Habitat association and population size of the Madeira Firecrest (*Regulus madeirensis*)

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Abstract

Basic population information is often lacking for recently recognised species, yet such information is essential for conservation and management. This study provides a detailed assessment of population size and habitat association in a recently recognised species, the Madeira Firecrest (*Regulus madeirensis*). Species abundance data and habitat data were collected using a point transect distance sampling method. Estimates of density per habitat type were made, in conjunction with presence and absence data derived from the Madeira bird atlas, to estimate population size and habitat associations. We estimate the population size of the Madeira Firecrest to be 698,300 (95% CI: 523,540 and 869,960) which greatly exceeds the 10,000 threshold for the IUCN 'Vulnerable' category. Distribution and abundance were strongly linked with laurel and heath forest, with 56% of the population found in these two habitat types. Historically, much of the native laurel and heath forest was lost on Madeira, but these native forest habitats are now protected. Based on the large population size and successful management of the laurel forest habitat, our results suggest there is a no immediate risk of a change in conservation status for the Madeira Firecrest.

Keywords

conservation, density estimates, endemic, , laurel forest, management.

The loss of biodiversity due to anthropogenic factors is recognised as one of the predominant conservation issues of our time and it is estimated that the extinction rate of species is up to 1,000 times greater than the natural background rate (Pimm *et al.* 1995). While the taxonomic categorisation of species is fundamental to biology, ecology and conservation of species (May 1990), it is thought that most species remain undescribed and effort is needed to identify, catalogue and evaluate species to help avoid extinctions (Bickford *et al*. 2006). The term species is ambiguous, with different concepts about what a species actually is; e.g., the biological species concept (BSC – defined as populations of species that cannot interbreed) and the phylogenetic species concept (PSC – defined as a group that shares at least one unique derived character) may arrive at different conclusions when studying the same group (Agapow *et al.* 2004). The rate at which new species have been recognized has increased rapidly with the development of new tools (e.g. molecular genetics, acoustic analysis) to identify distinct taxonomic units (Köhler *et al*. 2005; Sangster 2009). Thus, there has been rapid change in the recognition of species limits, with a general trend leading to a larger number of less inclusive taxonomic units (Agapow *et al*. 2004). The identification of such taxonomic units for conservation, described as a discrete population or populations comprised by a single species or variant thereof, has been recognised as conceptually and legally important in the context of conservation monitoring and management (Frankham *et al*. 2010; Tobias *et al*. 2010).

Recently recognised cryptic species constitute a special case because their conservation status may not be well understood and relevant data may be difficult to assemble or collect. Yet cryptic species are thought to be common across a variety of taxa and geographical regions (Pfenniger and Schwenk 2007). It has been suggested that the increasing recognition of cryptic species with genetics tools results in a significant challenge for conservation management, as it is concomitant with an increase in the recognized number of threatened or endangered species experiencing range or population size decline (Tobias *et al.* 2010; Agapow *et al.* 2004; Sangster *et al*. 2016). For example, in species exhibiting a wide geographical range, there might be several subspecies recognized or merely considered populations of the same species. However, if a discrete population becomes recognized as a distinct species, it follows that it is found in a smaller geographical range, and that a finite, global population size estimate may or may not be known (Isaac *et al.* 2004). A study by Lohman et al. (2010) on Southeast Asian bird species, using genetic and phylogenetic evidence with supporting morphological data, found cryptic diversity in a number of widespread species with findings that suggest that many insular populations of these widespread species may be overlooked endemics that lack protection and recognition. The Madeira Firecrest (*Regulus madeirensis*) provides an example of a cryptic, polytypic, recently recognized island endemic (Clarke 2006; Sangster *et al.* 2005). Yet, while it is categorized by the IUCN as 'Least Concern', there are limited data on habitat association, population size and susceptibility to disturbance (del Hoyo *et al.* 2006).

The Madeira Firecrest is one of six species in the genus *Regulus* (del Hoyo *et al.* 2006), formerly treated as a conspecific of *Regulus ignicapilla* but which is now recognized as a distinct species based on genetic divergence, morphology, and call structure (Päckert *et al.* 2003; 2006; Rodrigues *et al.* 2014). Globally, *Regulus* spp. are categorised as being of 'Least Concern', with the Madeira Firecrest recognised as 'Least Concern' in 2008 (IUCN 2016).
The Common Firecrest (*Regulus ignicapilla*) breeds in the west Palearctic between July isotherms of 16 and 24°C with the core distribution in Central Europe and Iberia (Snow and Perrin 1998; Hagenmeijer and Blair 1997). The Madeira Firecrest is found only on the main island of the Madeiran Archipelago (Clarke 2006). Firecrests tend to breed in broad-leaved and mixed woodland and their diet is primarily arthropods, including springtails (Collembola), spiders (Araneae), moth and caterpillars (Lepidoptera) and aphids (Aphidoidea) (Snow and

Perrins 1998; Martens and Päckert, 2018). The Madeira Firecrest has been observed in a range of habitats including laurel forest (*Laurus*), woody heath, mixed forest and mountain vegetation (low tree heath) (Oliveira et al. 2002; Oliveira and Menezes 2004; Martens and Päckert 2015). Until recently, the best population estimate was > 10,000 individuals globally (Oliveira and Menezes 2004); a more recent estimate by BirdLife International (2015) suggests the population was 100,000-200,000 individuals. However, because of the lack of quantitative data underlying these estimates, the extent to which the endemic Madeira Firecrest population meets or exceeds the IUCN's 'Least Concern' threshold of 10,000 individuals is unclear. Recent contraction of laurel forest (during the 20th century), due to introduced *Eucalyptus* plantations, is of conservation concern, potentially affecting the breeding success of Madeira Firecrest (del Hoyo *et al.* 2006; BirdLife International 2015). Finally, while the Madeira Firecrest is an endemic species, there is no specific management or conservation initiative directed towards the species (Oliveira and Menezes 2004).

The aim of this study was to estimate the population size and habitat use of the Madeira Firecrest to understand better the status of the newly recognised species and to inform its management and conservation. Specifically, the objectives of this study were to: (1) identify habitat correlates of Madeira Firecrest presence and abundance; (2) estimate population density as a function of habitat types; and (3) evaluate the effect of habitat disturbance on presence and density. We discuss our results in relation to the IUCN conservation status designation for a newly recognized species and, specifically, in the context of management of the Madeira Firecrest.

Methods

Study area

Madeira is a volcanic island located in the eastern Atlantic and is approximately 5.2 million years old (Jones *et al.* 1987). Madeira has an area of 742 km^2 with a maximum elevation of 1,861 m along a mountainous central ridge (Jones *et al.* 1987). The island consists of several habitat types including agriculture, urban, coastal, heath, upland, indigenous forest, and exotic forest (Jones *et al.* 1987*;* Oliveira and Menezes 2004*)*. Indigenous forest on Madeira is the Laurisilva or laurel forest that once covered most of the island and is considered a relict forest type (Clarke 2006; Jones 1988; Oliveira and Menezes 2004). Laurel forest (characteristic species include *Laurus azorica*, *Ocotea foetens and Myrica faya)* covers an area of approximately 15,000 ha representing around 20% of Madeira, a reduction from historical cover due to habitat loss and degradation as a result of clearance for crops and cattle (*Bos taurus*) grazing (Oliveira *et al*. 2002; Fernandez-Palacios *et al.* 2011; Marrero *et al.* 2004).

Data Collection

Distance sampling

Data on Madeira were collected between March and June during the breeding season in 2008, 2010, and 2011. Surveys were conducted using a point transect distance sampling method (Buckland *et al.* 2001). A total of 55 transects were conducted resulting in 584 census points. Transect locations were selected based on a stratified design to include all major habitat types on Madeira (any change in habitat type at a census point was noted). The starting point of each transect was chosen randomly in the field using a stopwatch (seconds and 1/100th of a second displayed were added together upon arrival in a survey area and this was then used to select the number of metres into the transect the start point was positioned). Habitat types sampled were categorised according to the predominant habitat types occurring on Madeira, laurel forest *,* heath forest (*Erica* spp.), planted exotic forest (mostly pine, *Pinus pinaster* or Eucalyptus*, Eucalyptus globules*), mixed forest (mixture of exotic and indigenous tree species), agriculture, upland (high altitude regions not dominated by forest), urban (evidence of human presence), and coastal (similar to Jones *et al.* 1987). At each census point, the percentage cover of each habitat type was estimated and the dominant habitat type was recorded (similar to Jones *et al.* 1987; Jones 1988).

Surveys were conducted in the morning between 07:00 and 11:30 (GMT +1) to coincide with the peak activity of forest birds (Bibby *et al.* 1999). However, surveys were not conducted during inclement weather (high winds, rainfall and low clouds). Point counts were positioned systematically at intervals of 200 m and conducted over 4-minute periods. Where points were positioned along paths, roads, or watercourses, they were positioned 10-30 m perpendicular to the transect when possible to avoid bias (Lee and Marsden 2008). A single observer (JN) was used throughout the study to remove the effect of inter-observer variability, although a digital recorder or a research assistant was used to record observations. Birds in flight were ignored unless their point of origin could be identified. However, birds disturbed or flushed before counts were recorded as present. Point counts were conducted immediately after arrival, as the use of a settling down period has been identified as negatively biasing the number of contacts of many bird species (Lee and Marsden 2008). A range finder (Bushnell Yardage Pro) was used to estimate distances to visual contacts and to train estimates for call contacts. The method of contact recorded (sight or sound) was also noted. The contacts identified by sound were placed in distance bands if an accurate distance could not be taken due to the likelihood of error in the estimation. The bands used were 0-10, 11-30, 31-100, and > 100 m. The presence of disturbance was also noted in the laurel and heath forest with the occurrence of exotic forest species or agriculture exceeding 10% at each point used as an indication of anthropogenic disturbance.

Madeira breeding bird atlas data

Information on the general distribution of firecrest on Madeira was provide by a systematic survey of Madeira carried out by the Parque Natural da Madeira. It was conducted over three breeding seasons from between 2009 and 2011 (inclusive) (Atlas das Aves do Arquipélago da Madeira 2011). The survey took place within an existing system comprised of 291 grid squares of 4-km^2 quadrats, 181 on the main island Madeira (where the Madeira Firecrest is found). Each quadrat was surveyed at least once (Atlas das Aves do Arquipélago da Madeira 2011). Each transect lasted 1-hour, split into six 10-minute increments walked at a constant speed (2.5-3 km/hour) using a GPS (Garmin eTrex) and a stopwatch. During each of the six transect increments, the total number of individuals observed, habitat type and any indication of breeding were noted. Habitat types recorded in the Madeira bird atlas have been placed into the broader habitat types defined in the distance sampling bird survey using the detailed description of each habitat type provided by the bird atlas for the purpose of this analysis.

Analysis

Density was estimated using the program Distance 6.2 (Thomas *et al.* 2010), following guidelines described in Buckland *et al*. (2001). Briefly, exploratory analysis was undertaken on the data to identify the presence of errors, outliers and variation in detectability based on the method used (sight or sound). Outliers were removed (contacts in the band > 100 m) and then contacts were placed into distance bands to improve the fit of detection curves. To maximise the number of contacts used in the analysis, both aural and visual contacts were used, with the type of contact added as a covariate to account for difference in detection between the two types of contact. Density and population size estimates were made at the habitat level using a global detection function with covariates added to account for difference in detectability between habitat types and also forest versus non-forest habitats. A visual inspection of detection curves and histograms was made. AIC was used to select the best model fit from a selection of detection functions and series expansions (Half-normal and Hazard-rate with cosine, hermite polynomial and simple polynomial series expansions)(Thomas *et al*. 2010), and goodness of fit test and visual inspection of histograms were used to select the covariate combination, truncation distance and number of intervals. Variance was estimated using bootstrapping for the final chosen model (Thomas *et al*. 2010).

The number of quadrats occupied in each habitat type from the Madeira bird atlas was used to estimate distribution and was then used in conjunction with the density calculated for each habitat type to estimate habitat-specific population estimates using Distance. Habitat-specific population estimates were then summed to estimate the total population size by multiplying habitat specific density estimates by the area represented by that habitat (e.g. see Newson *et al.* 2005). These estimates were then summed to calculate an overall population estimate. Chi-squared goodness of fit was used to examine the partitioning of the Madeira Firecrest density and population across habitat types (both measured in number of individual birds).

In order to determine whether habitat disturbance, modification, and human presence each has a significant effect on focal species presence using the bird atlas data, habitat types were ranked roughly from 1-8 based on the degree of anthropogenic disturbance and change they have been exposed to since the arrival of the first settlers (ad 1420–1430; Fernandez-Palacios et al. 2011); a score of 8 indicated the maximum level of disturbance represented by urban areas and a score of 1 the least amount of disturbance represented by the indigenous laurel forest. This now protected on Madeira, followed by indigenous heath forest which often buffering the laurel forest, both habitats being those least changed by humans (Jones et al, 1987) (8 = urban, 7 = coastal, 6 = agriculture, 5 = exotic forest, 4 = mixed forest, 3 = mountain, 2 = heath forest, 1 = laurel forest). A generalised additive model (GAM) with a binomial link function (Wood, 2006) and thin plate splines as smoothers (K = 5 as suggested by Keele 2008, in Zuur et al. 2009 for datasets with >100 observations) was used to determine if habitat disturbance has a significant effect on species presence using the R package 'mgcv' (Wood, 2003). The number of contacts per point was compared between pristine laurel forest and disturbed laurel forest using a t-test to examine the effect of disturbance. Average abundance per quadrat (mean individuals per quadrat) were calculated using the Madeira bird atlas sampling data. The relative abundance for each quadrat was then calculated (quadrat abundance / total species abundance across Madeira). Average relative abundance was mapped along with human disturbance level, which was categorised as low, which included laurel and heath forest, intermediate including mountain, mixed and exotic forest and high including agriculture, coastal and urban habitat to identify spatial patterns in relative abundance associated with habitat disturbance. Mapping was conducted in QGIS (QGIS.org, 2015). Spearman rank correlation was used to test for a correlation between relative abundance and human disturbance across Madeira. Unless otherwise specified, all analyses were conducted using R version 3.3.2 (R Core Team 2016).

Results

A Half-Normal model with truncation at 60 m and eight intervals was chosen to estimate density and population size with covariates for contact type and forest included to account for differences in detectability based on goodness of fit (summary in table 2). Density estimates are expressed as the number of individuals per km^2 (Table 1). The total population size of Madeira Firecrest, accounting for habitat weighting, was estimated to be 698,300 individuals (95% CI: 523,540 and 869,960). Density estimates for the Madeira Firecrest (Individuals per km^2), calculated for each habitat type are shown in Table 1. The highest density was observed in heath forest (3,716 /km^2), followed by laurel forest (2,572 / km^2) (Table 1). Madeira Firecrest population estimates within each habitat type are shown in Fig 1 and table 1. The population was not evenly distributed across habitat types (Chi-square: χ^2 = 464,840, df = 7, p < 0.001), with the largest density occurring in laurel forest (195,530 individuals; 28%) and heath forest (193,250, 27.67%). The remainder of the population was supported by exotic forest, mixed forest, upland and agricultural habitats with no individuals recorded in coastal and urban habitats during distance sampling (Fig 1, Table 1).

We found Madeira Firecrest presence to have a highly dependent, non-linear, negative relationship with habitat disturbance (GAM: Deviance explained= 29.8%, K = 5; p < 0.001; Fig 2). However, the number of contacts per point count did not differ between pristine laurel forest and disturbed laurel forest (t-test: t = 1.2, df = 169.3, p = 0.21). Spatially, we found a strong negative correlation between Madeira Firecrest abundance and habitat disturbance (Fig 3: Spearman Rank Correlation, rho = -0.56, df = 179, p < 0.001). The distribution of the Madeira Firecrest was concentrated in central and northern areas of the island that coincided with the distribution of primary habitat. High levels of relative abundance (proportion of total contacts observed in each grid square) were measured in low (laurel and health forest) or intermediate (mountain, mixed and exotic forest) levels of disturbance. Low relative abundance and absence of the Madeira Firecrest were associated with areas of high disturbance (agriculture, coastal and urban habitat; see Fig 3).

Discussion

In this study we present the most recent estimate of Madeira Firecrest population size based on detailed point counts across all prevalent habitat types on the island. We report an estimated population size for Madeira Firecrest of 698,300 individuals, which, although consistent with the IUCN designation as of 'Least Concern' (IUCN 2016), is higher than previous estimates. A high density of an island *Regulus* species has been observed by Carrascal *et al.* (2008) on La Palma, Canary Islands, with the Goldcrest (*Regulus regulus)* being the second most abundant terrestrial species. A significant percentage of the Madeira Firecrest population was concentrated in the laurel and heath forest (56%), with the primary range being much smaller than the estimated extent of occurrence. Approximately 20% of the island is covered by laurel forest (Marrero *et al*. 2004; Fernandez-Palacios *et al.* 2011; IUCN 2016). These remaining indigenous habitats are concentrated in the northern and central areas of Madeira (Oliveira *et al.* 1999). The 'Vulnerable' (VU) IUCN Red List criteria for area of occurrence is 20,000 km^2. Although a significant percentage of the Madeira Firecrest was concentrated in a small area of occurrence of <20,000 km^2, there is no evidence for a decline in population or habitat size or quality that is associated with the 'Vulnerable' IUCN classification (IUCN 2016). Martin (2009) suggested that the criteria set by the IUCN for distribution ranges may not be applicable equally to all taxa or when assessing the extinction risk and conservation urgency of island species that occur across small geographical areas naturally. Martin (2009) suggested that the natural restricted range of occurrence of island species is a factor must be taken into account in order to not overestimate the potential threat to a species and its IUCN classification.

We found evidence of a negative relationship between Madeira Firecrest presence and human disturbance. This relationship is possibly explained by a link between Madeira Firecrest and laurel and heath forest, habitats where anthropogenic disturbance is relatively low. However, the analysis from distance sampling and of bird atlas data suggest that the Madeira Firecrest utilises disturbed remnants of the indigenous forest on Madeira and, to a lesser extent, the exotic forest, which is consistent with previous observations (del Hoyo *et al.* 1996). While we also found the Madeira Firecrest in agriculture habitat, most of these sites were classified as "agriculture with forest nearby" (Atlas das Aves do Arquipélago da Madeira 2011). Some of the agriculture on Madeira is subsistence farming on terraces at relatively high elevations in close proximity to well-preserved laurel forest (Marrero *et al*. 2004), which may contribute to the population estimate attributed to this habitat class.

An association of Firecrest (*Regulus ignicapilla*) with mature, mixed hardwood forest has been identified by Kosicki *et al.* (2015) in a study in Poland, where the species avoided pine forest and favoured areas with high tree species richness. Kosicki *et al.* (2015) also found Firecrest (*R. ignicapilla*) to be abundant in upland regions, similar to our findings. Previous studies have found that the Firecrest (*R. ignicapilla)* will use a range of tree species (i.e. coniferous and non-coniferous (Leisler and Thaler 1982), will forage on a relatively wide species diversity of arthropods (Kralj *et al.* 2013) and exhibit relatively broad habitat choice (Hagenmeijer and Blair 1997) in comparison to otherwise ecologically similar, sympatric species (such as the Goldcrest, *Regulus regulus*). The Madeira Firecrest may be able to use resources that on the mainland may be limited by competition (such as food or nesting habitat), used by other firecrest (*R. Regulus*), tit (Paradae) and warbler (Sylviidae) species, which may promote the high densities found on Madeira. Further research could investigate whether any behavioural differences between the mainland Firecrest (*Regulus ignicapilla)* in the presence of the sympatric Goldcrest (*Regulus regulus*) and the Madeira Firecrest are present that may indicate niche change or expansion.

A large proportion of the Madeira Firecrest population occurs within nature reserves (around 56% in laurel and heath forest) under the jurisdiction of the Parque Natural da Madeira or Madeiran Natural Park (Oliveira & Menezes, 2004; Oliveira and Heredia 1995). This habitat is considered a priority habitat under the EU Habitat Directive, as part of the Macaronesian laurel forest (Oliveira and Menezes 2004; Oliveira and Heredia 1995). These protective measures have halted the impact of habitat loss, degradation, and fragmentation which reduced the native laurel forests to its present cover (Oliveira *et al.* 1999). In addition, the laurel forest features in the successful programme of conservation management for the endemic Madeira Laurel Pigeon (*Columba trocaz*; Oliveira and Heredia 1995), which has likely imparted indirect benefit to the status of the Madeira Firecrest.

Conclusions

While our findings are consistent with the classification of the recently recognised Madeira Firecrest as of 'Least concern', being a single-island endemic, it is inherently vulnerable to natural disasters and to anthropogenic habitat loss or introduced species (Pimm *et al.* 1995). Although our results suggest that conservation management has been effective for the Madeira Firecrest, continued monitoring remains important to enable intervention due to unforeseen changes in its status. Ideally, this would be through continuous monitoring or a census scheme, perhaps in conjunction with development of a volunteer based Madeira bird atlas project or breeding bird survey. This would provide information on any changes in species distribution and population trends on a continual yearly basis and would provide information on other bird species on Madeira. Madeira is also covered by the SPEA (Portuguese Society for the Study of Birds) Breeding Bird Atlas that is collected over 5 years that could also provide monitoring data. Finally, the loss and replacement of laurel forest with eucalyptus plantations may pose a potential threat to this species in the future. Madeira is an Endemic Bird Area (EBA) and so protection of its habitats and endemic species is a priority for the preservation of biodiversity (Martens and Päckert 2015). While we focussed on a single species, we suggest that population monitoring for island endemics, especially for newly recognised species, is crucial for species management, conservation and prevention of extinctions (Sangster *et al*. 2016).

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Figure legends

Fig 1. Population size and 95% confidence interval estimate for each habitat type on Madeira. Laurel, heath, exotic and mixed are all forest types. Coastal and urban habitat types are not shown in the figure as population size in these habitat types was 0) (based on data collected on Madeira between 2008 – 2011).

Fig 2. Non-linear effect of human presence and habitat disturbance on the presence of the Madeira Firecrest (1 = No disturbance – indigenous laurel forest; 8 = Maximum disturbance – Urban areas) (based on data collected on Madeira between 2008 – 2011).

Fig 3. Map of the relationship between habitat disturbance and the distribution and abundance of the Madeira Firecrest (based on data collected between 2008 – 2011).

Table 1. Madeira Firecrest density estimates (individuals per km^2) and population estimates across habitat types on Madeira (based on data collected between 2008 – 2011). Results are from a Half-Normal model with truncation at 60 m and eight intervals was chosen to estimate density and population size with covariates for contact type and forest included to account for differences in detectability (estimates bootstrapped – 999).

Habitat **(Quadrats survey / occupied)**	Density/ km^2	Coefficient of variation (%)	95% LCL	95% UCL	Population size (95% CI)
Laurel Forest **(19 / 19)**	2,527	13.01	1,938.5	3,229.9	195,530 (147,320– 245,470)
Heath Forest	3,716.3	11.91	2,833.2	4,530.6	193250

(13 / 13)					(147,320– 235,590)
Exotic Forest	769.43	25	442.92	1,172.2	104,640
(36 / 34)					(60,237 – 159,420)
Mixed Forest	2,367.5	15.58	1,680.6	3,142.3	66,289
(7 / 7)					(47,058 – 87,984)
Upland	901.97	18.98	609.25	1,259.2	46,902
(20 / 13)					(31,681 – 65,477)
Coastal	0	-	-	-	0
(10 / 3)					
Agricultural	533.08	27.82	274.88	841.37	91,690
(68 / 43)					(47,280 – 144,720)
Urban	0	-	-	-	0
(8 / 0)					
Total population estimate					698,300 (523,540 – 869,960)

Model	Key Function (Automatically selected in Distance using AIC)	AIC	Estimate (Individuals per km^2)	% CV	95 % CI		GOF Chi-p
*** Truncation 60 m (8 bands) Forest and Contact covariate**	**Half-normal (cosine)**	**1027.7**	**1404.9**	**7.14**	**1215.9**	**1623.2**	**0.238**
Truncation 65 m (8 bands) Forest and Contact covariate	Half-normal (cosine)	1029.4	1314.4	7.4	1137.7	1518.5	0.074
Truncation 60 m (6 bands) Forest and Contact covariate	Half-normal (cosine)	1052.1	1673.5	7.4	1448.1	1933	NA
Truncation 70 m (7 bands) Forest and Contact covariate	Half-normal (cosine)	1235.6	1511.7	7.2	1312.8	1740.9	NA
Truncation 80 m (8 bands) Forest and Contact covariate	Half-normal (cosine)	1272.4	1324.7	7.2	1151	1524.7	<0.001
Truncation 90 m (9 bands) Forest and Contact covariate	Half-normal (cosine)	1347.9	1120.85	7.2	973.6	1290.4	<0.001
Truncation 100 m (10 bands) Forest and Contact covariate	Half-normal (cosine)	1396	977.1	7.2	848.7	1124.8	<0.001

Table 2. Model summary with different truncations and bands. Key function selected from Half-normal and Hazard-rate with cosine, hermite polynomial and simple polynomial series expansions using AIC in Distance. CI – Confidence intervals. CV – Coefficient of variation. GOF chi-p – goodness of fit test results. * indicates model that was bootstrapped to calculate population estimates.