broadleaf Woodland Maximum Patch Size (5000m), North-South Aspect (3000m), Woodland Maximum Patch Size (3000m), Elevation (3000m), Woodland Proportional Cover (5000m), Surface Water Proportional Cover (5000m), Roughness (3000m), Slope (5000m), Distance to Nearest Conifer Forest (100m), Woodland Edge Density (5000m), Distance to Nearest Surface Water (100m), and Road Density (1000m) had statistically significant Kolmogorov-Smirnov test p-values, rejecting the null hypothesis that the Gower AONB and whole Wales distributions are the same (Figure 8).

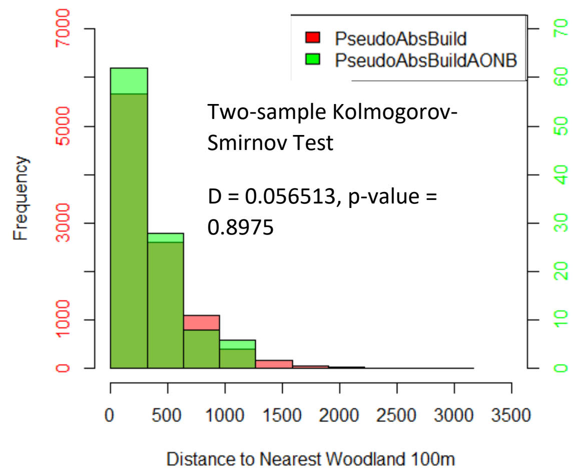
For random pseudo-absence, of the fourteen variables, only three variables showed a similar pattern of distribution across Gower AONB as they did for the whole of Wales: Building Proportional Cover (100m) (D=0.02366, p=1), Distance to Nearest Woodland (100m) (D=0.15522, p=0.0528), and Distance to Nearest Surface Water (100m) (D=0.13031, p=0.1543). Broadleaf Woodland Proportional

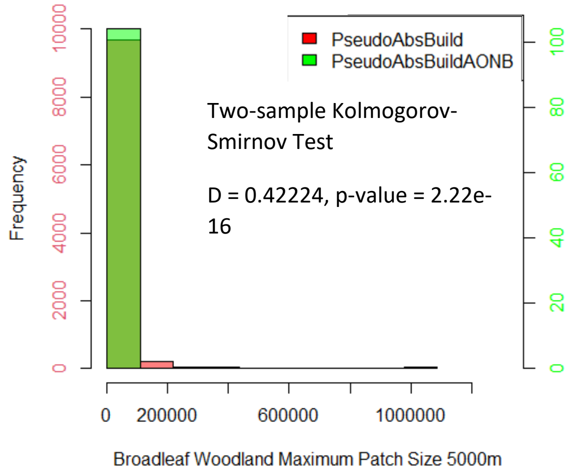
Cover (4000m), Woodland Edge Density (5000m), Woodland Proportional Cover (5000m), Broadleaf Woodland Maximum Patch Size (5000m), Elevation (3000m), Slope (5000m), North-South Aspect (1000m), Distance to Nearest Conifer Forest (100m), East- West Aspect (1000m), Road Density (5000m), and Surface Water Proportional Cover (5000m) had statistically significant Kolmogorov-Smirnov test p-values, rejecting the null hypothesis that the Gower AONB and whole Wales distributions are the same (Figure 9).

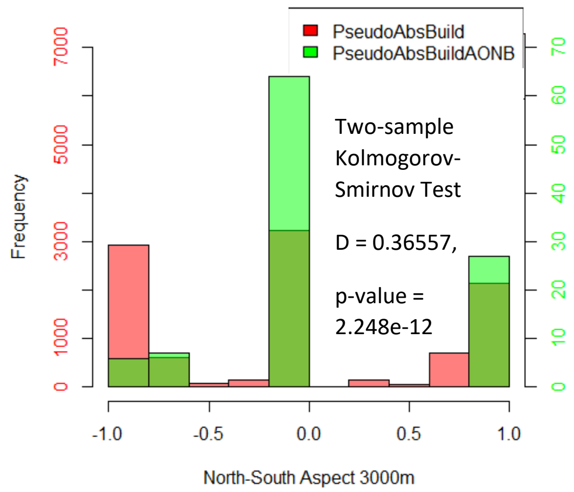
These distributions can be related to the environmental variable importance done by Fuller, Shewring, & Caryl (2018), to determine whether variables with distribution biases were important or not to *R. hipposideros* probability. Building Proportional Cover (100m) was the most important variable in both models, with Distance to Nearest Woodland (100m) the second and third most important for the random pseudo-absence model and building pseudo-absence model, respectively. Distance to Nearest Surface Water (100m) was the least important for random pseudo-absence, and East-West Aspect (500m) was eighth most important (Figure 10).

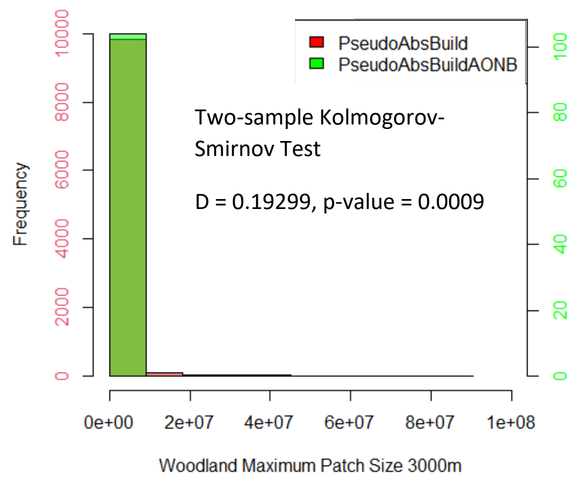

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.053292, p-value = 0.9319
Frequency
Building Proportional Cover 100m

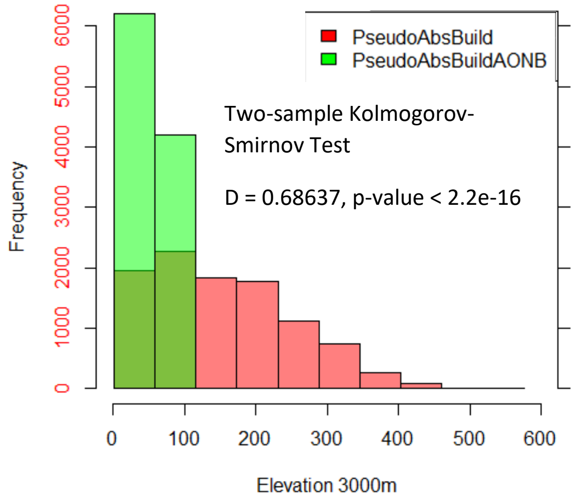

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.19975, p-value = 0.0005
Frequency
Broadleaf Proportional Cover 4000m

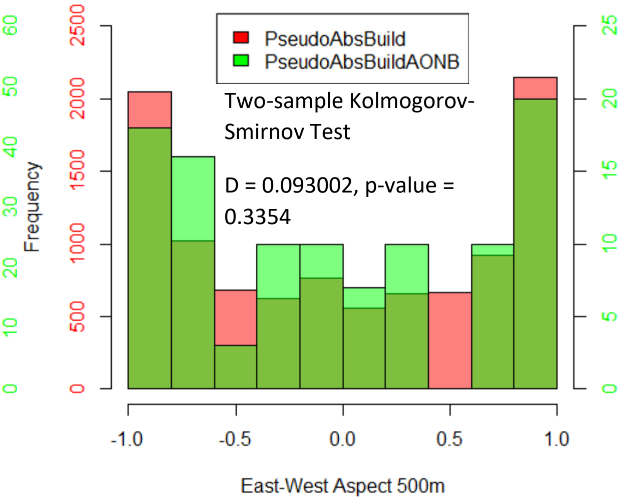

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.056513, p-value = 0.8975
Frequency
Distance to Nearest Woodland 100m

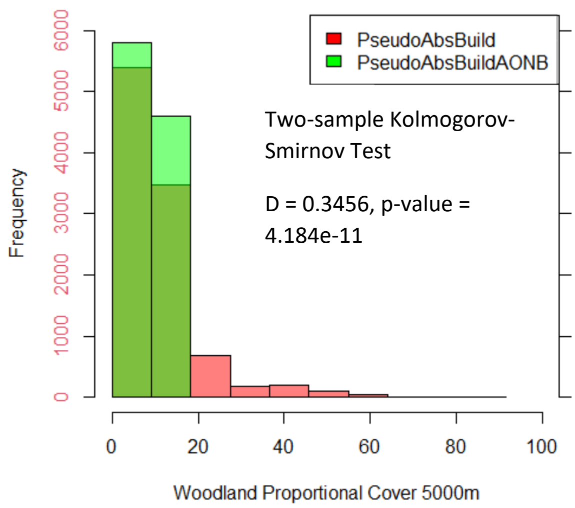

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.42224, p-value = 2.22e-16
Frequency
Broadleaf Woodland Maximum Patch Size 5000m

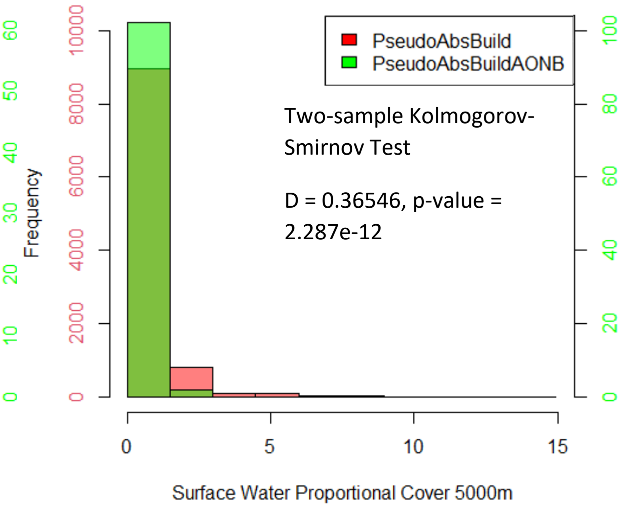

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.36557,
p-value = 2.248e-12
Frequency
North-South Aspect 3000m

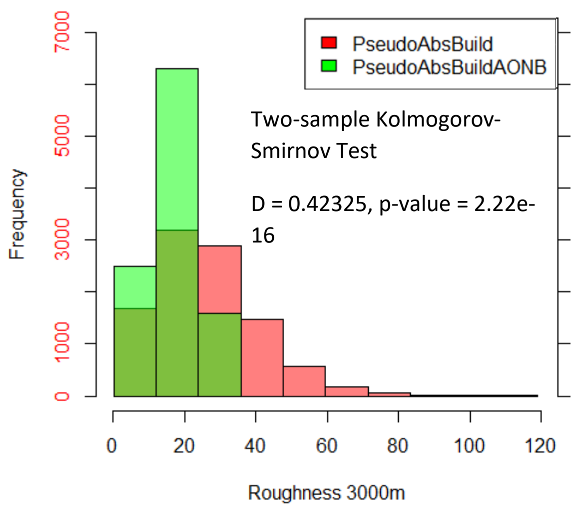

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.19299, p-value = 0.0009
Frequency
Woodland Maximum Patch Size 3000m

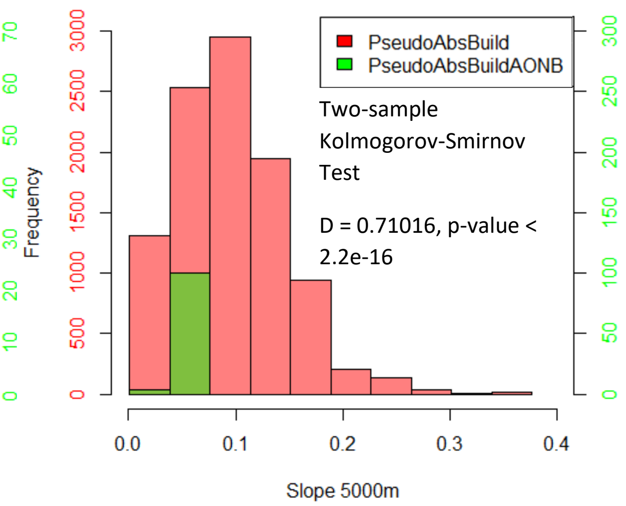

PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.68637, p-value < 2.2e-16
Frequency
Elevation 3000m


PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.093002, p-value = 0.3354
Frequency
East-West Aspect 500m


PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.3456, p-value = 4.184e-11
Frequency
Woodland Proportional Cover 5000m


PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.36546, p-value = 2.287e-12
Surface Water Proportional Cover 5000m


PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.42325, p-value = 2.22e-16
Frequency
Roughness 3000m


PseudoAbsBuild
PseudoAbsBuildAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.71016, p-value < 2.2e-16
Frequency
Slope 5000m

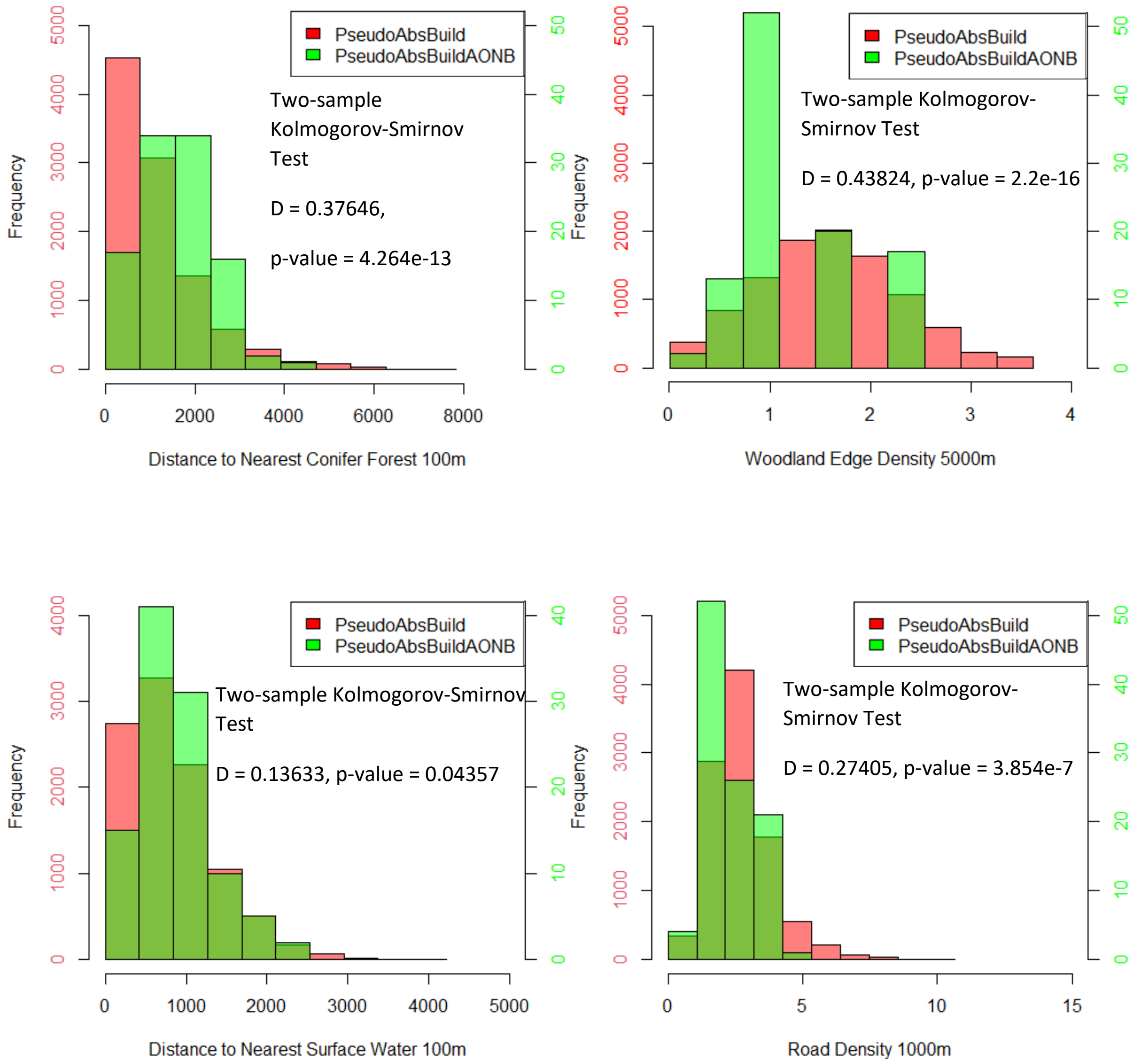
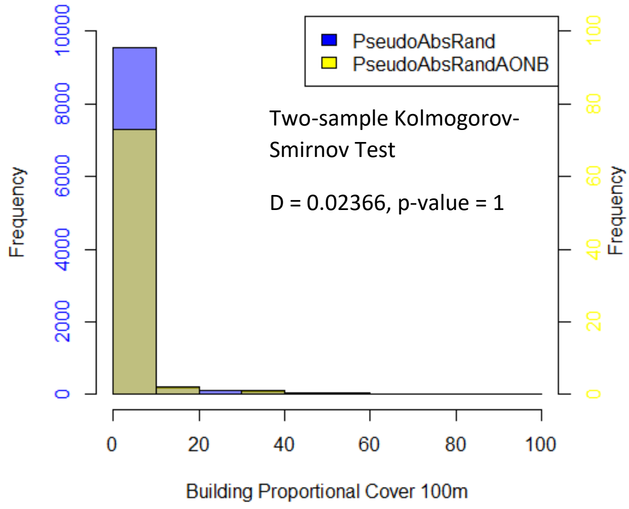
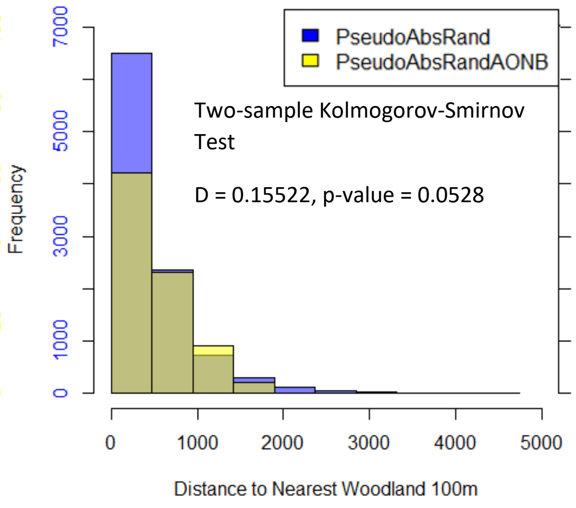
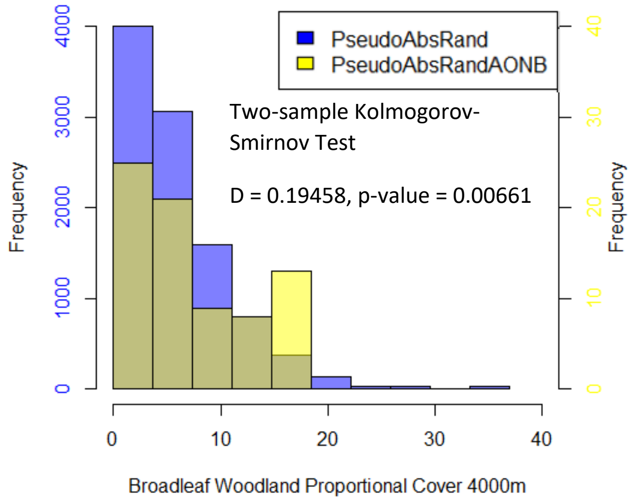
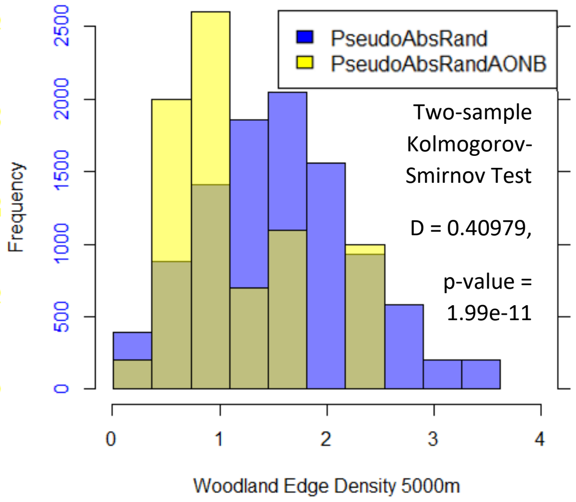


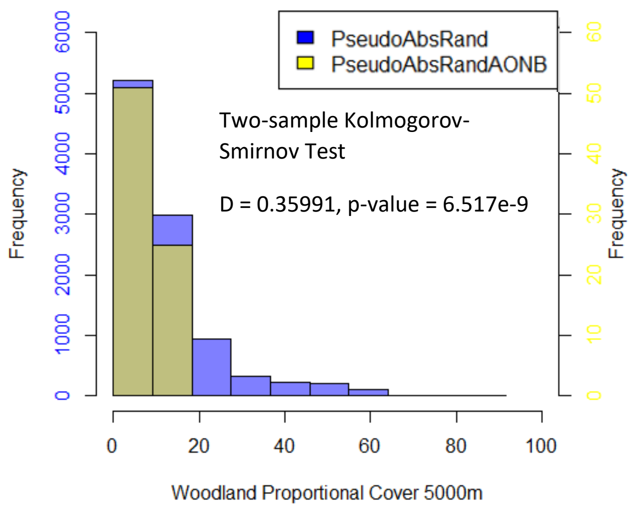
Figure 8. Histograms derived from environmental variables for "building pseudo-absence" across all of Wales (PseudoAbsBuild) compared with only across GowerAONB (PseudoAbsBuildAONB). Environmental Variables chosen are those considered most important in predicting *R. hipposideros* in AUC building pseudo-absence. Frequency axis for PseudoAbsBuildAONB were kept at 1/100th of the Frequency axis for PseudoAbsBuild to make histogram shape comparison across environmental variables concise.

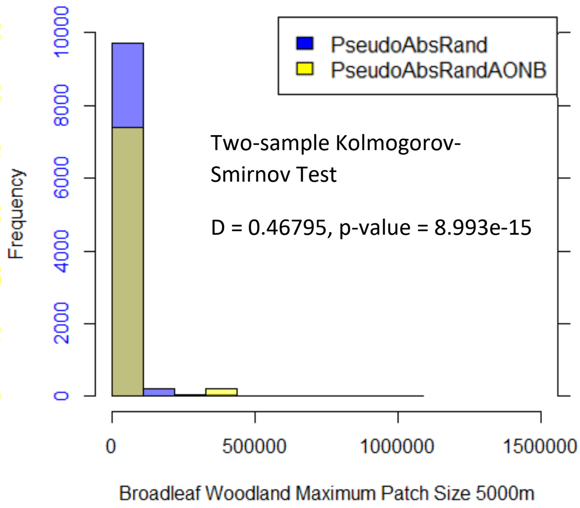

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.02366, p-value = 1
Frequency
0 2000 4000 6000 8000 10000
0 20 40 60 80 100
Building Proportional Cover 100m

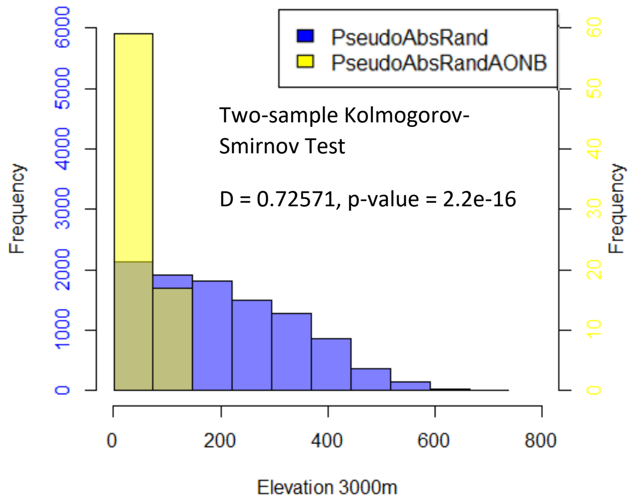

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.15522, p-value = 0.0528
Frequency
0 1000 3000 5000 7000
0 1000 2000 3000 4000 5000
Distance to Nearest Woodland 100m

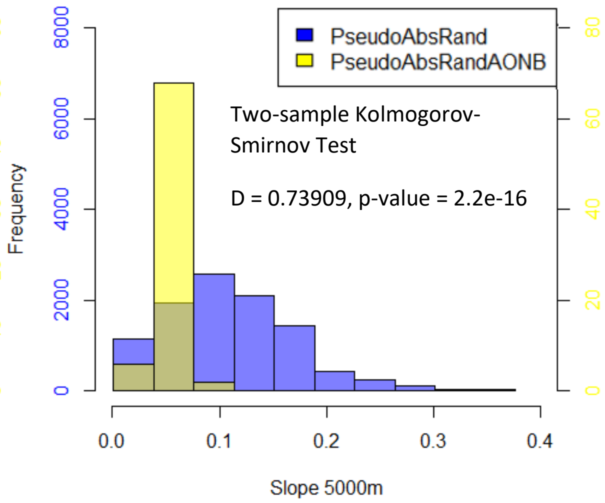

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.19458, p-value = 0.00661
Frequency
0 1000 2000 3000 4000
0 10 20 30 40
Broadleaf Woodland Proportional Cover 4000m

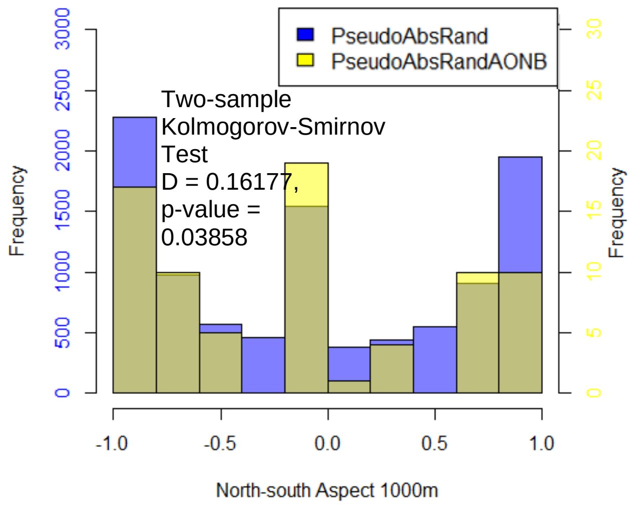

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.40979,
p-value = 1.99e-11
Frequency
0 500 1000 1500 2000 2500
0 1 2 3 4
Woodland Edge Density 5000m

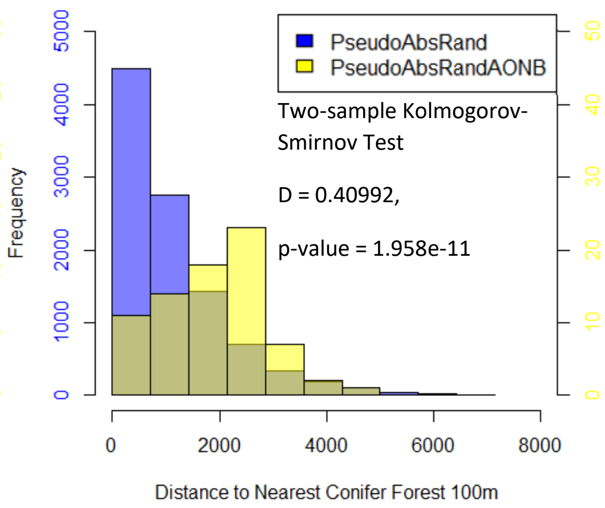

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.35991, p-value = 6.517e-9
Frequency
0 1000 2000 3000 4000 5000 6000
0 20 40 60 80 100
Woodland Proportional Cover 5000m

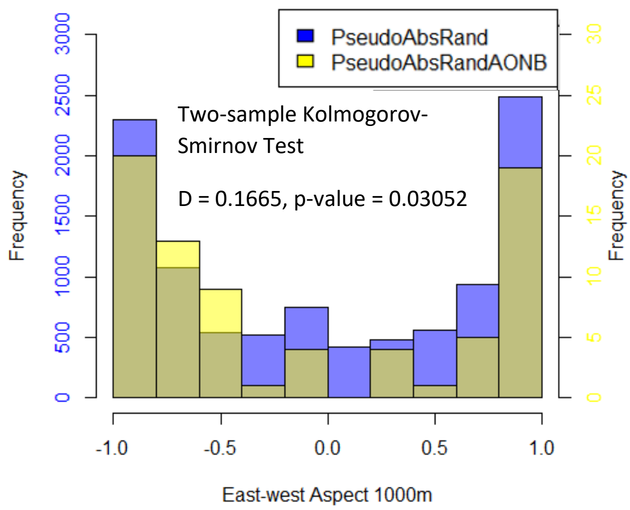

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.46795, p-value = 8.993e-15
Frequency
0 2000 4000 6000 8000 10000
0 500000 1000000 1500000
Broadleaf Woodland Maximum Patch Size 5000m

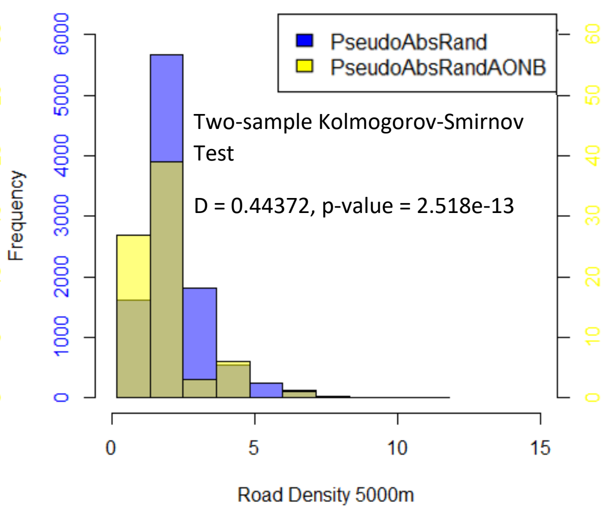

PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.72571, p-value = 2.2e-16
Frequency
Elevation 3000m


PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.73909, p-value = 2.2e-16
Frequency
Slope 5000m


PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.16177, p-value = 0.03858
Frequency
North-south Aspect 1000m


PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.40992,
p-value = 1.958e-11
Frequency
Distance to Nearest Conifer Forest 100m


PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.1665, p-value = 0.03052
Frequency
East-west Aspect 1000m


PseudoAbsRand
PseudoAbsRandAONB
Two-sample Kolmogorov-Smirnov Test
D = 0.44372, p-value = 2.518e-13
Frequency
Road Density 5000m

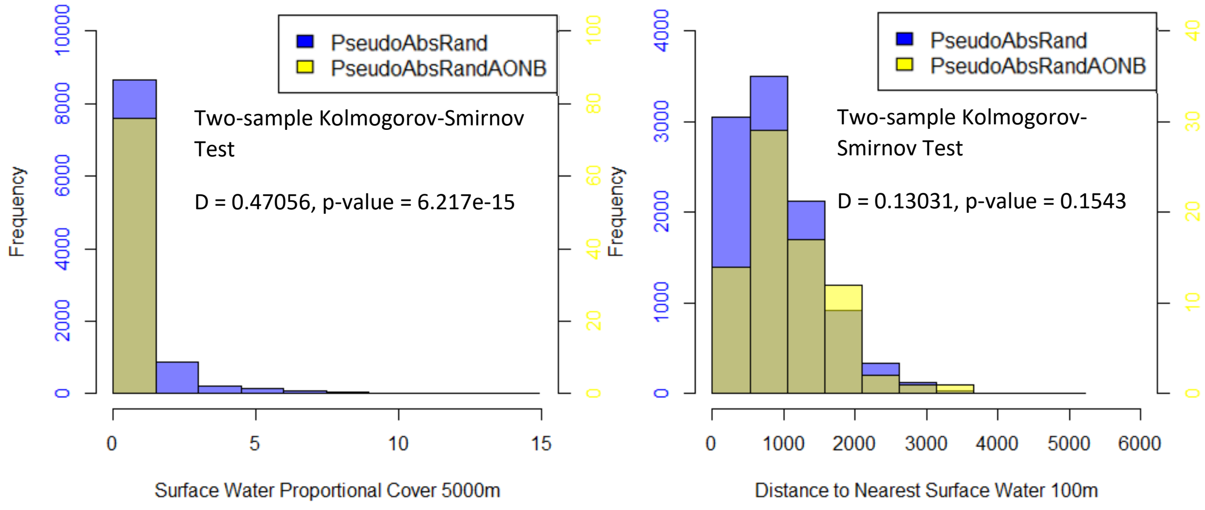


Figure 9. Histograms derived from environmental variables for "random pseudo-absence" across all of Wales (PseudoAbsRand) compared with only across GowerAONB (PseudoAbsRandAONB). Environmental Variables chosen are those considered most important in predicting *R. hipposideros* in AUC random pseudo-absence. Frequency axis for PseudoAbsRandAONB were kept at 1/100th of the Frequency axis for PseudoAbsRand to make histogram shape comparison across environmental variables concise.

Figure 10. Table of ‘Environmental Variable Importance (S5)’ from Fuller, Caryl, & Shewring (2018) Supplemental Material, with amendment to include D and p values for each variable from their Kolmogorov-Smirnov tests. Both models of pseudo-absences are included. Variables in bold have p-value >0.05.

RANDOM PSEUDO-ABSENCE				
Variable	Scale (m)	Importance %	D=	p-value=
Building Proportional Cover	**100**	**19.76**	**0.02366**	**1**
Distance to Nearest Woodland	**100**	**15.72**	**0.15522**	**0.0528**
Broadleaf Woodland Proportional Cover	4000	12.33	0.19458	0.00661
Woodland Edge Density	5000	10.87	0.40979	1.990E-11
Woodland Proportional Cover	5000	10.07	0.35991	6.517E-09
Broadleaf Woodland Maximum Patch Size	5000	7.43	0.46795	8.993E-15
Elevation	3000	7.02	0.72571	2.2E-16
Slope	5000	3.17	0.73909	2.2E-16
North-South Aspect	1000	2.88	0.16177	0.03858
Distance to Nearest Conifer Forest	100	2.71	0.40992	1.958E-11
East-West Aspect	1000	2.41	0.1665	0.03052
Road Density	5000	2.38	0.44372	2.518E-13
Surface Water Proportional Cover	5000	1.93	0.47056	6.217E-15
Distance to Nearest Surface Water	**100**	**1.33**	**0.13031**	**0.1543**

BUILDING PSEUDO-ABSENCE				
Variable	Scale (m)	Importance %	D=	p-value=
Building Proportional Cover	**100**	**20.25**	**0.053292**	**0.9319**
Broadleaf Proportional Cover	4000	15.49	0.19975	0.0005
Distance to Nearest Woodland	**100**	**12.38**	**0.056513**	**0.8975**
Broadleaf Woodland Maximum Patch Size	5000	11.48	0.42224	2.22E-16
North-South Aspect	3000	9.18	0.36557	2.248E-12
Woodland Maximum Patch Size	3000	8.95	0.19299	0.0009
Elevation	3000	4.71	0.68637	<2.2e-16
East-West Aspect	**500**	**2.95**	**0.093002**	**0.3354**
Woodland Proportional Cover	5000	2.63	0.3456	4.184E-11
Surface Water Proportional Cover	5000	2.46	0.36546	2.287E-12
Roughness	3000	2.3	0.42325	2.22E-16
Slope	5000	2.1	0.71016	<2.2e-16
Distance to Nearest Conifer Forest	100	1.58	0.37646	4.264E-13
Woodland Edge Density	5000	1.52	0.43824	2.2E-16
Distance to Nearest Surface Water	100	1.5	0.13633	0.04357
Road Density	1000	0.52	0.27405	3.854E-07

3.4 Assessing the accuracy of Wales HSM across Gower AONB

Histograms for PIV's of pseudo-absence points for the whole of Wales and for Gower AONB, plus PIV's of bat presences, were constructed for both random and building pseudo-absence HSM's.

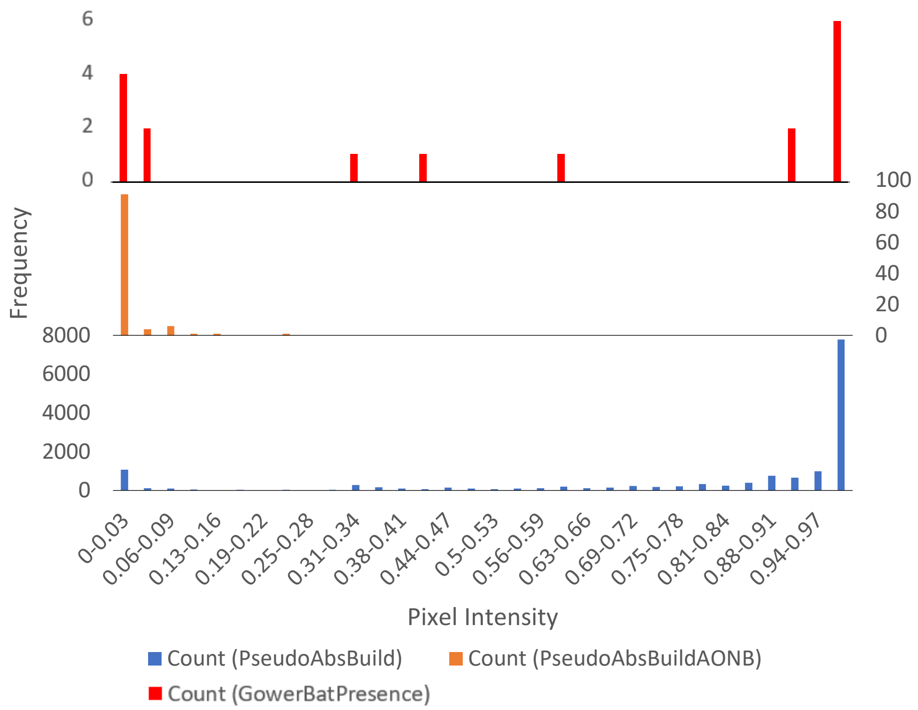


Figure 11. Pixel Intensity Values of all Building pseudo-asbence locations (PseudoAbsBuild; n=14,833) against Building pseudo-absence locations within GowerAONB+0.5BUFFER (PseudoAbsBuildAONB; n=104) and Bat Presence Data within GowerAONB+0.5BUFFER (GowerBatPresence; n=17, mean=0.548)

The distribution of building pseudo-absences across the whole of Wales was highly skewed towards high pixel intensity (Figure 11), indicating high predicted probability of presence. This is not consistent with the expectation that pseudo-absences should be in locations with low predicated probability in an effective HSM. However, building pseudo-absences within Gower AONB did conform to the expectation of generally being associated with low predicted probability (Figure 11). Predicted PIV's at locations where bats were observed (Figure 11) were spread across the whole range of values, with four bats at locations 0 < PIV < 0.03, and six bats at locations with 0.97 < PIV < 1.00. This suggests the building pseudo-absence model may have poor performance in predicting habitat suitability for *R. hipposideros* in Gower AONB.

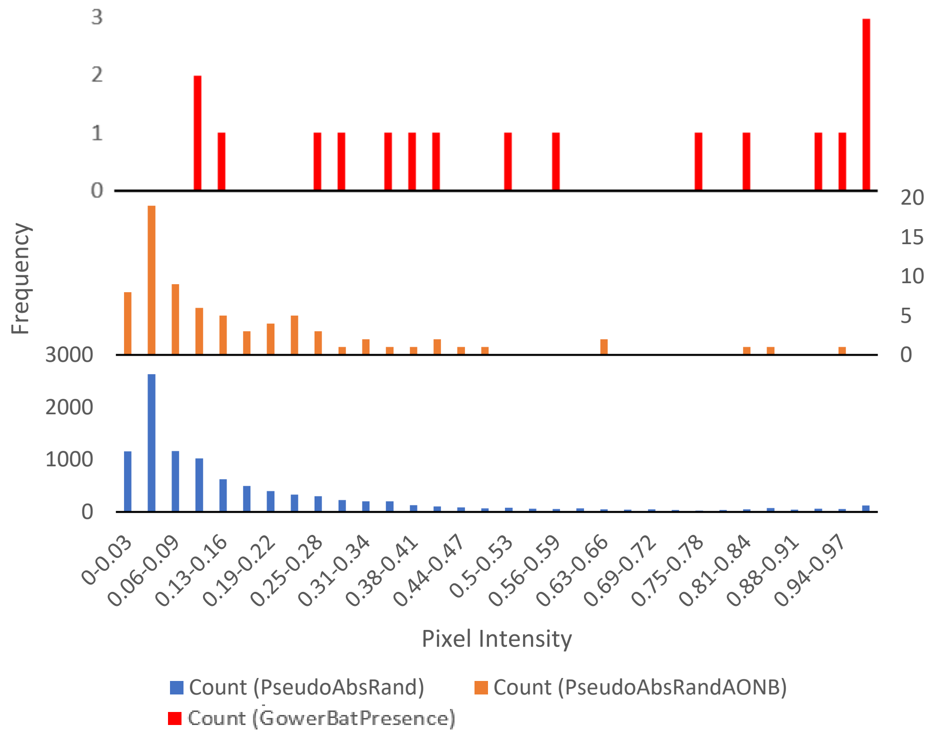


Figure 12. Pixel Intensity Values of all Random pseudo-asbence locations (PseudoAbsRand; n=10,077) against Random pseudo-absence locations within GowerAONB+0.5BUFFER (PseudoAbsRandAONB; n=76) and Bat Presence Data within GowerAONB+0.5BUFFER (GowerBatPresence; n=17, mean=0.57)

The distribution of random pseudo-absences across the whole of Wales was highly skewed towards low pixel intensity (Figure 12), indicating low predicated presence probability. Random pseudo-absences within Gower AONB (Figure 12) showed a very similar distribution. Predicted PIV's at locations where bats were observed (Figure 12) were spread across the whole range of values, from PIV=0.09 to PIV=1.00. However, when compared to the distribution of random pseudo-absences, the lowest PIV for bats had a higher PIV than 4954/10,077 pseudo-absences across Wales, with 14/17 having a higher PIV than almost 75% of random pseudo-absences across Wales.

Overall, this indicates that the building pseudo-absence HSM has 1) bias in environmental basis for Gower AONB, thus predictions, and 2) poor ability to discriminate between presence and (pseudo-) absence. Also, random pseudo-absence HSM has 1) relatively unbiased environmental basis, and 2) good ability to discriminate between presence and (pseudo-)absence.

3.5 Assessing potential roost sites of Lesser Horseshoe Bats in Gower AONB

An ensemble model, BuildRandAONB, was created by combining both random and building pseudo-absences (Figure 14) in ArcGIS Pro. An AUC value was calculated from an ROC curve generated in R Studios (Figure15) in the same manner as was done to produce Figure 7.

Given the average PIV of known bat roosts in Gower AONB for building pseudo-absence, random pseudo-absence, and ensemble pseudo-absence HSM's (Figure 13) was 0.548, 0.57, and 0.571 respectively, the ensemble pseudo-asbence HSM was scrutinized in ArcGIS Pro to determine buildings with a PIV of 1.00. However, no buildings were found, so the random pseudo-absences HSM was scrutinized instead, and three buildings were found with a PIV of 1.00. Although the average Bat Presence PIV of 0.57, and AUC value of 0.787 for random pseudo-absences are similar to the ensemble pseudo-absence, the scores are still low, and should be considered when investigating possible bat roosts at these sites. The latitude/longitude coordinates of these buildings using the British National Grid are: (51.5809, -4.1010), (51.5742, -4.1706), and (51.5792, -4.0313). Alternatively, the Easting and Northing coordinates are also provided: (254522, 188985), (249678, 188381), and (259346, 188660).

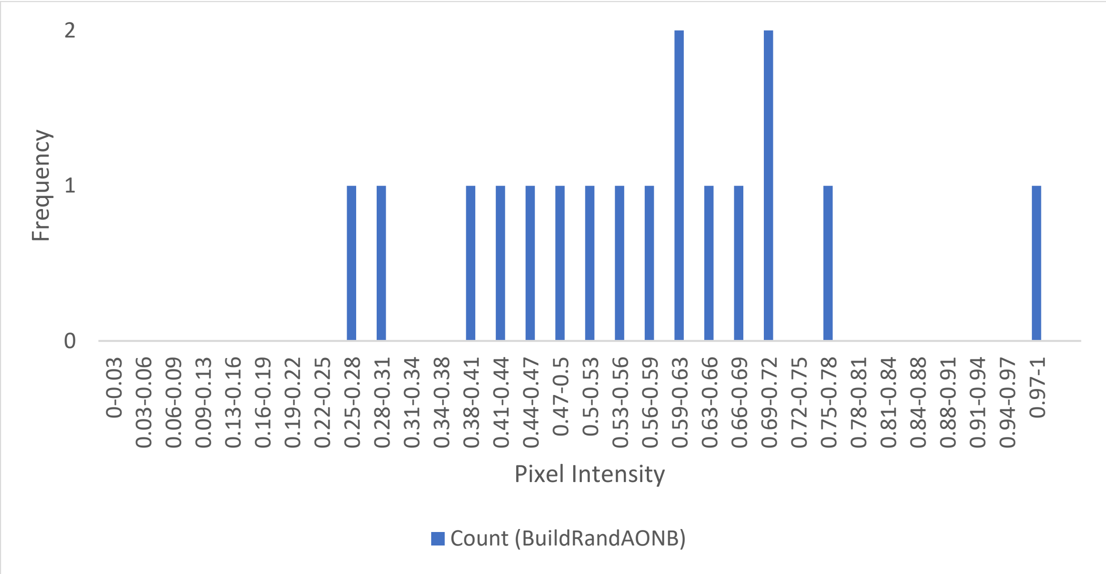


Figure 13. Pixel Intensity Values of all Bat Presence Data within GowerAONB+0.5BUFFER (GowerBatPresence; n=17, mean=0.571) for the ensemble model, BuildRandAONB

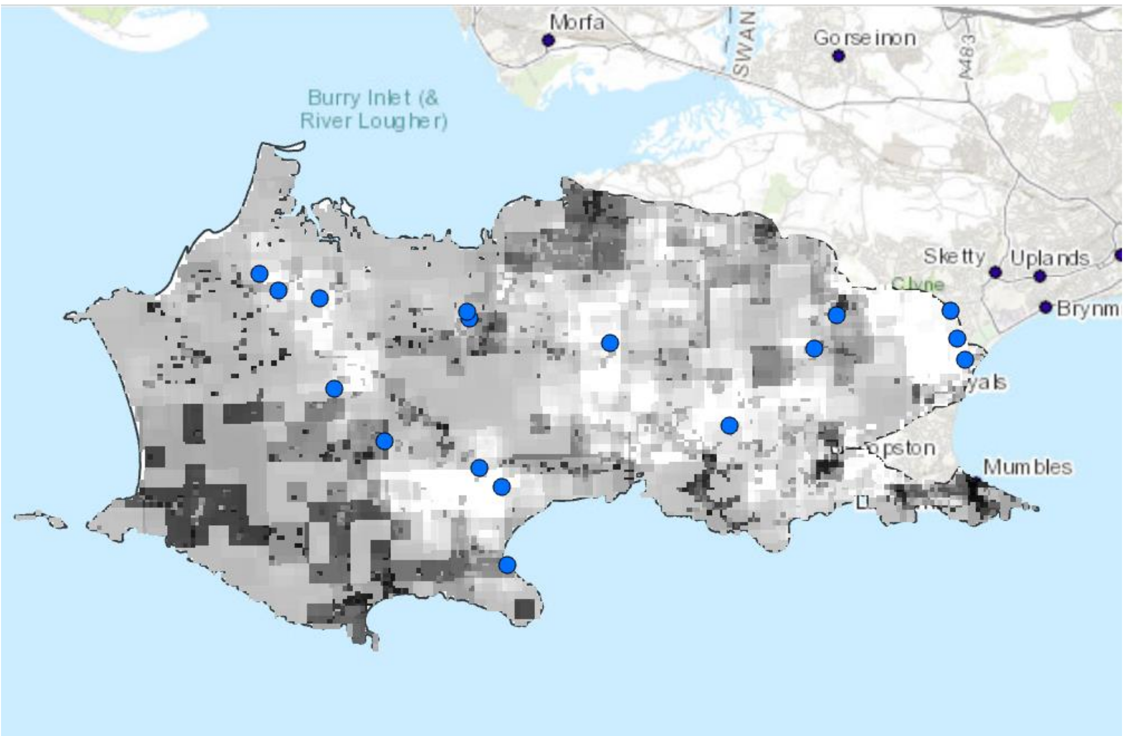


Figure 14. GowerAONB+0.5BUFFER overlayed with Pixel Intensity Value grey-scale for BuildRandAONB and Bat Presence data (BLUE points)

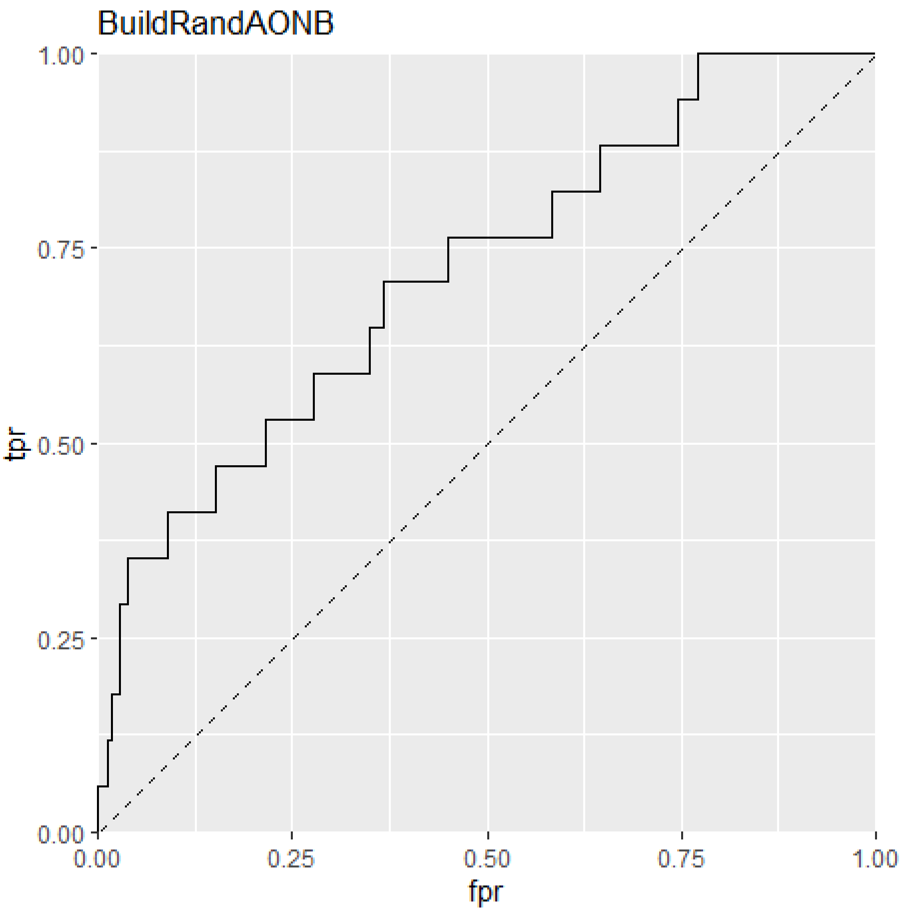


Figure 15. ROC 'curve' (solid line) for the ensemble pseudo-absence HSM (BuildRandAONB) for Gower AONB. The diagonal line represents random prediction (AUC = 0.5), with tpr = 'true positive rate' (sensativity), and fpr = 'false positive rate' (1-specificity).

The AUC value was 0.700 for the ensemble pseudo-absence HSM. This AUC value was less than both the building pseudo-absence HSM AUC value of 0.782, and the random pseudo-absence HSM AUC value of 0.787.

4.0 Discussion

As mentioned previously, the aims and objectives of this study are to test the hypothesis that national-scale models are not appropriate for use in making accurate predictions at local scales. The HSM was successfully reproduced to cover only the Gower AONB (first aim). The environmental variables of the pseudo-absence points of both models were assessed using Kolmogorov-Smirnov tests, which demonstrated just have dissimilar the Gower AONB is from the whole of Wales at an environmental level (second aim). Using AUC statistics, the random pseudo-absence model, building pseudo-absence model, and ensemble pseudo-absence models all had 'fair' predictive performance, however, only the random pseudo-absence model was reliable at discriminating between pseudo-absences and true bat presences (third aim). As a result, the random pseudo-absence model was used to determine potential *R. hipposideros* roost sites (fourth aim). With the aims and objectives of this study in mind, the key findings of this study are detailed below.

4.1 Reproduced HSM

The HSM was reproduced from data provided by Fuller, Shewring, & Caryl (2018), and covered the whole of Wales for both random and building pseudo-absence data. Reproducing this model was important for forming the basis for this study, providing the groundwork HSM for which to compare environmental variables and discuss bat presence prediction accuracy within Gower AONB. The low accuracy (which is discussed later) of the HSM in predicting bats in Gower AONB suggests similar inaccuracies would be found throughout the whole Wales HSM, inaccuracies only noticed when 'zooming in' to local scales. These smaller scale regions would thus suffer from the inaccuracy of the HSM, where true bat roosts are not predicted and therefore are not investigated. Without knowing where these roosts are, and if currently unknown true roosts are not predicted by the HSM and thus get overlooked, conservation efforts to protect buildings or landscapes cannot be enacted. Fuller, Shewring & Caryl (2018) produced an informed HSM with statistical tests to determine predictive performance was acceptably high, but only discussed anecdotal evidence in determining whether their HSM successfully predicted bat roosts that were as of then not known about. Known bat presence data provided by the Bat Conservation Trust in this study was used to assess the HSM's true accuracy. It can thus be suggested that the whole Wales HSM could be improved by including more bat presence data for smaller scale regions with significantly different environmental structure to that of "average" Wales environmental structure. Fuller, Shewring & Caryl (2018) had limited bat presence data when creating their HSM (see their Supplementary Figure S1), so updating such a model continuously as more bat presence data is made accessible would also benefit the overall accuracy. Including presence data from a broad range of environment structures would similarly benefit any HSM of any species, where inaccuracies related to significantly different environmental structures skew the predictive performance over a large regional scale. Applying more dedicated survey efforts to these environmentally different regions would provide presence data that would enable a HSM, such as this study's, to accurately predict roosts in regions that would otherwise be overlooked.

4.2 Environmental variables assessed

A simple way in which to determine whether the environment of the Gower AONB differs from the whole of Wales was presented through the pseudo-absence points generated by Fuller, Shewring, & Caryl (2018). Kolmogorov-Smirnov tests for each histogram provided a statistical method of investigating distribution differences between the whole of Wales, and Gower AONB environmental data. The histograms' shape, relative to scale, visualised this comparison, and the considerable difference in environmental variables between the two. Given the null hypothesis that 'Gower AONB and whole Wales distributions are the same' was rejected for both building and random pseudo-absences, the environmental variables difference would support the hypothesis that national-scale models are not appropriate for use in making accurate predictions at local scales.

Building Proportional Cover (100m) and Distance to Nearest Woodland (100m) were the only variables considered that had a Kolmogorov-Smirnov p-value greater than 0.05 for both Building Pseudo-Absence (PseudoAbsBuildAONB) and Random Pseudo-Absence (PseudoAbsRandAONB), suggesting, in these two regards, Gower AONB was statistically similar to the whole of Wales. Given the reliance *R. hipposideros* has on the connectivity between forested regions and buildings for roosting (Tournant *et al*, 2013), having these environmental variables be similar across Gower AONB as they are across Wales helps provide a good point of reference in describing the differences between Gower AONB and Wales. Building Proportional Cover (100m) was the most important variable in predicting *R. hipposideros* for both building and random pseudo-absences, with Distance to Nearest Woodland (100m) being second and third most important for random and building pseudo-absences, respectively (Figure 10). Building Proportional Cover (100m) and Distance to Nearest Woodland (100m) combined make up 35.48% and 32.63% of the environmental variables total importance in predicting *R. hipposideros* for random and building pseudo-absences, respectively, not even half. This explains why, even though Building Proportional Cover (100m) and Distance to Nearest Woodland (100m) are both very important in predicting *R. hipposideros* roost sites, they alone are not enough to reject the hypothesis that national-scale models are not appropriate for use in making accurate predictions at local scales. To be truly representative, the HSM needs to have a greater degree of environmental similarity in the less important variables as well, something that is impossible to achieve across the spectrum of environments of local scales across Wales. The HSM may be as effective in local scales with similar environments to the whole of Wales, but will grow less effective in local scales with increasing more varied environmental structure due to decreasing predictive performance.

Furthermore, East-West Aspect (500m) for building pseudo-absences (with 2.95% importance), and Distance to Nearest Surface Water (100m) for random pseudo-absences (with 1.33% importance) were the only other variables with a Kolmogorov-Smirnov p-values greater than 0.05, highlighting the dissimilarity in the environment structure GowerAONB has when compared to Wales. This highlights why a national-scale HSM is not appropriate in making accurate predictions at local levels: the environment the HSM is based off is too dissimilar in its structure. There is a noticeable lack of similar studies in literature with which to compare findings to, but a great number of studies on HSM's. This interest in HSM use, but lack of study into scaling HSM's, suggests this study is a novel investigation and would benefit from further study to elucidate the HSM literature.

A further example of the dissimilarity between Gower AONB and Wales is shown using Pixel Intensity Values of pseudo-absence points. Comparing whole Wales pseudo-absences against only those that were generated within Gower AONB visualises whether the HSM generates pseudo-absences reasonably at local scales. This means that, what should be expected of pseudo-absences in Gower AONB, is they should predominantly have low PIV's for low probability of having *R. hipposideros* presence. Random pseudo-absence points for both Wales as a whole and Gower AONB do indeed predominantly have low PIV's. Building pseudo-absences across Wales, however, are unusual: they act entirely the other way around, with predominantly high pixel intensity values, for high probability of *R. hipposideros*. Building pseudo-absences within Gower AONB have entirely low pixel intensity values though, highlighting an unusual discrepancy between pseudo-absences in Wales compared to Gower AONB. This could be explained by the method for pseudo-absence selection ("random selection of 10,000 buildings from non-urban areas") in Wales, which would only select areas already likely to have a high probability of presence. Fuller, Shewring, & Caryl (2018) mention as much. However, it is not as clear as to why, then, building pseudo-absences within Gower AONB have predominantly low probability. *R. hipposideros* have been shown to have preference for where in buildings they roost in previous studies (Seckerdieck, Walther, & Halle, 2005), but the HSM here does not account for building structure or available roosting space. *R. hipposideros* are known to prefer historic buildings, those with large attic spaces and cellars, which can be accessed by flying directly into from outside (Howard, 2014). Therefore, such details could enhance the building variables used in the HSM's: such data could be accessed from (https://datamap.gov.wales/layers/inspire-wg:Cadw_ListedBuildings). Furthermore, given buildings were randomly selected across Wales for pseudo-absence data, it is likely a lot of urban buildings would have been selected. The inclusion of urban buildings, given *R. hipposideros* is sensitive to urban build-up (Jung & Threlfall, 2016), would likely make for a difficult comparison of the HSM to the Gower AONB, which is not urbanised. Examining the building pseudo-absences within Gower AONB with PIV grey-scale overlayed shows a mostly white map, suggesting open fields have a higher probability of having presence than areas near houses. This is likely due to the model predictions being focused on pseudo-absence of buildings but highlights the dissimilarity between Gower AONB and Wales at the model's prediction level. It would have been interesting to provide a table of environmental variables most important for bat presence probability in the Gower AONB, to compare against the whole of Wales, but it was decided early that there was not enough data of bat presences in the Gower AONB to calculate importance values.

<u>4.3 Accuracy assessed</u>

Using PIV's, it can be assessed whether the HSM accurately predicts *R. hipposideros* presence by mapping known presence data onto Gower AONB alongside building and random pseudo-absences. Presence data for PseudoAbsBuildAONB (Figure11) has low accuracy with 0.548 PIV average, with Presence data for PseudoAbsRandAONB (Figure12) having similarly low accuracy with 0.57 PIV average. This indicates that both HSM's will, on average, correctly predict bat presences for less than 60 predictions out of 100. The known presences of *R. hipposideros* across Wales could potentially be affecting the HSM. As discussed by Hirzel, Lay, Helfer, Randin, & Guisan (2006), a lack of known presence sites of a species, such as *R. hipposideros*, as well as a lack of understanding of environmental variables favoured by a specific species, could skew an HSM. This skew would likely be compounded when "zoomed-in" to smaller regions within the initial sample area, leading to a drop in HSM accuracy.

Fuller, Shewring, & Caryl (2018) included 118 known roost sites in their study for bat presences, a small number to cover all of Wales, especially given 17 were separately provided for Gower AONB. This demonstrates a lack of known roost sites for this species, which highlights a gap in our knowledge of this species' preference for choosing roost sites. Comparative studies have investigated both lesser horseshoe bats (*Rhinolophus hipposideros*) and greater horseshoe bats (*Rhinolophus ferrumequinum*), discussing the similarity between the two, including calls, diet, and environment preferences (Jones & Rayner, 1989). This introduces the possibility that observation data for *R. hipposideros* could include *R. ferrumequinum*. This lack of known Welsh roost sites would restrict the HSM's ability to predict roost sites due to a limited understanding of environmental predictors, whilst observation data including other horseshoe bat species would likely widen the HSM's predictive performance, but only because it is predicting the wrong species' roost sites. Use of niche overlap comparison between the two bat species would further improve the predictive performance by allowing for the removal of overlap regions, as demonstrated by Gaulke, Hohoff, Rogness, & Davis (2023), but would require an HSM for *R. ferrumequinum* that was not available in this study.

R. hipposideros avoids being preyed upon by emerging from roosts when it is darkest (Duvergé, Jones, Rydell, & Ransome, 2008), as birds typically consider them prey, as do other more surprising predators, such as otters (Forman, Liles, & Barber, 2004). Furthermore, *R. hipposideros* could suffer from competition for food with other animals, such as pipistrelle bats (Arlettaz, Godat, & Meyer, 2000). Both predation and food competition were not applied to the HSM in Fuller, Shewring, & Caryl's (2018) work. A lack of consideration for potential predation on, and competition with, *R. hipposideros* in the environmental variables would likely skew the predictions to over-predicting roosts where they may not be due to predation-pressures and competitor-pressures, further supporting the need to investigate niche overlap. Lastly, predictions within Gower AONB would have the bias of Fuller, Shewring, & Caryl's (2018) HSM being four years old as of this study, so any change in environment in those years would not be accounted for, such as deforestation and fragmentation, as well as loss or addition of roads or houses. HSM studies have demonstrated the differing predictive outputs between current environmental factors and predicted-future environmental factors (Gupta, Sharma, Rajkumar, Mohammad, & Khan, 2023), thus the effects of environmental change. Consistent yearly reapplication of the HSM to updated environmental parameters across Gower AONB would eliminate the risk of having outdated predictions.

With the average PIV of Bat Presence for random pseudo-absences within Gower AONB and building pseudo-absences within Gower AONB being 0.57 and 0.548 respectively, the HSM is not predicting *R. hipposideros* presences in Gower AONB to within a 0.05 margin of error (assuming the Bat Presence points should have a Pixel Intensity Value of 1). Razgour, Hanmer, & Jones (2011) demonstrate how different scales of HSM associate the study species with differing environmental variables due to the resolution. This could explain the low accuracy, as the smaller scale of Gower AONB might result in the importance of the environmental variables assessed varying from their importance to the whole Wales HSM. Fuller, Shewring, & Caryl (2018) discuss ensemble modelling having better predictive performance, thus producing an ensemble model for Gower AONB using both random and building pseudo-absences within Gower AONB should perform better than its composite HSM's. Given the average PIV for the ensemble model was 0.571, and the AUC value was 0.700, this suggestion isn't supported in this instance. Ensemble modelling of HSM's has been shown to perform better than its composite models (Rew, Cho, Moon, & Hwang, 2020), so BuildRandAONB's negligible increase in accuracy is unexpected. This could be a criticism of the HSM's applicable use, using Bat Presence to determine actual-performance, or this could highlight the need to include more than the two pseudo-absence models used here. Additional pseudo-absences considering broadleaf cover within 100m (Bellamy *et al*, 2020) could further increase the ensemble accuracy.

4.4 Possible Lesser Horseshoe Bat roost sites determined

As stated above, providing informed suggestions for possible *R. hipposideros* roost sites in the Gower AONB for the Bat Conservation Trust is made challenging due to the lack of accuracy of the HSM across GowerAONB. Furthermore, the ensemble model is only as accurate as either random pseudo-absences or building pseudo-absences, and the likely reason for there being no buildings with a PIV of 1 is because of PseudoAbsBuildAONB predicting buildings being absence points. Further buildings could be suggested (those with PIV's of 0.95, for example), though to do this would extract buildings with diminishing reliability. Therefore, the buildings located at the three sites of PseudoAbsRandAONB PIV=1 [British National Grid Latitude/Longitude: (51.580860, -4.1009581), (51.574212, -4.1706216), and (51.579242, -4.0312962)] are to be recommended for survey efforts into locating further *R. hipposideros* roost sites.

4.5 Wider Impacts

Habitat Suitability Models are popular in biodiversity, ecology, and conservation research literature. Since their inception, HSM's have been created for several species, including *Rhinolophus* bats (Le Roux *et al*, 2017) or more broad bat species (Bellamy, Scott, & Altringham, 2013), to more general use, like large mammals (Boitani *et al*, 2007). HSM's for *Rhinolophus hipposideros* have also been done outside of Wales (Bendjeddou *et al*, 2022). There is, however, a lack of study on the use of HSM performance on a smaller scale than initially designed for. Although this study found that the pseudo-absence HSM's investigated did show a lack of statistical accuracy regarding predicting *R. hipposideros* roost sites, the ultimate success will be determined by whether bat roosts are found at the recommended sites. The use of AUC and pseudo-absences has previously been criticised for its ability to predict species presences (Cianfrani, Le Lay, Hirzel, & Loy, 2010). This study serves to further inform HSM research, regardless of the species of interest or the environment in question, demonstrating that HSM use on smaller scales than was designed for: 1) provides insight into HSM on a region when a HSM exists on a larger scale of that region, predicting presence sites with fair performance, but 2) has low predictive accuracy that comes from scaling down a complex environmental variable-based model. Scale likely plays a key role in the accuracy of the HSM; Gower AONB is ~1% of the whole of Wales, yet the scale of the environmental variables is not changed. Although the creation of a species-specific HSM should be constructed from raw data to scale with the region being investigated, downscaling a HSM to a region would need to consider downscaling the environmental variable resolution to match.

4.6 Conclusions

Habitat Suitability Models are an effective way of determining the extent of a species suitable habitat, effectively informing policy and conservation through statistical predictive modelling. Lesser horseshoe bats (*Rhinolophus hipposideros*), threatened as they are in the UK, are one such species that would benefit from effective HSM's. Utilizing a HSM previously produced by Fuller, Shewring & Caryl (2018) for *R. hipposideros*, it was investigated whether this HSM was effective when 'zoomed-in' on a region within the original HSM's predictive range. This investigation was directed with four main aims and objectives, laid out in the Introduction. The ability to achieve those aims and objectives is summarised thusly:

1. The HSM was successfully reproduced from the data provided by Fuller, Shewring & Caryl (2018). It was essential to reproduce this HSM for the purposes of manipulating its parameters and focusing in on the Gower AONB, as it provided the basis for which to conduct statistical performance tests from the probability predictions generated across all of Wales.
2. Pseudo-absence points, random and building, from the whole of Wales and only within Gower AONB were assessed by comparing their environmental variable spread as

histograms, with Kolmogorov-Smirnov tests used to provide statistical measure of similarity. These assessments demonstrated the environmental dissimilarity between Gower AONB and the whole of Wales, preluding the HSM's inaccuracies across Gower AONB. This was contrasted by AUC statistics of "fair" performance of the HSM's predictions.

3. To assess the accuracy of Wales HSM across Gower AONB, PIV's for random and building pseudo-absences were compared, alongside PIV's for known bat presences. Random pseudo-absences demonstrated low presence probability compared to generally high presence probability for known bat presence, whilst building pseudo-absences only showed low presence probability across Wales, having high presence probability across Gower AONB, yet also having high presence probability for known bat presences.
4. To assess potential roost sites of *Rhinolophus hipposideros* in Gower AONB, an ensemble model, consisting of both random and building pseudo-absences in Gower AONB, was constructed. This model demonstrated similar levels of bat presence accuracy and slightly lower predictive performance than random and building pseudo-absences. This likely contributed to the ensemble model's inability to determine any potential bat roosts. The random pseudo-absence model, with generally better accuracy and predictive performance, was instead used to determine potential bat roosts, resulting in three suggested areas for further observation.

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Appendices

A1. Pseudo-absence points for building pseudo-absence HSM within Gower AONB (PseudoAbsBuildAONB), including Easting-Northing British National Grid coordinates

Number	X	Y	Pixel Intensity Value
1	253001	194623	0.002333
2	253082	194595	0.001992
3	249744	192322	0.006055
4	242965	193311	0.008414
5	248255	192509	0.007629
6	242052	192636	0.009539
7	242985	193008	0.008414
8	244796	193180	0.0269
9	252776	194233	0.001657
10	251756	193882	0.001144
11	251729	194246	0.000951
12	252456	193598	0.001144
13	253561	193550	0.010594
14	253815	193529	0.010594
15	253854	193951	0.003739
16	252464	193437	0.001144
17	250572	192642	0.00768
18	250498	192701	0.00614
19	254636	193432	0.00555
20	254237	193493	0.012176
21	250074	192103	0.004239
22	253535	191347	0.00565
23	253981	189646	0.003815
24	254489	190617	0.010021
25	254211	191052	0.008112
26	249660	192360	0.007972
27	249233	191284	0.002532
28	249620	191845	0.00394
29	248493	192048	0.007629
30	247940	190020	0.020118
31	247430	190961	0.036743
32	247580	191687	0.002509
33	248195	191699	0.002703
34	248208	192453	0.007629
35	247061	189441	0.001842
36	247154	189531	0.001842
37	246430	193360	0.032413
38	246375	190876	0.023469
39	246912	190725	0.097018
40	246570	192963	0.156778
41	246281	190372	0.001548

42	245050	193186	0.0269
43	245083	193209	0.0269
44	245418	193482	0.004746
45	245813	191524	0.017671
46	257571	190883	0.006362
47	257498	190570	0.002642
48	257493	190879	0.002642
49	257962	192065	0.021865
50	255663	190326	0.049242
51	255710	190422	0.001499
52	255214	192840	0.004216
53	255282	191772	0.003619
54	254226	191275	0.00565
55	254330	191055	0.008112
56	255566	193554	0.002083
57	256923	187030	0.008496
58	255785	188209	0.078036
59	255419	188878	0.080606
60	255519	188987	0.079109
61	255181	187789	0.24823
62	243899	193330	0.011101
63	244686	193169	0.0269
64	244065	192407	0.009693
65	244200	192566	0.011101
66	242115	190991	0.009622
67	243695	190065	0.001587
68	242877	187951	0.001305
69	242684	187313	0.001051
70	255083	189078	0.048948
71	254956	188835	0.075493
72	254909	188094	0.069753
73	254778	188966	0.066557
74	253379	188426	0.004194
75	253362	189203	0.003243
76	252542	188430	0.003242
77	252733	188623	0.004737
78	251401	188573	0.004124
79	251556	188559	0.003551
80	250975	188604	0.003521
81	249772	186586	0.004414
82	250282	186456	0.003978
83	249896	188544	0.017737
84	250063	186545	0.003978
85	250148	187157	0.003978
86	245278	189244	0.004865
87	245301	189055	0.002687

88	246034	188967	0.002288
89	248856	189018	0.011159
90	246097	189258	0.002556
91	246462	189364	0.002288
92	247147	189028	0.001944
93	249322	187825	0.01636
94	248055	189100	0.013508
95	249365	186762	0.001482
96	249295	187087	0.001482
97	248676	186007	0.001032
98	246451	185440	0.011057
99	246847	184807	0.001359
100	246857	185253	0.006422
101	252318	195418	0.010493
102	257022	194412	0.00297
103	255647	194554	0.003069
104	252254	195423	0.00545

A2. Bat Presence points for building pseudo-absence HSM within Gower AONB (PseudoAbsBuildAONB), including lat./long. British National Grid coordinates

Number	X	Y	Pixel Intensity Value
1	51.34513	-3.56812	0.312227
2	51.60435	-3.99917	1
3	51.34249	-3.55081	1
4	51.61327	-4.2253	0.032413
5	51.23611	-3.54393	0.629302
6	51.61034	-4.17287	0.926086
7	51.58536	-4.07999	0.05601
8	51.60222	-4.04978	0.006362
9	51.6034	-4.12228	0.025714
10	51.58187	-4.2024	0.414465
11	51.59341	-4.22014	0.99509
12	51.57183	-4.16077	0.995157
13	51.57584	-4.16877	0.928975
14	51.55444	-4.15895	0.001623
15	51.60964	-4.04184	0.003004
16	51.61506	-4.23983	0.995698
17	51.61862	-4.24665	0.999999

S3. Pseudo-absence points for random pseudo-absence HSM within Gower AONB (PseudoAbsRandAONB), including Easting-Northing British National Grid coordinates

Number	X	Y	Pixel Intensity Value
1	245250	185250	0.03783
2	246850	185350	0.180391
3	246150	185650	0.040833
4	247750	185750	0.023796
5	249950	185750	0.07137
6	246950	186550	0.029269
7	248050	186650	0.045872
8	245650	186950	0.031525
9	255550	187150	0.01753
10	251050	187350	0.082004
11	254350	187350	0.055211
12	241350	187450	0.040545
13	250550	187550	0.475917
14	245850	187650	0.363796
15	243950	188050	0.021106
16	257450	188150	0.644246
17	252850	188350	0.031937
18	245550	188550	0.040545
19	250850	188650	0.424391
20	242050	188750	0.036841
21	245050	188750	0.064321
22	251350	188850	0.039001
23	243150	188950	0.040467
24	255950	188950	0.209905
25	249250	189150	0.135978
26	248750	189350	0.064546
27	241950	189550	0.037162
28	259750	189550	0.069283
29	256050	189750	0.465172
30	243150	189850	0.025683
31	259450	189850	0.027475
32	261050	189850	0.332786
33	243250	189950	0.025969
34	258450	189950	0.228625
35	242950	190050	0.05327
36	248650	190050	0.038452
37	254950	190150	0.221089
38	257150	190150	0.24345
39	260350	190250	0.069107
40	255550	190350	0.953676
41	256350	190850	0.212107
42	246050	190950	0.105401
43	259350	190950	0.150974

44	246750	191050	0.427908
45	259250	191050	0.147594
46	246050	191250	0.080832
47	248750	191350	0.040438
48	260550	191350	0.648702
49	247250	191450	0.334076
50	247550	191450	0.11169
51	244950	191550	0.260926
52	255650	191750	0.167261
53	251850	191850	0.290234
54	248550	192150	0.040143
55	261350	192150	0.820901
56	252550	192350	0.391356
57	247850	192450	0.080897
58	257950	192650	0.081394
59	248950	192950	0.090937
60	252150	192950	0.126268
61	251550	193050	0.246293
62	246250	193150	0.871468
63	252750	193150	0.149891
64	246150	193350	0.21331
65	247150	193450	0.097624
66	258350	193650	0.230564
67	258550	193750	0.257211
68	255150	193850	0.275554
69	256350	193950	0.187364
70	244750	194050	0.156705
71	245750	194250	0.093917
72	247350	194350	0.063821
73	251850	194450	0.21955
74	246250	194650	0.040545
75	252350	194750	0.055861
76	244450	195750	0.048436

S4. Bat Presence points for random pseudo-absence HSM within Gower AONB (PseudoAbsRandAONB), including lat./long. British National Grid coordinates

Number	X	Y	Pixel Intensity Value
1	51.34513	-3.56812	0.773875
2	51.60435	-3.99917	0.434845
3	51.34249	-3.55081	0.526152
4	51.61327	-4.2253	0.824201
5	51.23611	-3.54393	0.14716
6	51.61034	-4.17287	0.117212
7	51.58536	-4.07999	0.971835
8	51.60222	-4.04978	0.992681

9	51.6034	-4.12228	0.960687
10	51.58187	-4.2024	0.126351
11	51.59341	-4.22014	0.300252
12	51.57183	-4.16077	0.975878
13	51.57584	-4.16877	0.27877
14	51.55444	-4.15895	0.589746
15	51.60964	-4.04184	0.930617
16	51.61506	-4.23983	0.351388
17	51.61862	-4.24665	0.388552

S5. Bat Presence points for ensemble pseudo-absence HSM within Gower AONB (BuildRandAONB), including lat./long. British National Grid coordinates

Number	X	Y	Pixel Intensity Value
1	51.34513	-3.56812	0.543051
2	51.60435	-3.99917	0.717422
3	51.34249	-3.55081	0.763076
4	51.61327	-4.2253	0.428307
5	51.23611	-3.54393	0.390775
6	51.61034	-4.17287	0.521649
7	51.58536	-4.07999	0.626799
8	51.60222	-4.04978	0.587825
9	51.6034	-4.12228	0.493201
10	51.58187	-4.2024	0.270408
11	51.59341	-4.22014	0.647671
12	51.57183	-4.16077	0.985518
13	51.57584	-4.16877	0.603872
14	51.55444	-4.15895	0.295684
15	51.60964	-4.04184	0.46681
16	51.61506	-4.23983	0.673543
17	51.61862	-4.24665	0.694275