LETTER

Intraspecific application of the mid-domain effect model: spatial and temporal nest distributions of green turtles, *Chelonia mydas*, at Tortuguero, Costa Rica

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Abstract

The mid-domain effect (MDE) model was developed to evaluate patterns of species richness. We applied the MDE model to intraspecific distribution patterns – the spatial and temporal nest distributions of green turtles, *Chelonia mydas*, at Tortuguero, Costa Rica, from 1972 to 2000. Spatial and temporal distributions of green turtle nests at Tortuguero did not exhibit significant annual variation over this time period. The spatial and temporal distribution of nests largely conformed to the predictions of the MDE model, although the spatial model has a better fit. Environmental factors that may cause deviations from the MDE model are discussed. The model also indirectly provided a first estimate of the mean spatial nesting range of individual green turtles at Tortuguero: 10.1 km (SD 8.7 km). The MDE model provides insight into intraspecific as well as interspecific distribution patterns.

INTRODUCTION

Colwell & Lees (2000) proposed the mid-domain effect (MDE) model to explain geographical patterns in species richness. The MDE model demonstrates that randomly placing the ranges and/or range midpoints of various species within a single shared geographical domain with defined boundaries will produce a unimodal curve in species richness with the greatest species richness at the centre of the domain. Similarly, interspecific overlap in the temporal ranges of a biological event such as flowering phenology within a defined temporal domain would result in a mid-domain peak (Colwell & Lees 2000; Morales *et al.* 2005). In the absence of environmental constraints within the domain, the MDE is an inevitable result of geometrical constraints when ranges of species are placed randomly within the boundaries of the domain (Colwell & Lees 2000).

The MDE model has been evaluated in numerous multi-species systems (Colwell *et al.* 2004), but apparently not for intraspecific distribution patterns. Some researchers have expressed concerns about the validity of the MDE as an explanation for patterns in species richness including the dimensionality of the habitat, the hardness of habitat boundaries, and the probability that range sizes change with environment (Hawkins & Diniz-Filho 2002; Zapata *et al.* 2003). However, the MDE is less problematic and its assumptions are better met for our evaluation of one-dimensional distributions than for the original phenomenon (continent-scale latitudinal variation in species richness) that the MDE was proposed to explain.

We assessed the spatial and temporal distributions of green turtle (*Chelonia mydas* L.) nests at Tortuguero, Costa Rica, the largest rookery in the Atlantic system, based on surveys conducted along the 30-km beach from 1972 to 2000. We applied the MDE model to Tortuguero green turtles by replacing the ranges of species with the spatial or temporal nesting ranges of individual females within a nesting season. An individual female green turtle deposits several egg clutches within a season at *c.* 12-day intervals and chooses nesting sites within her spatial nesting range defined by her degree of site fixity, the tendency of a female to place successive nests in close proximity (Carr & Carr 1972).
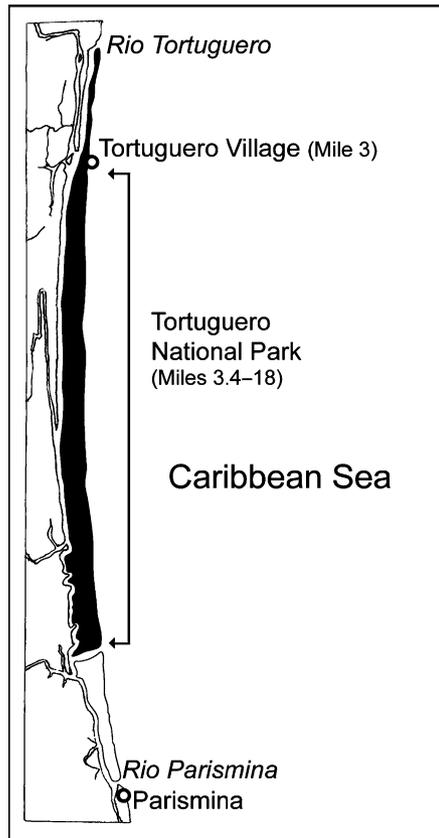
Figure 1 The Tortuguero green turtle nesting beach (shown in solid black) is bounded by Rio Tortuguero.

Spatial and temporal nesting ranges of individual females are smaller than the population ranges. As required by the MDE model, the spatial and temporal nesting ranges at Tortuguero have defined boundaries. Spatially, Rio Tortuguero defines hard boundaries at the northern and southern ends of the beach and separates the beach from the mainland, making the beach an island (Fig. 1). Hard boundaries are more difficult to define temporally; although a few nests may be deposited in every month of the year on Tortuguero Beach, the main nesting season occurs between July and October. Thus, the spatial and temporal distributions of nests may conform to the MDE. Deviations from the predicted curve indicate the role of biological or environmental factors influencing the distribution.

Before applying a MDE model to assess whether spatial and temporal nest distributions are consistent with its predictions, we must confirm that these distributions are constant across years. Increasing population size [the annual number of nests deposited doubled between 1971 and 2000 (Bjorndal *et al.* 1999; Solow *et al.* 2002)], wide dispersal of females throughout the Greater Caribbean between reproductive seasons, variable intervals of 2–4 or more years

between successive nesting seasons for individual females, variable annual number of nests per individual (Carr *et al.* 1978), a highly dynamic beach environment, and environmental stochasticity could all contribute to significant annual variation in seasonal spatial and temporal patterns, which would complicate interpretation of the MDE model.

MATERIALS AND METHODS

Study site and data collection

The 18-miles (30-km) long Tortuguero nesting beach lies on the northern Caribbean coast of Costa Rica and is separated from the mainland by Rio Tortuguero (Fig. 1). Historically, data have been collected in units of miles on this beach with mile 0 at the north end. Tortuguero village lies at *c.* mile 3, and in recent years, construction of tourist lodges has spread northwards to mile 1. The area between miles 3.4 and 18 is designated as Tortuguero National Park. The beach is backed by low-lying tropical rainforest.

Females emerge from the sea at night to nest on the beach, leaving visible tracks in the sand. An experienced observer can distinguish between tracks of females that nested successfully and tracks of females that returned to sea without laying eggs (non-nesting emergences). In 1971, Archie Carr initiated surveys of nests and non-nesting emergences at Tortuguero. Surveys have been conducted since 1971 at approximately weekly intervals by an observer walking the beach early in the morning and counting the number of nests and non-nesting emergences from the previous night for every 0.125 miles. Initially, these surveys were only conducted during the main nesting months between June/July and October/November, but since 1997 the beach has been surveyed throughout the year. Between 1971 and 1985, survey coverage alternated between the northern 11 miles and the entire 18 miles. From 1986 to 2000 the entire 18-mile beach was surveyed.

Analyses of within and among year variation

Data on nests collected from 1972 to 2000 during the main nesting period between 1 July and 31 October were analysed for spatial and temporal patterns. Data were aggregated into 0.5-mile intervals for analyses. To ensure that samples were large enough to provide a representative spatial pattern, only surveys that had more than 70 nests per day (equivalent to the potential for two nests per half mile) were used. Additionally, for spatial analyses within a year, at least two surveys in each month were required. Data from 25 (1972, 1977–2000) and 8 years (1986, 1988, 1991, 1993, 1994, 1998–2000) met the criteria set for spatial analyses among and within years respectively. Years with at least one survey in each half-month period between 1 July and 31 October

were used for temporal analyses. Data from 12 years (1972, 1976–1978, 1988, 1991–1994, 1998–2000) met the criteria; only the northern 11 miles were considered for temporal analyses, because of the availability of a larger data set. The northern 11 miles consistently account for *c.* 60% of the nesting each year (Carr *et al.* 1978; Bjorndal *et al.* 1999).

Spatial and temporal distributions of nests were modelled statistically using a nonparametric regression approach (generalized additive models [GAM]: Hastie & Tibshirani 1990; Crawley 2002) incorporating a logit link and a binomial distribution corrected for overdispersion (see below, Table 1). The spatial distribution models had one response variable (proportion of nests on each half mile) and three potential covariates (half-mile, day-of-year and year). The temporal distribution models had one response variable (proportion of nests on each day-of-year) and two potential covariates (day-of-year and year). To evaluate whether the potential covariates were statistically significant, analyses were repeated with each potential covariate excluded, and the nested models were compared with analyses of deviance. For models with overdispersion ratios (residual deviance/residual d.f.) > 1, F-tests rather than chi-squared tests were used for model evaluation, and standard errors were multiplied by the square root of the over-

Table 1 Summaries of generalized additive regression models (logit link, binomial distribution) for spatial and temporal distributions of nests on Tortuguero Beach*

Models	r^2	d.f.	F-test	P-value
Spatial nest distribution model				
Covariates: half-mile, day, year				
Model simplification	–	28 7911	0.0006	1
Reduced model: half-mile	0.522	8 7911	1091	< 0.0001
Temporal nest distribution model				
Covariates: day, year				
Model simplification	–	1 182	2.874	0.092
Reduced model: day	0.767	4 182	152	< 0.0001

*Years analysed for spatial trends: 1972, 1977–2000. Years analysed for temporal trends: 1972, 1976, 1977, 1978, 1988, 1991–1994, 1998–2000. r^2 = (null deviance − residual deviance)/null deviance. d.f. is degrees of freedom (numerator and denominator). F-tests are used for analyses of deviance tests of significance because of overdispersion. Response variable is the proportion of nests and is a two-column matrix. Covariates: half-mile, spline half-mile; d.f. = 8; day, spline day-of-year; d.f. = 8. Nested non-significant model simplification (analysis of deviance) indicates that the covariates removed from the full model do not have a significant effect.

dispersion ratio (Crawley 2002). The r^2-values were calculated as (1 − residual deviance/null deviance).

MDE model simulations

To evaluate the predictions of the MDE model for this system, a null distribution of nest densities along the 18-mile beach was simulated. The MDE model described by Colwell & Lees (2000) assumes that species ranges are known and simulates the random placement of these ranges within the domain. However, because there are insufficient data on nesting range sizes (the length of beach over which a female deposits her clutches within a nesting season) from Tortuguero, the nesting range size distribution was estimated from the distributional data, assuming that the distribution of range sizes among females followed a gamma-distribution. In the absence of data and ecological justification for using some other range size frequency distribution, the gamma-distribution provides a more parsimonious approach. The gamma-parameters (shape and scale) that provided the best fit between the simulated null (MDE) pattern and the observed data were determined. Data on number of nesting females are unavailable as only nest counts are conducted on the 18-mile beach, but Carr *et al.* (1978) estimated a mean of three clutches per female at Tortuguero. Therefore, a total of 24 000 turtles each with a mean of three clutches was simulated with the model, equivalent to the mean annual number of 72 000 nests laid at Tortuguero (modified from Bjorndal *et al.* (1999) for the years 1992–1996). For each turtle, a range size was picked at random from a gamma distribution with particular shape and scale parameters. An assumption of the MDE model is that all areas of the beach are equally suitable for nest deposition. Thus, the location of the centre of each range along the 18-mile beach was selected from a uniform distribution of potential points along the beach, such that the nesting range always lay within the boundaries of the beach. The location within this range of each of the three clutches was then selected at random from a uniform distribution along this range. The beach was divided into 36 half-mile segments and the segment of the beach within which each clutch was placed was recorded. This process (simulating 72 000 nests) was then repeated 20 000 times and averaged to calculate the expected distribution of nests along the beach. The sum of squares was calculated from both the observed numbers of clutches and the simulated (mean) nest distribution in segments along the beach. The Nelder–Mead optimization method (R Development Core Team 2004) was used with tolerance values of 0.001, and varying numbers of simulations, to find the sum of square estimates of the shape and scale parameters of the spatial nesting range distribution. The 95% confidence intervals on the best-fit curve were derived by running 20 000 simula-

tions and taking the 0.025 and 0.975 quantiles for each beach segment. The sum of square gamma-parameters were also used to calculate the estimated mean and standard deviation of nesting range sizes at Tortuguero.

To evaluate whether temporal distribution of nests conformed to the MDE model, nest distribution was simulated using clutch frequency and inter-nesting interval data published for Tortuguero. The number of simulated clutches laid by a turtle in the model was randomly selected from a Poisson distribution with a mean of 3, truncated to include only values between 1 and 7 (Carr *et al.* 1978). Using data sampled from the clutch frequency distribution provided by Carr *et al.* (1978) produces identical results. The Carr *et al.* (1978) distribution has a higher variance than the distribution used in our model, but it probably overestimates the probability of small numbers of clutches considerably because of missed resightings of nesting females. Inter-nesting interval, assumed to be constant within each female, was selected from a gamma distribution whose shape and scale parameters were determined by fitting a curve to the inter-nesting interval distribution data provided by Carr *et al.* (1978) allowing for missed sightings. Temporal nesting range was calculated from inter-nesting interval and the number of clutches laid by each female. An important assumption of the MDE model was that all days during the nesting season were equally suitable for egg deposition. Range centre was picked randomly from a uniform distribution between July and October, such that the temporal nesting range always fell within the boundaries of the season. This model assumes that no nesting takes place in the other months of the year. In each simulation, *c.* 72 000 nests were placed in the beach to calculate the temporal distribution. This procedure was repeated 1000 times to calculate the mean temporal distribution and the 95% confidence intervals.

Expected distributions under the null hypothesis of the MDE model were compared with the observed data (spatial mean values across years and temporal distributions estimated from the generalized additive model) both visually and by fitting a generalized linear regression between expected and observed and testing against the null hypothesis (slope = 1, intercept = 0). The generalized linear model allowed for spatial autocorrelation in prediction errors that dropped off exponentially with distance (Pinheiro & Bates 2000); similar results are obtained with a model where autocorrelation drops off linearly. S-PLUS (S-PLUS 2000 Professional Release 2; Insightful, Seattle, WA, USA) was used for the generalized additive models. The R-software environment (version 2.0.1: R Development Core Team 2004) was used for the MDE simulation models (Appendix), and the nonlinear mixed effects library (version 3.1–56; Pinheiro & Bates 2000) was used for generalized linear regressions.

RESULTS AND DISCUSSION

Spatial distribution

Spatial distribution patterns of green turtle nests at Tortuguero have been remarkably stable over the past 30 years, both within and among years. The GAM analyses indicated that the proportion of nests laid within a particular half-mile was constant within seasons and across years (insignificant day-of-year and year effects, $P > 0.99$: Table 1, Fig. 2). The small number of nests deposited to the north or south of Tortuguero Beach (Bjorndal *et al.* 1999; S. Troëng, pers. comm.) suggests strong selective pressure to nest between the river mouths, particularly as spatial nesting ranges of individual females can be quite large. This distribution has been attributed to lower egg predation on the island of Tortuguero Beach compared with that on the mainland (Carr 1967; Carr *et al.* 1978).

The sums of squares estimates for nesting between miles 0 and 18 (Fig. 3a) were shape = 11.69 and scale = 0.88, corresponding to a mean spatial nesting range of 10.3 miles (SD 3.0 miles) [16.6 km (SD 4.8 km)]. Within the boundaries of Tortuguero Beach, the spatial distribution of nests has a strong central tendency, as predicted by the MDE model. Without correcting for spatial autocorrelation, the null hypothesis observed = expected is rejected, but when autocorrelation is included in the model, the null hypothesis cannot be rejected (intercept: 949 ± 93111 SD, $P = 0.99$, slope: 0.62 ± 0.25 SD, $P = 0.15$). However, comparing the spatial distribution of nests from miles 0 to 18 and the generated null curve reveals a major deviation around
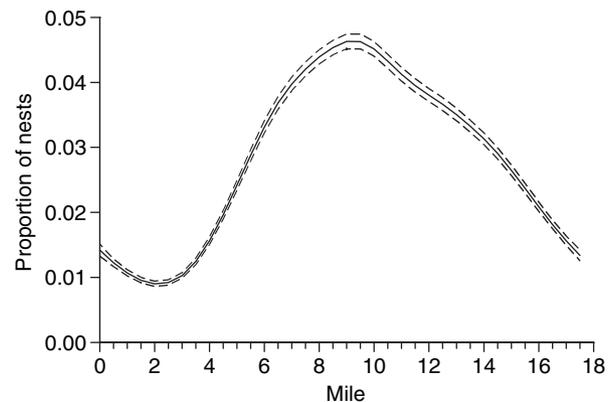

Figure 2 Spatial distribution of proportions of green turtle nests on each half mile at Tortuguero, Costa Rica. Solid line is the fitted smooth (cubic smoothing spline, d.f. = 8) and dashed lines are error bands (± 2 standard errors, adjusted for overdispersion, see text) from generalized additive regression models with binomial distribution and logit link. See text for years included in the analysis.
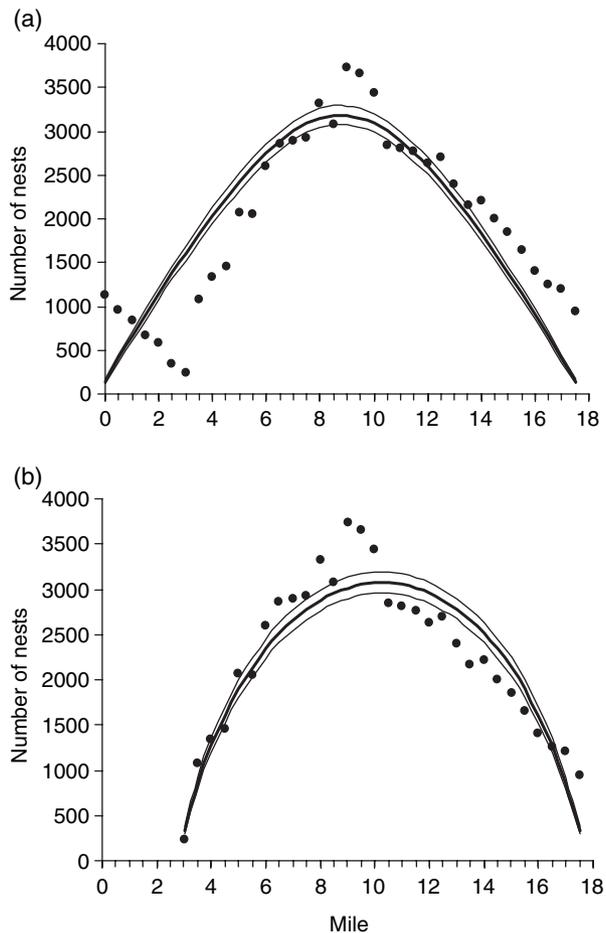
(a)

(b)

Figure 3 Simulated null curves fitted to the observed mean spatial distribution of nests for (a) miles 0–18 and for (b) miles 3–18. Bold lines are the simulated spatial distributions of the mean annual number of nests laid on the beach and the thinner lines represent 95% confidence intervals. Solid circles represent the observed data. See text for gamma-parameters.

Tortuguero village (Fig. 3a). Carr & Carr (1972) suggested that the low numbers of nests around the village may have resulted from the historical unrestricted harvest of nesting females in that section of beach. This dip may have persisted as a result of disturbance from lights and human activities (Witherington 1992; Jacobson & Lopez 1994). Another deviation in nesting from the null curve lies in the central section of the beach, suggesting the influence of environmental factors.

To adjust for the presence of Tortuguero village (Fig. 1), nest distribution was simulated between miles 3 and 18 only (Fig. 3b). In this model, we assume that the village forms a hard boundary for the domain and that no nesting takes place north of this boundary, i.e. between miles 0 and 3. Although this assumption is useful to explore the fit of the

MDE model in the absence of village effects, it technically violates the hard-boundary assumption of MDE by ignoring individuals beyond the boundary. A model that adds additional structure to estimate avoidance of the beach around the village and adjust for the presence of the village without truncating the domain would be a logical next step. The new sums of squares estimates were shape = 1.38 and scale = 4.57, corresponding to a mean spatial nesting range of 6.3 miles (SD 5.4 miles) [10.1 km (SD 8.7 km)]. With this added constraint, the curve matches the data much better (intercept: 304 ± 3282 SD, $P = 0.93$, slope: 0.86 ± 0.19 SD, $P = 0.48$), although there are still systematic deviations around miles 9–10 and 18. By accommodating a major environmental variable (presence of the village), but assuming random distribution of nesting ranges over the remaining domain, the MDE model provides a better fit. Rangel & Diniz-Filho (2005) made a similar argument for incorporating additional factors in MDE models. The remaining deviations from the MDE curve, presumably resulting from environmental factors, are similar among years.

Characteristics suggested to affect spatial nesting patterns on other sea turtle nesting beaches include offshore contours (Mortimer 1995), offshore currents (Richard & Hughes 1972), and physical profile of the beach (Provancha & Ehrhart 1987; Kikukawa *et al.* 1996, 1999). Variation has not been quantified for any of these features along Tortuguero Beach.

The sums of squares estimates of the mean individual spatial nesting ranges or nest site fixity (miles 0–18: mean = 16.6 km, SD 4.8 km; miles 3–18: mean = 10.1 km, SD 8.7 km) represent a first attempt to estimate these values for green turtles nesting at Tortuguero. The large standard deviations suggest that range sizes may vary tremendously among individuals. These indirect estimates need to be verified with direct empirical data.

Temporal distribution

Temporal distribution of nests has, like the spatial distribution, been very consistent over the past 30 years; the proportion of nests laid on a particular day-of-year, irrespective of location, was constant across years ($P = 0.092$: Table 1, Fig. 4). Like the spatial distribution, the temporal distribution of nests has a strong central tendency, as predicted by the mid-domain model, rather than a uniform distribution (Fig. 5). However, the model fits fairly poorly, with the slope of expected vs. observed significantly different from 1 even when accounting for autocorrelation (intercept: 38.0 ± 22.8 SD, $P = 0.098$, slope: 0.48 ± 0.07 SD, $P = 6.26e\text{-}8$). Major deviations from the simulated null model may be driven by environmental variation or ecological interactions.
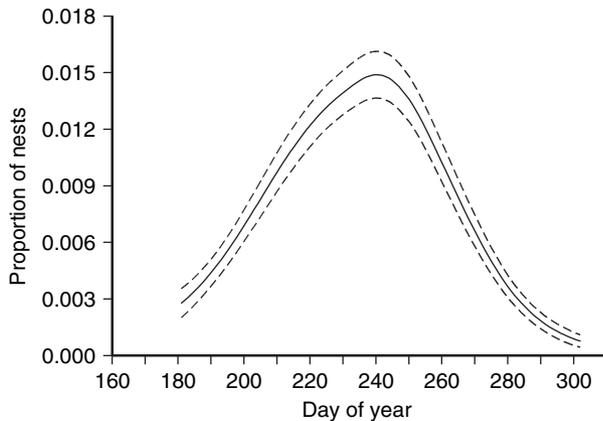
Figure 4 Temporal distribution of proportions of green turtle nests deposited on each day at Tortuguero, Costa Rica. Solid line is the fitted smooth (cubic smoothing spline, d.f. = 8) and dashed lines are error bands ($\pm$ 2 standard error, adjusted for overdispersion, see text) from generalized additive regression models with binomial distribution and logit link. See text for years included in the analysis.
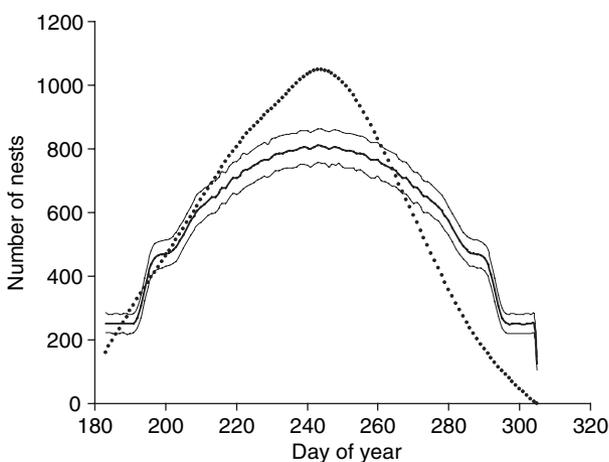

Figure 5 Simulated null curve for mean temporal distribution of nests (bold line with thinner 95% confidence interval lines) and the observed mean temporal nest distribution (solid circles).

Seasonal nesting patterns in sea turtles have been associated with ocean temperature (Hughes 1974; Williams-Walls *et al.* 1983), air and sand temperatures at the nesting beach (Godley *et al.* 2002), and photoperiod (Tiwari 2004). However, data on clutch frequency for Tortuguero used in the simulation were collected only within the northern 5 miles of beach. Consequently, clutch frequency data are biased towards fewer nests and shorter temporal nesting ranges because of incomplete coverage and tag loss. The degree of curvature of the mid-domain curve depends on the combination of range sizes; a steeper curve

is generated when larger range sizes are allowed in the model (Colwell & Lees 2000; Colwell *et al.* 2004). When more accurate data on clutch frequency for individual females are available, the temporal nest distribution at Tortuguero should be re-evaluated for the MDE.

In conclusion, although Colwell & Lees (2000) proposed the MDE to explain patterns of species richness, we demonstrate that intraspecific spatial and temporal patterns of nest distributions within well-defined spatial and temporal domains can be evaluated within the context of the MDE model. The model fits the spatial distribution well (once a single environmental factor, presence of humans, is taken into account). The temporal distribution has a poorer fit but should be re-evaluated when more data on clutch frequency are available. Other intra-specific distribution patterns should be evaluated to determine the extent to which such distributions are consistent with the MDE model.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online from http://www.Blackwell-Synergy.com:

Appendix S1 R-code for mid-domain models.

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