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# Effects of greenway development on functional connectivity for bats

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## 1 ABSTRACT

Fragmentation of ecosystems is continuing worldwide, posing increasing pressures to and loss of biodiversity. Disused transport corridors such as old railways and tramways often return to semi-naturalness, and are increasingly upcycled into multi-use, non-motorised public Greenway infrastructure. This study examines bat activity within a proposed rural Greenway corridor in Ireland. Development scenarios are simulated to predict impacts to woodland ecosystem functional connectivity using Probability of Connectivity (PC) index. Generalised Linear Modelling predicts associations of species activity to Greenway corridor habitat and habitat structure. Spatially explicit connectivity models indicate significant impacts to ecosystem connectivity can arise from Greenway development scenarios, such as decreasing connectivity in half, or increasing connectivity four-fold. Species activity modelling identified habitat conditions along the Greenway route that suggest on-going corridor effects and associations to particular habitats and structure, emphasising the importance to consider a sensitive approach to developing disused infrastructure into Greenways.

*Conservation implications:* Potential significant increases in woodland ecosystem reachability for bats are achievable by conserving canopy cover over Greenway corridors. Species-specific habitat modelling results presented are directly applicable to guide woodland enhancement for the sensitive conservation of Greenway woodland habitat, maximising their multi-functional use and connectivity potential. Opportunities therefore exist for European Greenways to conserve and enhance ecosystem connectivity, providing landscape-scale solutions to the problem of increasing ecosystem fragmentation.

## 1. Introduction

Increasing fragmentation of semi-natural and natural habitat through intensified land use is generally recognised as one of the significant threats to biodiversity and ecosystem services (Secretariat of the Convention on Biological Diversity, 2014). The gradual fragmentation of European landscapes through cumulative alterations has been caused largely through socio-economic drivers such as transport infrastructure (European Environment Agency, 2011) and urban sprawl (European Environment Agency, 2016). The negative effects of fragmentation can be reduced by increasing connectivity between

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habitat patches, thus increasing species movement through the landscape (Bennett et al., 2006) and improving ecosystem resilience (Olds et al., 2012). In this context, landscape connectivity is defined as 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al., 1993). Measuring landscape connectivity currently falls under two approaches; *structural connectivity*-largely defined as the arrangement and proximity relationship between patches of a habitat type or matrix within that landscape, and *Functional connectivity*-the ability or probability for a given species to move and reach between or within patches (Taylor et al., 1993; Rosenberg et al., 1997; Tischendorf and Fahrig, 2000; Belisle, 2005; Vogt et al., 2009; Crouzeilles et al., 2013). Although structural connectivity is widely used for quantifying landscape connectivity and is generally supported in theory, its association with increased species movement has been ambiguous in the past (Rosenberg et al., 1997). According to Vogt et al. (2009) and Pierik et al. (2016), to achieve a better connectivity measurement, analyses should consider both structural and functional connectivity.

Analysing functional connectivity can be complex, involving species-specific attributes such as dispersal capabilities within landscapes (Closset-Kop et al., 2016). Species presence and dispersal data can serve to calculate probabilistic and binary functional connectivity indices such as Probability of Connectivity (PC) and Integral Index of Connectivity (IIC) (Saura and Torné, 2009). These indices can determine the importance of identified structural habitat features and their contribution to the overall landscape connectivity (Saura and Rubio, 2010). The use of an ecological indicator species representing a host of additional species requires precise definition and consideration (Landres et al., 1988), and determining a suitable functional connectivity indicator species for dispersal characteristics can be challenging (Closet-Kopp et al., 2016). Measuring functional connectivity of a hypothetical organism based on various dispersal ranges and habitat requirements has also been demonstrated in past studies (e.g. Vogt et al., 2009; Niculae et al., 2016). However, examples of studies employing a given indicator species with distinct dispersal characteristics to evaluate functional connectivity in various conservation contexts has been demonstrated (Van Looy et al., 2014; Loro et al., 2015).

Determining an indicator species whose requirements encapsulates the habitat connectivity characteristics required by additional species can be challenging (Closset-Kop et al., 2016). The selection of an indicator species is typically based on knowledge of the species characteristics and responses to environmental stressors and their similarity to other species responses or ecosystem health and function (Landres et al., 1988). Although the extent of their use as bioindicators has been questioned (Park, 2015), bats have been generally recognised as excellent indicator species. They are recognised for their ease of acoustic monitoring and their response to the modification of landscape composition resulting in changes of species activity and distribution (Jones et al., 2009; Boughey et al., 2011b; Russo and Jones, 2015). Activity has been directly related to the availability and density of linear vegetation corridors (Verboom and Huitema, 1997; Hein et al., 2009; Lachoeuilhe et al., 2016), while species community structure alterations and a reduction in richness have been associated with urbanisation (Threlfall et al., 2012; Russo and Ancillotto, 2015).

Landscapes with good structural and micro-habitat features can be important to bats (Tournant et al., 2013; Kerbiriou et al., 2018) and habitat connectivity is important for their survival (Schofield, 1996; Bontadina et al., 2002; Froidevaux et al., 2017). Linear woodland features such as hedgerows within the landscape can serve as preferred foraging and corridor habitat for bats, and are important for the orientation of many species (Verboom and Huitema, 1997; Downs and Racey, 2006; Lundy et al., 2011; Zeale et al., 2012; Hacecková et al., 2014; Pinaud et al., 2018). Such corridors can provide a greater abundance of prey and cover from weather and predators (Verboom and Spoelstra, 1999). Establishing and managing hedgerows along transport infrastructures can also benefit from informed actions tailored to providing the best outcome for biodiversity. Vandevelde et al. (2014) note the importance of recognising railway corridors as important bat corridors and their appropriate complimentary management should be considered. The interaction of disused European railway corridors with substantial woodland networks of treelines and hedgerows has the potential to make them nationally and internationally important corridors for biodiversity. Across Europe, Greenway infrastructure projects 'upcycle' disused transport corridors such as rail and tramways into multi-use, non-motorised public infrastructure (European Greenways Association, 1998). Research has been conducted to inform Greenway design in order to provide both recreational and ecological functions (Fumagalli and Toccolini, 2012; Carlier and Moran, 2019). European Greenway networks expand and interconnect, substantial opportunities are emerging to create pan-European ecological conservation corridors and to contribute to the establishment of Green Infrastructure (European Commission, 2007). The hypothesis of this study is that Greenway development can provide functional connectivity for bats through i) understanding bat species habitat associations along proposed corridors and ii) simulated infrastructure development scenarios predicting species habitat connectivity. Through understanding bat associations with Greenway habitats, specific habitat structures and conditions that may exist can inform recommendations towards either maintaining or enhancing Greenways as corridors for bats. Furthermore, simulating the impact of Greenway development scenarios to functional woodland connectivity may present yet another reason towards the preservation and addition of linear woodlands along such infrastructure. In summary, this research helps fill major knowledge gaps that exist as to how Greenways can be optimised to be established as Green Infrastructure and conservation corridors, towards their realisation as true sustainable projects.

## 2. Materials and methods

The study followed a two-step approach; 1) sampling bat activity and determining associations with the Greenway habitat characteristics, and 2) simulating Greenway development scenarios to evaluate impacts to woodland ecosystem functional connectivity. Fig. 1 provides a schematic outline of the steps taken.

### 2.1. Study area

A study area extending 70 km in length and 1 k wide was based along a disused railway in the North West of Ireland (Atlantic European Biogeographical Region) (Fig. 2). The study area width was based on guidelines available from the Chartered Institute of Ecology and Environmental Management (2013) for infrastructure corridor studies. This railway is proposed as a cross-border Greenway connecting the Republic of Ireland and Northern Ireland (United Kingdom). The lowland landscape (22 m–200 m above sea level) is underlained by limestone, shale and sandstone. The landscape is dominated by High Nature Value farmland (HNVf (European Environmental Agency, 2004)) in undulating drumlin landscape of predominantly rushy pastures; semi-improved agricultural and wet grasslands, typically enclosed by a dense network of hedgerows and treelines (Sullivan et al., 2017). Small pockets of semi-natural woodlands (principally wet-willow alder ash woodland) and mixed broadleaf woodlands are found throughout the study area, and further habitat detail is available in Carlier and Moran (2018).

Ireland has nine resident bat species; Lesser Horseshoe bat; (*Rhinolopus hipposideros*), Common (*Pipistrellus pipistrellus)*, Soprano (*Pipistrellus pygmaeus*) and Nathusius (*Pipistrellus nathusii*) pipistrelles, Leislers (*Nyctalus leisleri*), Daubentons (*Myotis daubentoni*), Natterers (*Myotis nattereri*), whiskered (*Myotis mystacinus*) and brown long-eared (*Plecotus auritus*). All bat species are protected under European legislation (Habitats Directive, 1992), under the Irish Wildlife Act 1976 in Ireland and under the Wildlife (Northern Ireland) Order 1985. Common species include *P. pipistrellus and P. pygmaeus*, both found in urban and rural areas across Ireland (Roche et al., 2014). Research suggests all Irish species have positive associations with broadleaf woodland (Lundy et al., 2011), some more strongly associated with woodlands (Entwistle et al., 1997; Bontadina et al., 2002; Kanuch et al., 2008; CIBR, 2011). Bat commuting distances vary for individual species capabilities, for example 1.5 km for *P. auritus* (Entwistle et al., 1996), 4 km for *M. nattereri* (Siemens et al., 1999), and over 13 km for *N. leisleri* (Shiel et al., 1999)- varying in response of commuting habitat availability, surrounding habitat matrix and numbers present (Aughney et al., 2011).

### 2.2. Sampling strategy

Stratified random sampling was carried out by applying an overlay of three occurring landscape character types (Valleys & Lowlands, Lakelands, Uplands) (Geological Survey of Ireland, 2004) onto the study area and using the ArcGIS 'Create Random Points' tool. Twenty-three circular sites (320 m diameter) containing hedgerows and treelines adjacent to the Greenway route were sampled using two passive recorders (see Fig. 3.) to simultaneously record bat echolocation calls over a period of three nights of sampling. Acoustic recorders used were Song Meter SM4BAT Full Spectrum (Wildlife Acoustics, 2019) with new SMM-U1 omnidirectional ultrasonic microphones, erected at a height of 2 m. Recorder gain setting was set to default (12 dB) and microphone signal to noise ratio (SNR) plots range from 103 to 76 dB relative to frequency, (available from Wildlife

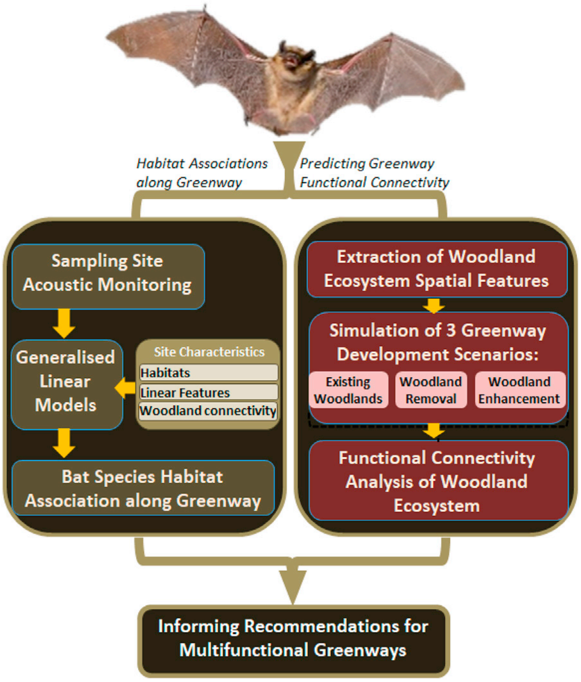

**Fig. 1.** Schematic outline of the methodology process flow.

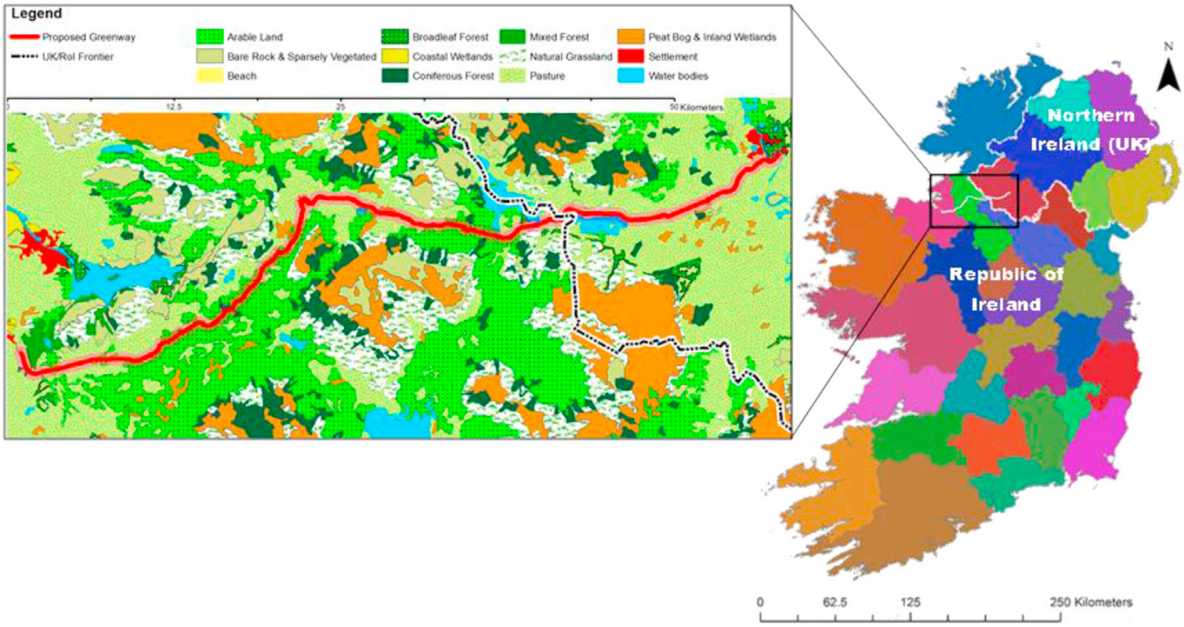

**Fig. 2.** Location of the Study Area and principal land uses within the four Counties in Ireland (left to right): Sligo, Leitrim, Cavan(Republic of Ireland) and Fermanagh (United Kingdom). Land use data adapted from Corine Land Cover 2012.

Acoustics SM4BAT FS product specification sheet [https://www.wildlifeacoustics.com/products/song-meter-sm4bat/specifications#plots]). Recorders were programmed to record 30 min before sunset until 30 min post sunrise. This resulted in an average of 9 h 20 min sampling time per night per unit (June to September 2017).

### 2.3. Bat data inventory

Exact numbers of individual bats foraging or commuting through an area is impossible to determine using passive acoustic monitoring. However, relative bat activity can be measured as a function of triggered recordings where periods of detected activity (a triggered event or bat pass) are recorded by the recorder. A bat pass is a sequence of greater than two echolocation

**Fig. 3.** Example of an aerial image of sampling site (320 m diameter) centred on the Greenway route (dotted line) with two recorder locations illustrated; recorder 1 typically positioned to detect activity related to the surrounding landscape, recorder 2 positioned to detect activity related to the Greenway route.

calls made as a single bat flies past the microphone (Lintot et al., 2015; Hundt, 2012; Walsh and Harris, 1996). Relative bat activity can be measured from the search-phase echolocation calls of bats or, more commonly, from bat passes or sequences of echolocation calls, 'where a bat pass or sequence is a series of calls that can be attributed to an individual bat' (Reason et al., 2016).

Bat call data was analysed with Kaleidoscope Pro v4.5.4 (Wildlife Acoustics, Inc., Concord, USA) Analysis Software, using the Irish classification from Bats of Europe v4.3.0 for the Auto-ID classification of individual species.

### 2.4. Sampling site characteristics for analysis

Sampling sites habitat structure, class, connectivity and spatial characteristics were obtained for statistical analysis. Hedgerow structural data was obtained from Carlier, J and Moran, J (unpublished data) and habitat spatial data was obtained from Carlier and Moran (2018). Morphological Spatial Pattern Analysis (Soille and Vogt, 2008) of linear woodland and broadleaf habitat patches occurring within the sampling sites (as determined in Carlier and Moran (2019)) was further analysed in GUIDOS software (Vogt and Riitters, 2017) using 'Network' analysis. Network analysis measures core habitat areas (e.g. woodlands) and linking features (features too narrow to contain core-e.g. hedgerow) between cores, determining networks of structurally connected woodlands. An output of Network analysis are individual features importance values for the maintenance of overall woodland habitat availability within the study area. Importance values are based on the equation in Saura and Rubio, 2009:

$$\mathrm{dPC} = dP\mathrm{cintra} + dPCflux + dPCconnector$$

where importance values corresponds to the term dPCconnector only (contribution of the linking or core feature to connectivity between other features as a stepping stone or connecting element). Importance values for woodland features present within sample sites were summed to provide an indication of the site's overall woodland structural connectivity importance. Nineteen landscape explanatory variables were used to characterise conditions within each sample site. Temperature data was calculated as average temperature during the full day over the three recording periods and was obtained from the nearest Met Eireann weather station (Markree, County Sligo-this weather station was adjacent to the study area in County Sligo and 55 km from the furthest sampling site in County Fermanagh). Table 1 provides a list of explanatory variables and a brief description.

### 2.5. Statistical analyses

All statistical analyses were performed in SPSS v.24 (IBM Corp., 2016) and ArcGIS v10.5.1 (ESRI, 2017).

Spatial autocorrelation of sampling sites was calculated using ArcGIS Geoprocessing based on site location and species diversity values using Global Morans Index (Moran, 1950). Differences in species activity along the Greenway route (*recorder 2*) and off the route (*recorder 1*) were investigated using a Mann-Whitney *U* test (Mann and Whitney, 1947). A covariance matrix of variables used for modelling was calculated using SPSS. Variables with a Spearmans rho >0.7 were omitted to avoid collinearity, retaining the variable most associated with bat species (Dormann et al., 2013). Simpsons Diversity Index was calculated for species activity across the 23 sampling sites. Generalised linear models (GLM) in SPSS were used to develop predictive models measuring the influence of the landscape elements and structural connectivity on individual species activity, species diversity and total activity. Negative binomial distribution models with log link function were fitted to *species activity* and *total activity*, and a normal distribution model for *species diversity* response variables. Further sequential backward elimination of non-significant variables ($p \geq 0.25$) (e.g. Lindborg and Eriksson, 2004; Wood et al., 2017) was applied to reduce the number of explanatory variables and to obtain a reduced model that describes the data and provides lower AICC values, while avoiding the critiqued full step-wise reduction (Whittingham et al., 2006). Finally, a test of normality was applied to the model residuals, a plot of standardised residuals against predicted values and cooks distance were explored to check the model adequacy (McCullagh and Nelder, 1989). All final full model parameters are provided in the supplementary material file.

### 2.6. Functional connectivity analysis

**Step 1:** Greenway development scenarios were prepared using ArcGIS (Fig. 4). Scenario one simulated existing conditions, where all broadleaf and broadleaf-conifer mix habitats and linear woodland were merged into one feature class. For scenario two, the previously combined woodland feature class was cut and 5 m either side from the centre of the Greenway was removed route to simulate woodland removal that could result from a corridor development of the route. In scenario three, additional woodland features were digitised onto the route to simulate a merging canopy structure either side of the route corridor (appropriately not applied onto built areas).

**Step 2:** Functional connectivity was calculated using *Probability of connectivity* (*PC*) index (See Saura and Pascual- Hortal, 2007) of woodland patch and linear habitat features using Conefor 2.6 software (Saura and Torné, 2009). Increases in habitat connectivity results in increases in *PC* (ranging between 0- no habitat, to 1- entire landscape composed of habitat). All broadleaf woodland area and linear habitat features from the three simulated Greenway development scenarios were

**Table 1**
Summary table of scaled explanatory landscape variables used for statistical analyses.

| | Variable | Description | Format |
|---|---|---|---|
| Areal Habitat Classes | GS | Semi- natural grassland | % of site area |
| | GA | Improved grassland | % of site area |
| | WD4 | Conifer plantation | % of site area |
| | Broadleaf | Semi- natural woodland and mixed broadleaved woodland | % of site area |
| | FL | Lakes and ponds | % of site area |
| | BL | Built land | % of site area |
| | PB[a] | Bogs | % of site area |
| Linear Habitats | Linear woodlands | Total linear woodlands density | km/site |
| | Total Linear features | Total linear features density | km/site |
| Woodland Features Connectivity Importance | $dPC_k$ | The importance of woodland feature k for the maintenance of overall habitat availability in the landscape | Sum of all k importance values present within sample site |
| Hedgerow Structure | Height | Average height of hedgerows | m/site |
| | Width | Average width of hedgerows | m/site |
| | Boxed | Percent of hedgerows that were boxed- profile | %/site |
| | Hedgerow gaps | Percent of Hedgerows with gaps >5 m | %/site |
| | Overgrown | Percent of hedgerows that were overgrown | %/site |
| | Remnant | Percent of hedgerows that were overgrown | %/site |
| Nearby Suitable Habitat | Distance to woodland habitat | Distance from sample site to nearest suitable habitat | m/site |
| | Distance to aquatic habitat | Distance from sample site to nearest suitable habitat | m/site |
| Temperature | Temperature average | Average temperature during site survey (three nights) | °C |

[a] Bogs (PB) habitat was cutover bog mostly regenerating back into heath and bog woodland with occasional and localised turf cutting.

extracted as a layer in ArcGIS and node (woodland habitat) and link (distances between woodland habitats) connection files were calculated for bat species. To avoid calculating all distances within the study area and save processing time, a ‘partial connection file’ was measured-limiting the maximum distances calculated to 3 km, determined by Core Sustenance Zones (CSZ) (Bat Conservation Trust, 2016) mean-maximum foraging radius. A set of dispersal distance thresholds between woodland features (nodes) were also determined to simulate the range of distances individual species may fly over non-woodland habitat; 10, 25, 50 and 100 m, and were input into Conefor for index calculations. The resulting calculation of the deviation of probability of connectivity (*dPC*) (Saura and Rubio, 2010) in Conefor provides an output containing node and link rank relative to its importance in maintaining existing connectivity levels within the landscape by measuring changes in the overall connectivity by the removal of the respective node or link. An additional output *Equivalent Connected Area* (*ECA*) is calculated from *PC* in Conefor, defined as ‘the size of a single patch (maximally connected) that would provide the same probability of connectivity than the actual habitat pattern in the landscape’ (Saura et al., 2011). *ECA* was used to calculate overall changes in landscape connectivity as a result of Greenway development scenarios. Fig. 5 provides a schematic outline of the steps taken to carry out functional connectivity analysis.

## 3. Results

A total of 154 GB of acoustic data was recorded, with mean recording time of 7.3 s and a mean sequence of echolocation pulses of 22.3 per recording. Eight species of bats were detected and 38,253 bat passes were recorded within 23 sites over the length of the Greenway route. *Pipistrellus pygmaeus* was most frequently detected (25,168 recordings) and *P. nathusii* was least frequent (217 recordings) (Table 2). Both *P. nathusii* and *P. auritus* were present in the least number of sites.

Distances between sampling sites were not considered to influence species diversity (Global Morans index *p-value* = 0.550; *z-score* = 0.599) and thus sites were considered independent and spatial autocorrelation did not occur. The activity recorded on the two recorders were not significantly different to each other ($p = 0.324$) and both recorder recording data were combined per sampling site for further analysis.

Autocorrelation determined ‘semi-natural grassland’* was negatively correlated with ‘improved grassland’ (Spearman's rho = −0.796), ‘linear woodlands’ was positively correlated with ‘total linear features’* (Spearman's rho = 0.801), hedgerow ‘width’ was positively correlated with hedgerow ‘height’* (Spearman's rho = 0.845), ‘boxed’ hedgerows was negatively correlated with ‘overgrown’* (Spearman's rho = −0.795), (*denotes the variable retained). Results of Generalised Linear Models for each species recorded are shown in Table 3; models for *P. pygmaeus*, *P. auritus*, *M. nattereri* and *total bat activity* were considered a poor representation of the actual data due to high cooks distance and standardised residuals values (Tabachnick and Fidell, 2013) and were omitted from further analysis. *Myotis daubentonii* had a strong positive association with ‘built’ and ‘total linear features’, a moderate association with ‘conifer’ and a weak negative association with ‘remnant’ hedges. *Myotis mystacinus* had a strong positive association with $dPC_k$, a moderate association with ‘total linear features’, a

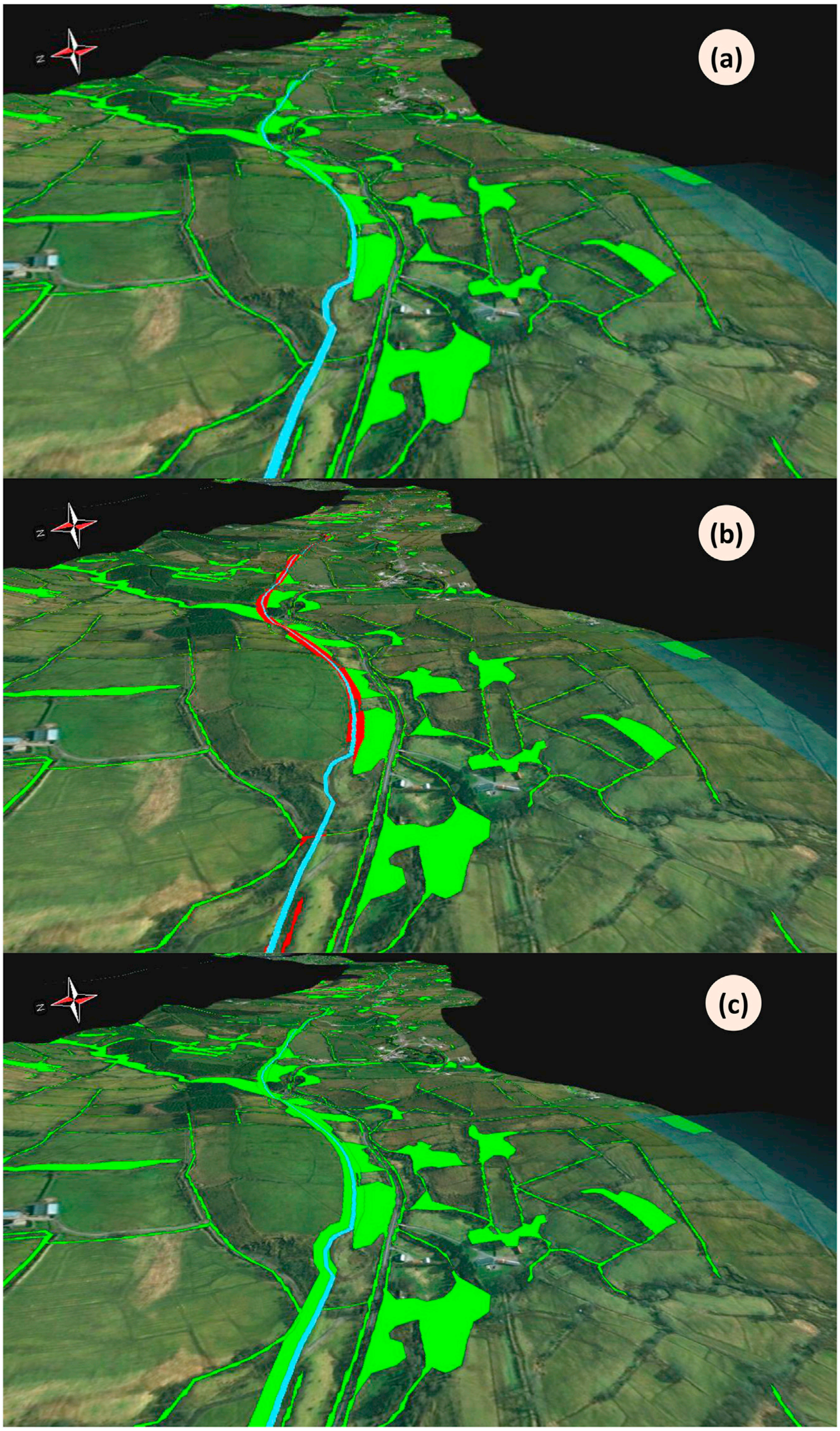

**Fig. 4.** Examples of ArcGIS maps of woodland feature class (bright green) with proposed Greenway route (blue). Existing woodland conditions (a) are cut 5 m either side of the Greenway route (indicated in red) to simulate woodland removal (b) and added to simulate woodland enhancement (c). These maps illustrate the three Greenway development scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

weak association with 'semi-natural grassland' and 'peatland', and a strong negative association with 'broadleaf'. *Nyctalus leisleri* associated strongly with 'conifer' and 'overgrown' hedges, moderately with hedge 'height' and 'temperature' and a moderate negative association with 'broadleaf' and 'total linear features'. *Pippistrellus. nathusii* had a strong positive association with 'total linear features' and moderate association with 'semi-natural grassland' and 'peatland', and moderate

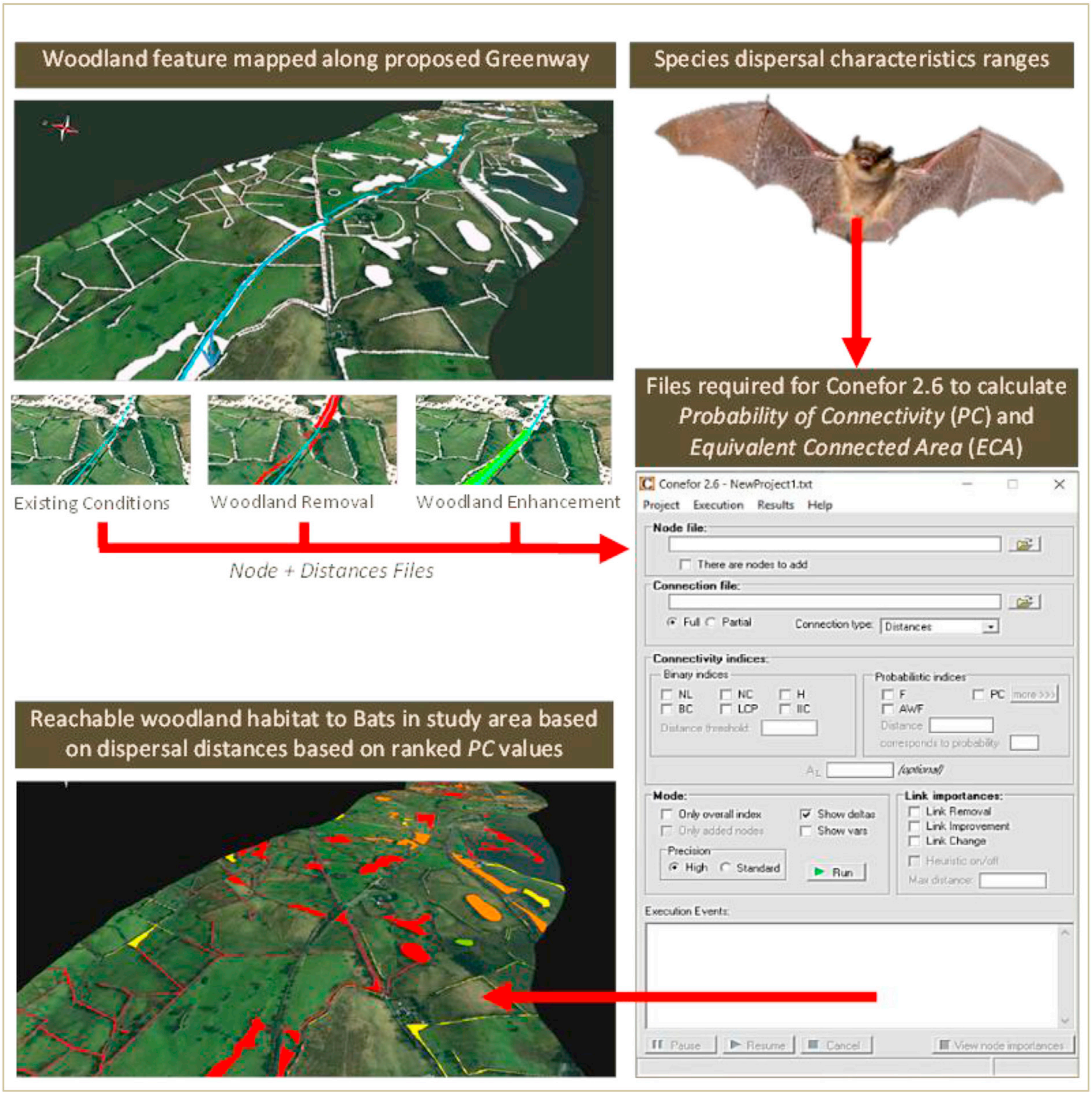

**Fig. 5.** Schematic outline of the methodology steps used for the analysis of reachable habitat for bats under the three Greenway development scenarios.

**Table 2**
Summary table listing species detected and activity across the Greenway route.

| Species | Total passes | representation | Occurrence ($p \leq 0.05$*) |
|---|---|---|---|
| Pipistrellus pygmaeus | 25168 | 66% | 100% |
| Pipistrellus pipistrellus | 7535 | 20% | 100% |
| Myotis mystacinus | 2291 | 6% | 87% |
| Nyctalus leisleri | 1034 | 3% | 100% |
| Myotis daubentonii | 855 | 2% | 52% |
| Plecotus auritus | 828 | 2% | 35% |
| Myotis nattereri | 325 | 1% | 87% |
| Pipistrellus nathusii | 217 | 1% | 35% |

* P-value is related to Kaleidoscope auto-classification detection: presence P-values based on Maximum Likelihood Estimator using confusion matrices (see Wildlife Acoustics Inc, 2017a,b Kaleidoscope Pro Classifier Performance Chart).

**Table 3**
Generalised linear model (GLM) results: bat species (N. of sites presence) activity association with landscape explanatory variables. Values shown represent the best-fit model post elimination of non-significant variables ($p \geq 0.25$). Significance levels: ***<0.001, **<0.01, *<0.5, —— not significant.

| Variable[a] | Bat Activity | | | | | |
|---|---|---|---|---|---|---|
| | *M.dau* (12) | *M.mys* (20) | *N.lei* (23) | *P.nat* (8) | *P.pip* (23) | Bat Diversity |
| Built | 2.133* | | | | −1.839** | .449** |
| Semi-natural Grass | | .237 * | —— | .235* | —— | |
| Conifer | 1.144** | | 1.386*** | | 1.282** | |
| Peatland | —— | .463* | | .672** | | -.251* |
| Broadleaf | | −1.477** | -.848** | | -.834** | —— |
| Tot Linear Features | 1.941*** | 1.806* | -.923** | 1.962** | | |
| Hedgerow Gaps | —— | | | | .022*** | .003*** |
| Remnant Hedge | -.057*** | —— | | -.128*** | -.030** | |
| Hedge Height | | | .702** | -.875* | | -.077* |
| Overgrown Hedge | | —— | 1.468*** | —— | | —— |
| Temperature | | —— | .385*** | -.278* | | .059*** |
| Dist. to Aqua Body | | | | .008*** | | |
| Dist. to Woodland | | —— | .002* | | | .001* |
| $dPC_k$ | | 4.475** | —— | | | |

[a] Variable descriptions are provided in Table 1.

negative association with 'remnant' hedges, hedge 'height' and 'temperature'. *Pippistrellus pipistrellus* had a strong positive association with 'conifer', a strong negative association with 'built' and moderate negative association with 'broadleaf'. *Bat Diversity* had a strong association with 'built', and a moderate negative association with 'peatland'.

Simulated Greenway development scenarios had a range of effects on the amount of reachable woodland habitat (*Equivalent Connected Area* (*ECA*)) under the four bat dispersal distance thresholds (Table 4). The greatest impact on overall woodland habitat reachability was the *enhancement* scenario (a), which increased the amount of functionally connected habitat by x 59% (±5%) across the four analysed bat distance thresholds. The *removal* scenario (b) resulted in an x 8% (±3%) decrease of reachable woodlands from *existing* woodlands (a). A minimum of 14% of woodland area was accessible to bats under the *existing* scenario (a) - (10 m distance threshold) to a maximum of 24% (100 m distance threshold). The *removal* scenario (b) resulted in a net loss of 40 ha and the *enhancement* scenario (c) resulted in a net gain of 80 ha of woodland habitat area.

Respective *Probability of Connectivity* (*dPC*) values were joined to attributes tables for each woodland feature under the three Greenway development scenarios (previously used to calculate *ECA* in Table 4) in ArcGIS. *dPC* values were then used to classify woodland habitat features within a sample section of the study area (Fig. 6) to illustrate the effect of each scenario on woodland functional connectivity. *dPC* values were Log-normalised and four indicative classes were defined in ArcGIS ranging from red (low connectivity value) to green (high connectivity value). Although isolated, certain features (example encircled in Fig. 6 (a)) provide a degree of connectivity within the study area through intrapatch connectivity (internal patch connectivity). In general, a decrease in feature connectivity from green to yellow colour classes is observed when comparing existing woodlands (a) to woodland removal (b) development scenarios, and increases in connectivity of woodland features from orange to yellow and yellow to green colour classes when comparing to woodland enhancement (c) in Fig. 6. Decreases in connectivity value of certain isolated features (yellow to orange) occur in woodland enhancement (Fig. 6. (c)) as the connectivity importance of smaller feature patch areas are reduced due to relative connectivity gains of the added Greenway woodland canopy within the study area.

## 4. Discussion

A Greenway development can present an excellent opportunity for conserving and enhancing cultural and natural heritage (Fabos, 1995; Ryan et al., 2004) and also the potential to preserve large networks of linear woodland elements within

**Table 4**
Graph of functional connectivity results displaying percentage amount of ECA-reachable broadleaf habitat to bats within the study area under various Greenway development scenarios, respective to dispersal distance (m) thresholds. Percentage values were based on each scenario resulting total woodland area.

| Development Scenario | Bat Dispersal Distances Thresholds | | | | Total Woodland Area (ha) |
|---|---|---|---|---|---|
| | 10 m | 25 m | 50 m | 100 m | |
| (a) Existing: % reachable woodland | 14% | 16% | 19% | 24% | 709 |
| (b) Removal: % reachable woodland | 10% | 10% | 11% | 12% | 669 |
| (c) Enhancement: % reachable woodland | 60% | 66% | 72% | 79% | 789 |

landscapes facing increasing land use intensification (Carlier and Moran, 2019). This study assessed the effect of landscape feature composition and structure on bat species activity along a disused European railway to inform future Greenway design in order to conserve and enhance landscape connectivity for bat species present. The research applied an interdisciplinary approach (as recommended in LaPoint et al., 2015); determining species presence, modelling species habitat associations, and simulating impacts to functional connectivity as a result of Greenway development scenarios. While the study applied the use of a relatively reliable bat auto-identification software (Brabant et al., 2018) with a limited number of species, it is accordingly advised to consider species-level results with a degree of prudency (Russo and Voigt, 2016).

**Fig. 6.** Example maps of study area displaying woodland habitat colour classified with respect to Probability of Connectivity values (dPC) for each feature under woodland- (a) Existing, (b) Removal and (c) Enhancement Greenway development scenarios at a 100 m bat dispersal threshold. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Continuous linear woodland, broadleaf woodland and semi-natural pastures are generally important habitat features for bats (Entwistle et al., 1997; Boughey et al., 2011a; Lundy et al., 2011; Pinaud et al., 2018, Claireau et al., 2019). The presence of broadleaf habitat is considered favourable for roosting habitat and important for the occurrence of Irish bat species (Lundy et al., 2011). Conversely, models in this study found *M.mystacinus, N.leisleri* and *P.pipistrellus* bat activity to be negatively associated with the presence of broadleaf woodland within the immediate landscape matrix (particularly). However, contribution of woodland features to connectivity within the study area present within the sample sites had a strong positive effect on *M.mystacinus*— considered a woodland generalist species in Ireland (Lundy et al., 2011; Buckley et al., 2012). This result suggests *M.mystacinus* prefer structurally connected woodland networks rather than isolated woodland patches that provide little or no structural connectivity. It therefor remains important to increase connectivity to woodland habitat, possibly via the establishment of linear woodland along the Greenway.

Previous studies suggest bats do not generally associate with conifer plantations (e.g Smith and Racey, 2008; Boughey et al., 2011b). However, recent research found this woodland type can support foraging activities of *Pipistrellus* species, although preferring plantation stand edges (Kirkpatrick et al., 2017). The strong, positive association in this study may therefore be a response to a combination of factors such as the double linear stand edge effect bounding either side and the open, clutter-free middle corridor of the abandoned railway within plantations. This is similar to woodland corridor use described in Hein et al. (2009), where woodland corridor edge reported greater bat diversity and activity when compared to dense corridor interior within managed landscapes. Given *N. leisleri* preference for broadleaf and mixed woodland habitat in Ireland (Lundy et al., 2011), it is interesting to note its strong, positive association with conifers in this study also. Further targeted investigation of potential corridor function is needed; until further research is carried out it may be precautionary to assume that Greenways traversing conifer dominated landscapes can provide essential foraging corridors and links to more suitable habitat for these species. The conservation and future management of Greenway corridor semi-natural grassland edges, particularly corridor sections between peatland areas, may be beneficial to *P. nathusii* and *M.mystacinus.*

*Pippistrelus nathusii*, *M. daubentonii* and *M. mystacinus* were positively influenced by linear features (positively correlated with hedgerows) with substantial effect size for each positive association. This reflects the positive correlation between density of features and bats (particularly linear vegetation) within the wider landscapes of the British Isles (Barr et al., 2005). Smaller species from these genus are noted for their reliance on linear elements in landscapes (Limpens and Kapteyn, 1991) whereas larger and faster species (e.g. *Nyctalus* spp) typically fly higher and directly to foraging grounds. *Nyctalus leisleri* are subsequently more susceptible to colder temperatures (Froideveaux et al., 2016), as shown in the results, and their more direct flight path may explain the moderate negative association with general linear feature density (similarly reported in Boughey et al. (2011a)).

Hedgerow structure had mixed influence on bat activity, highlighting a potential need for varied linear woodland management to suit the range of species recorded. The present study found a general negative association between *M. Daubentonii, P. nathusii* and *P. pipistrellus* and remnant hedgerows (i.e. hedges loosing base structure and density), though with a relatively weak effect. This contrasted with a positive association with overgrown hedgerows among *N. leisleri*. Hedgerow height (a covariate of width) had conflicting associations between the two species *N. leisleri* (positive) and *P. nathusii* (negative). Hedgerow height is considered generally important for bats (e.g. Wickramasinghe et al., 2003) and low, overtrimmed hedgerows are avoided (Russ and Montgomery, 2002). In order to benefit multiple bat species, a specific Greenway corridor may require a mixture of treelines (achieving height), dense, boundary-functioning hedgerow understorey (opposite of remnant) and the conservation of a relatively homogenous height profile to suit small and medium range echolocation species (see Froideveaux et al., 2016; Graham et al., 2018).

Bat activity levels detected along linear woodland features of the proposed Greenway route did not differ from activity detected along those within the surrounding landscape matrix. This suggests that the occurrence of suitable foraging habitat features along the Greenway corridor were spatially well connected and of similar structure to the surrounding landscape matrix. The composition and spatial arrangement of the surrounding habitat matrix can influence bat tendencies to cross open ground between woodland features (Abott et al., 2012), with different bat species willingness to cross open spaces varying depending on size (Limpens and Kapteyn, 1991) and their ability to avoid predation (Waters et al., 1999). The Greenway development scenarios aimed to determine the respective amount of reachable woodland habitat within a range of bat dispersal distances. It is important to recognise that functional connectivity was measured within the context of the study area only: *Probability of Connectivity* was calculated within a delimited study area, and it is probable that additional connectivity interactions exist outside of the study area that may influence species activity in a wider landscape context.

The woodland functional connectivity analysis of different Greenway development scenarios, demonstrated through the amount of theoretical reachable habitat and illustrated as classified maps, indicates the respective effects of the removal or addition of woodland habitat along a Greenway corridor. The removal of a 5-m section of woodland vegetation from the centre of the Greenway corridor significantly reduces functional connectivity within the immediate landscape. However, the addition of woodland habitat area to the Greenway route corridor is demonstrated to significantly increase functional connectivity within the immediate landscape. Furthermore, as bat activity varies with respect to structural and compositional make-up of habitat matrices (e.g. Klingbeil and Willig, 2009; Wood et al., 2017; Dias-Silva et al., 2018), species-specific models determined in this study provide practical insight towards conserving and enhancing habitat characteristics associated with high activity. The present study highlights both potential positive and negative impacts of Greenways development on linear woodland network functional connectivity and informs the management of these for the provision of a conservation corridor for bats.

***Existing Woodland Conditions:*** Given the extent of linear woodland features within the region (Minogue, 2002; Foulkes, 2006) and the increased density of field boundaries associated with High Nature Value farmlands (Matin et al., 2016), the total ‘functionally’ connected woodland area for an aerial species remained markedly low (under ‘existing’ woodland conditions). This suggests a significant portion of woodland habitat features within the study area were not functionally accessible to bats. Isolated woodland patches surrounded by open areas has been noted to result in less bat activity (Limpens and Kapteyn, 1991). This finding may coincide with the negative association to broadleaf woodland habitats for *M. mystacinus, N. leisleri* and *P. pipistrellus* in the generalised linear models.

***Woodland Removal***: The potential for the significant loss and fragmentation of woodland habitat is demonstrated under scenario 2 (woodland removal) by the very low habitat reachability that results across all species distance thresholds. This demonstrates that habitat removal not only results in net loss of total woodland habitat area (5.5% overall loss), but also has wider implications for functional connectivity at larger spatial scales; up to half of existing connectivity is lost. The removal of linear woodland can be detrimental to local bat populations, resulting in a loss of potential roosting sites (Barr et al., 2005) and wind shelter-reducing bat food (Harris and Woollard, 1990). Although mortality of bats due to Greenway development and use is unlikely, avoidance of associated open habitat could occur, resulting in the fragmentation of woodland networks either side of the route.

***Woodland Enhancement:*** Although this simulated scenario results in an 11% net gain of woodland habitat area, up to four-fold increases in functional connectivity are observed. This scenario would likely significantly increase reachable habitat for smaller species (i.e. *P. auritus*, *M. daubentonii* and *P. pipistrellus*) which have a greater dependency on continuous landscape features because of limited echolocation range (Limpens and Kapteyn, 1991; Entwistle et al., 1996; Barr et al., 2005).

Prioritising research on accurate predictions of habitat connectivity configurations and surrounding matrix composition can promote functional connectivity and help focus conservation efforts that are usually limited (Villard and Metzger, 2013). Rural European Greenways, typically re-using existing abandoned infrastructure corridors such as railways, could offer low-cost opportunities to establish linear woodlands-creating functioning woodland corridors and becoming multi-functional infrastructures. Such Greenway design should take into consideration the implications of development scenarios on woodland habitat in order to conserve or increase bat functional connectivity. These corridors could not only increase reachable habitat within the immediate landscape, but also could ultimately form an integral part of the European Green Infrastructure network, providing substantial ecological fluxes and conservation corridors at member state and international scales. At these larger scales, Greenway networks may benefit other species of conservation importance that are heavily dependent on linear woodland and that currently have restricted distributions-e.g. *R. hipposideros* (Lundy et al., 2011). Targeted woodland ecosystem enhancement and management in Greenway landscapes can be informed by ecosystem connectivity characterisation (e.g. Carlier and Moran, 2019) and using the species-specific recommendations in this study, providing larger landscape-scale solutions to the problem of increasing natural and semi-natural habitat fragmentation.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00613.

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