

2015

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### Recommended Citation

Isdell, Robert; Chambers, Randolph M.; Bilkovic, Donna M.; and Leu, Matthias, Effects of terrestrial–aquatic connectivity on an estuarine turtle (2015). *Diversity and Distributions*, 21(6), 643-653.  
DOI: 10.1111/ddi.12289

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# Effects of terrestrial–aquatic connectivity on an estuarine turtle

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## ABSTRACT

**Aim** Estuaries world-wide have been modified or fragmented due to human stressors in their terrestrial and aquatic components. Estuary fragmentation often results in reductions in species richness, diversity and connectivity. Effects of human modification on estuaries have been well studied, but less is known about how land use alters connectivity of the terrestrial–aquatic ecotone. We studied the relationship between terrestrial–aquatic connectivity and the distribution of an estuarine turtle, diamondback terrapin (*Malaclemys terrapin*).

**Location** Chesapeake Bay, Virginia, USA.

**Methods** We conducted diamondback terrapin surveys at 165 sites from late spring to mid-summer in 2012 and 2013. We evaluated associations between terrapin occurrence, land use, salt marsh, shoreline armouring and crabbing intensity in concentric–circular neighbourhoods ranging from 0.27 to 2 km to cover daily and annual terrapin movements. We used occupancy modelling and model averaging to identify key terrestrial and aquatic variables explaining heterogeneity in terrapin occupancy. We evaluated the final model with an independent data set and identified occurrence thresholds for key variables.

**Results** Diamondback terrapin occupy areas with  $\geq 10\%$  of marsh within a 750-m neighbourhood,  $\leq 17\%$  armoured shoreline within a 1-km neighbourhood,  $\leq 20\%$  of agriculture within a 500-m neighbourhood,  $\leq 33\%$  low-density housing within a 270-m neighbourhood and  $\leq 9$  active crab pots within a 270-m neighbourhood. Our model performed well when evaluated with an independent data set.

**Main conclusions** We are the first to identify thresholds and quantify negative associations between the distribution of diamondback terrapin and alterations to terrestrial–aquatic connectivity from land development, shoreline armouring, and fishing activity. Because diamondback terrapin responses are reflective of changes in coastal habitats, especially marshes, terrapin occurrence can be used to direct wetlands conservation and restoration efforts.

## Keywords

Aquatic–terrestrial ecotone, connectivity, crab pots, diamondback terrapin, salt marsh, shoreline development.

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## INTRODUCTION

The degree of spatial and temporal exchange of energy, material and organisms constitutes functional landscape connectivity (Wu, 2013). The majority of research on the connectivity of ecological processes has occurred within either terrestrial or aquatic systems, while connectivity at the terrestrial–aquatic interface, which includes physical (Ells &

Murray, 2012), biogeochemical (Carpenter *et al.*, 1999), and biological interactions (Nakano & Murakami, 2001; Cristol *et al.*, 2008), is less understood (Talley *et al.*, 2006). Research primarily has focused on terrestrial effects on aquatic systems through processes such as eutrophication (Kemp *et al.*, 2005; Worm & Lotze, 2006), shoreline armouring (Morley *et al.*, 2012), land use (Seitz *et al.*, 2006; Bilkovic & Roggero, 2008), and non-native invasive species (Silliman & Bertness,

2004; Chambers *et al.*, 2012). Disturbance in either the terrestrial or aquatic system has the potential to decrease connectivity. However, beyond physical phenomena such as waves, tides, and flooding, comparatively few studies have demonstrated connectivity from aquatic to terrestrial ecosystems (Bouchard & Bjorndal, 2000; Cristol *et al.*, 2008).

Of all anthropogenic modifications, landscape/seascape fragmentation has the greatest effect on estuarine connectivity (Rizkalla & Swihart, 2006). The largest estuary in the United States, the Chesapeake Bay, exemplifies estuarine fragmentation (Jantz *et al.*, 2005). For centuries, humans have modified both terrestrial and aquatic systems within this region by extracting resources for sustenance, defence, and social and economic gain (Bradley, 2011). The ongoing fragmentation has led to reductions in species abundance, richness, diversity, and distribution (King *et al.*, 2005; DeLuca *et al.*, 2008).

We investigated associations between the spatial distribution of the diamondback terrapin (*Malaclemys terrapin*; terrapin hereafter) throughout the Chesapeake Bay, Virginia, and factors that can influence functional connectivity at the terrestrial–aquatic ecotone. Terrapin feed, mature and mate in tidal salt marshes and adjacent open water, but, like all reptiles, the terrapin must lay its eggs on dry land (Brennessel, 2006). Human activities can disrupt the connection between the near-shore aquatic and terrestrial ecosystems the terrapin inhabits. For example, shoreline structures (i.e. bulkheads, riprap and docks) are common throughout much of the Chesapeake Bay (Isdell, 2014). Shoreline structures and armouring block terrapins from moving from the water to nesting habitat above the tideline (Roosenburg, 1991; J. M. Winters pers. comm.). Additionally, shoreline armouring is associated with changes in species composition, and reductions in species richness and structural complexity of nekton and benthic macroinvertebrate communities (Bilkovic *et al.*, 2006; Seitz *et al.*, 2006; Bilkovic & Roggero, 2008). These changes may reduce the availability and diversity of prey for the terrapin. The abundance of terrapin in Virginia has not been estimated.

Coastal development increases the abundance of synanthropic terrapin-nest predators (animals that thrive in human developed areas (Johnston, 2001)) such as raccoons (*Procyon lotor*) and crows (*Corvus* spp.; Hart & Lee, 2006; Ernst & Lovich, 2009). Terrapins also die as bycatch in active or derelict blue crab (*Callinectes sapidus*) pots that have been placed within their home ranges. Numerous studies have shown that whether baited or unbaited, terrapins enter pots and drown, sometimes in massive numbers (Roosenburg *et al.*, 1997; Grosse *et al.*, 2011; Morris *et al.*, 2011).

Our objectives for this study were to use occupancy modelling (MacKenzie *et al.*, 2006) to (1) determine the distribution of terrapins throughout the southern Chesapeake Bay, Virginia, (2) assess which habitat and human activities affected their distribution, (3) explore possible connections between terrapin distribution and terrestrial–aquatic linkages and (4) identify management targets for restoration and conservation of estuaries in the Chesapeake Bay. We hypo-

thesized that terrapin occupancy relates positively to their primary habitat (salt marsh) and negatively to elevated levels of human stressors, such as crabbing activity, shoreline armouring, and coastal development.

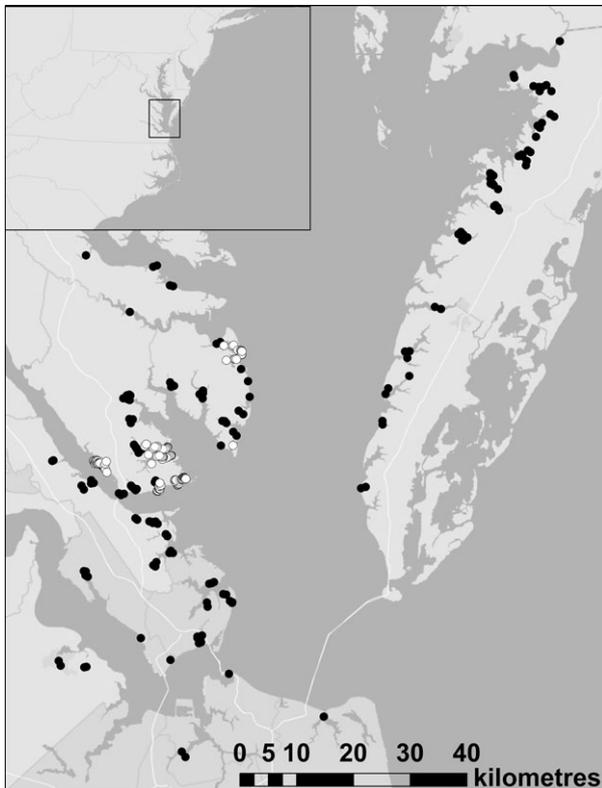
## METHODS

### Study area

The Chesapeake Bay is located between the eastern and western shores of Maryland and Virginia, USA. Approximately 15,000 km of the bay's shoreline falls within Virginia (NOAA NGDC, 2000), where land use varies from wildlife management in refuges to agriculture, housing, and commercial and industrial activities. An estimated 18% of the tidal shoreline has been armoured to prevent erosion, 32% of riparian land cover has been converted to residential or commercial development, and approximately 47,000 docks have been constructed (Titus *et al.*, 2009; Center for Coastal Resources Management, 2011). Commercial crabbing in the nearshore waters is extensive throughout the Chesapeake Bay, with more than 385,000 pots permitted in Virginia in 2013 (Bilkovic *et al.*, 2014). Annually, approximately 20% of pots are lost (Havens *et al.*, 2008), and Bilkovic *et al.* (2014) conservatively estimated 50,000 derelict crab pots (those pots lost or abandoned by fishermen) are added to the Virginia portion of the Bay each year.

### Survey design

We used a priori stratified, random sampling to select survey points (Fig. 1) across gradients of variables previously determined to influence terrapin presence or absence (henceforth occurrence) either positively (marsh) or negatively (shoreline armouring and crabbing pressure; Roosenburg, 1991; Rook *et al.*, 2010). For a detailed explanation of our survey point selection methodology, see Appendix S1 in Supporting Information. We visited each point by kayak on three occasions. We conducted surveys from early May through late July (2012) or early August (2013); we extended the field season in 2013 because of adverse weather during May and June. We used a Garmin GPSmap 60Cx to navigate to each survey point, where we anchored our kayak  $50 \pm 5$  m from the shoreline. Before the start of each survey, we measured weather variables that might affect detection probabilities (see Appendix S1). We scanned the open water for 15 min, sufficiently long to detect any emerging terrapin during months of peak activity (Brennessel, 2006) when average diving time is  $8.4 \pm 5.7$  min (Baker *et al.*, 2013). We recorded the time of each detection and used an 8× monocular laser-rangefinder (Zeiss Victory PRF; Oberkochen, Baden-Württemberg, Germany) to estimate the distance between the observer and a terrapin. At the end of each survey, we recorded the distance from the observer to each crab-pot buoy and used the number of pots within 270 m as a measure of current crabbing intensity.



**Figure 1** The study area in the southern Chesapeake Bay. Black circles indicate survey points; white circles indicate evaluation points.

### Site-specific covariates

We selected different landscape and seascape features to explain the observed variation in terrapin distribution. We obtained three terrestrial variables, low-intensity development, agriculture, and marsh, from SEGAP (Biodiversity & Spatial Information Center, 2010). First, because terrapin eggs and juveniles are known prey of synanthropic predators, we predicted that low-intensity development would have a negative effect on terrapin distribution. Terrapins have also been observed nesting in agricultural fields (Roosenburg, 1994; Feinberg & Burke, 2003). We hypothesized that as the amount of suitable nesting beach in an area declined due to human development, terrapins might turn to agricultural fields as an alternate nesting substrate. Therefore, we predicted that agriculture might have a positive effect on terrapin distribution. Terrapins occurring along the Atlantic coast have been shown to rely on marshes for both food and shelter (Roosenburg *et al.*, 1999; Brennessel, 2006; Butler *et al.*, 2006). We hypothesized that terrapin occupancy would be positively related to the amount of marsh in an area.

We also included variables at the terrestrial–aquatic ecotone to explain the observed heterogeneity in terrapin distribution. We included shoreline armouring because it prevents terrapins from moving from the water to land above the tide-line (Roosenburg, 1991; J. M. Winters pers. comm.). For

shoreline armouring data (Center for Coastal Resources Management, 2011), we calculated the proportion of shoreline armouring for the total shoreline length in a given area. Additionally, to account for the heterogeneous distribution of armoured shoreline within an area, we generated the biological distance (i.e. not the shortest distance but the distance based on area where terrapins would traverse) from each survey point along the shoreline to the nearest section of armouring. All spatial analyses were conducted in ARCGIS 10.0 (ESRI, 2011).

To account for aquatic threats, we included derelict and active blue crab pots in our analyses. A Marine Debris Location and Removal Program conducted in Virginia over four consecutive winters (2008–2012) recovered nearly 32,000 spatially referenced derelict (lost or abandoned) pots using side-scan sonar (Bilkovic *et al.*, 2014). We used this data set as both a way to assess the potential impact of derelict crab pots on terrapin distribution as well as a proxy for crabbing pressure prior to the beginning of this study. Because no spatial data set of active pots existed, we used the mean number of pots counted at each survey point. As crabbing pressure varies throughout the season, we divided the mean number of pots per site by the SE + 1; we added one to the SE to avoid dividing by SE = 0 for sites where crab pot counts were homogenous. We used mean adjusted by SE as it weighted sites with consistent crabbing pressure higher than sites with sporadic crabbing pressure.

All site-specific covariates (with the exception of active pots) were evaluated in concentric–circular neighbourhoods ranging in radii from 270 m to 2 km with intervals of ~250 m. Neighbourhood extents overlap with daily and annual terrapin habitat use. We used focal statistics to calculate either proportion or intensity within neighbourhoods for all survey points.

### Occupancy models

We used single-season occupancy models (MacKenzie *et al.*, 2006) to estimate detection probability ( $P$ ) based on survey-specific covariates and occupancy ( $\psi$ ) on the basis of site-specific covariates at all neighbourhood sizes. We conducted all occupancy modelling in package ‘Unmarked’ (Fiske & Chandler, 2011) in R (R Development Core Team, 2011). We first identified the best neighbourhood size for each site-specific covariate using univariate analyses where the neighbourhood size with the lowest Akaike’s information criterion (AIC) value was retained. Any survey-specific covariate and the neighbourhood size for each site-specific covariate that received a lower AIC value than the null model was then selected for inclusion in a global model. We then used Pearson’s correlation coefficient to test multicollinearity among selected variables. If two or more variables had a correlation coefficient  $> 0.7$ , we retained the variable that we hypothesized had the strongest relationship with occupancy (Leu *et al.*, 2011). Additionally, we plotted dependent and independent variables to check for linear and nonlinear associations (Zuur *et al.*, 2010). We centred and

scaled all of the variables on the basis of means and standard deviations from all points.

We included all statistically independent variables in a global model and ran models with all possible combinations of those variables (Doherty *et al.*, 2012). Although we estimated detection probability as a function of survey-specific covariates (see Table S1), those associations were not our focus. We model-averaged parameter estimates for variables included in the set of models for which AIC model weights summed to 0.95 of the cumulative AIC weight (Burnham & Anderson, 2002). We included the model-averaged parameter estimates in a final model to estimate probability of occurrence at each point. We assessed model predictive capabilities by computing the area under the receiver-operator curve (AUC). We used package 'ROCR' (Sing *et al.*, 2013) in R (R Development Core Team, 2011) to derive the cut-off value – the probability of occurrence at which the model predicts false positives and false negatives with equal accuracy (Metz, 1978). Although Lobo *et al.* (2008) questioned the use of AUC to assess model predictive capabilities, a high AUC in combination with model evaluation typically increases confidence in the predictive capabilities of a model.

We spatially applied the final model to create a predictive surface map. All predictions were restricted to within 1500 m of the shoreline based on radio telemetry estimates of terrapin movement patterns (Tulipani 2013).

### Model evaluation

To determine whether the final model effectively predicted occurrence beyond the original data set, we used an independent data set of terrapin presence locations collected by boat surveys during summer 2011 (Bilkovic *et al.* 2012). Surveys were conducted across a large portion of Virginia's middle peninsula (Fig. 1), and each of the 174 terrapin presence locations was georeferenced. For each observation, we extracted predicted occupancy values from the final model. Because our evaluation data set only included presence locations, we binned the extracted and study area-wide occupancy probabilities into deciles (i.e. 0–10%, 11–20%, ..., 91–100%) and calculated the proportion of the study area in each bin. We estimated the expected number of observations in each bin as

$$\frac{B_i N \bar{\Psi}_i}{\sum_{i=1}^{10} (B_i N \bar{\Psi}_i)} \times N \quad (1)$$

where  $B_i$  is proportion of the study area in the  $i$ th bin,  $N$  is number of observations in the validation data, and  $\bar{\Psi}_i$  is median value of the predicted probability of occurrence for the  $i$ th bin. We used linear regression to assess fit between model predictions and observations. A perfect model would have a slope of 1 and an intercept of 0.

### Thresholds

We identified thresholds for spatial predictor variables above or below which terrapins were present using the Dose

Response Calculator for ARCGIS (Hanser *et al.*, 2011). Thresholds for spatial variables were determined where the predicted occupancy curve intersected the predicted occupancy cut-off value derived from the sensitivity–specificity analysis (Liu *et al.*, 2005). We calculated the predicted occupancy curve across the range of values for each spatial variable while keeping all other variables in the model at mean value. The intersection value was then used to estimate the threshold for each spatial predictor variable. We fit a loess curve to the predicted probability of occurrence and its upper and lower 95% confidence intervals. The same methods were used to derive the threshold for the active crab pots (local variable), but rather than using occupancy values derived from the entire study area, we used study site-specific values.

## RESULTS

We surveyed a total of 165 sites (85 in 2012, 80 in 2013; Fig. 1), with an average distance between sites of  $1,011 \pm 159$  m (mean  $\pm$  SE). Terrapins were observed at 55 of the 165 sites (naïve occupancy = 33%). Of sites where terrapins were detected, 66% had  $\leq 3$  terrapins in total (range 1–14 terrapins) across three surveys. Two detection covariates, starting time and precipitation, explained heterogeneity in detection probabilities. Estimates of detection probability did not differ substantially between the null model ( $0.49 \pm 0.05$ ) and the averaged models ( $0.46 \pm 0.07$ ). We found no nonlinear associations between the dependent and independent variables, nor any multicollinearity among variables that had lower AIC values than the null model. Our model structure consisted of six site-specific and two detection covariates.

Terrapins were susceptible to anthropogenic stressors at multiple scales, ranging from 270 to 1,000 m. Within the home range scale, terrapin occurrence was affected by the proportion of low-intensity development within a 270-m neighbourhood, the number of active crab pots within a 270-m neighbourhood, the proportion of agriculture within a 500-m neighbourhood and the number of derelict crab pots within a 500-m neighbourhood. The proportion of marsh within a 750-m neighbourhood and the proportion of armoured shoreline within a 1-km neighbourhood had an effect on terrapin occurrence at or just above the terrapin home range scale. Cost–path distance from sites to shoreline armoured was not an important predictor of terrapin occupancy (see Table S2 for AIC values and variable selection).

Proportion of marsh within a 750-m neighbourhood had the strongest positive effect and proportion of agriculture within a 500-m neighbourhood had the strongest negative effect on terrapin occupancy. Both current crabbing intensity and per cent armoured shoreline within a 1-km neighbourhood had intermediate negative effects on occupancy (Table 1). The final, spatially applied model (Fig. 2) was based on 45 models accounting for 95% of the total AIC weight (see Table S3).

**Table 1** Model-averaged regression coefficients and standard errors for variables included in the 45 models for which cumulative Akaike's information criterion (AIC) weights summed to 0.95. Variables were centred and scaled to make the  $\beta$ -values directly comparable.

Variable	Neighbourhood (m)	$\beta$	SE	AIC cumulative weight
Intercept		-3.69	0.85	
Proportion of marsh	750	2.64	1.05	1.00
Proportion of agriculture	500	-1.37	0.67	0.89
Current number of crab pots	270	-0.90	0.40	0.72
Percentage of shoreline armoured	1000	-0.80	0.49	0.48
Percentage of low-intensity development	270	-0.48	0.37	0.44
Number of derelict crab pots	500	0.11	0.06	0.54

The sensitivity–specificity analyses showed an optimal occupancy cut-off of 0.39 and AUC = 0.91, indicating a robust predictive model. Model-based conditional estimates of occupancy (points where terrapins were observed or predicted probability of occurrence was > 0.39) indicated 73 of 165 sites (44%) were likely occupied (versus our 33% naïve occupancy estimate). Most of these occupied sites were within extensive marshes. Our model suggested that 26% of the shoreline in our study was occupied by terrapin and that the most extensively occupied areas were along the north-east sector of our study area (Fig. 2a) and along the western shore near the open waters of the Chesapeake Bay. These areas are relatively far from urban development.

We found that our final model predicted well when evaluated with independent terrapin presence data collected in the western portion of the study area. Predicted and observed values related positively ( $P < 0.001$ ). Neither the intercept ( $\beta_0 = 2.59$ , SE = 2.42) nor the slope ( $\beta_1 = 0.85$ , SE = 0.08) varied significantly ( $\alpha = 0.05$ ) from the expected values of 0 and 1, respectively. The adjusted  $R^2$  for the model was 0.92.

We ran dose–response calculations to estimate terrapin occupancy thresholds for proportion of salt marsh, agriculture, low-intensity housing, armoured shoreline, derelict crab pots and active crab pots (Fig. 3). Terrapin were unlikely to occur in areas with < 10% (17.6 ha) of salt marsh within a 750-m neighbourhood (Fig. 3a). On the basis of this threshold, approximately 72% of shoreline in the study area is unsuitable for terrapin. Thresholds for the other variables, above which terrapin presence was unlikely, were  $\geq 17\%$  armoured shoreline within a 1-km neighbourhood,  $\geq 19.6\%$  (15.4 ha) of agriculture within a 500-m neighbourhood,  $\geq 33\%$  (7.6 ha) of low-intensity housing within a 270-m neighbourhood and  $\geq 9$  active pots within a 270-m neighbourhood (Fig. 3b–d, f). Because the upper confidence interval for derelict crab pots did not cross the occupancy threshold, we were unable to define a threshold for this variable.

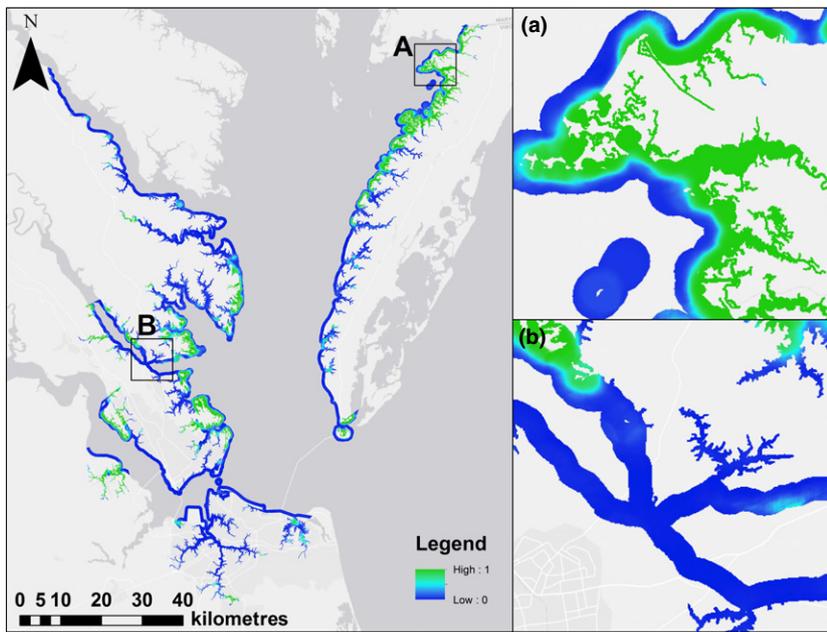
## DISCUSSION

We are the first to quantify multiple-scale associations between terrapin distribution and habitat variables. Our

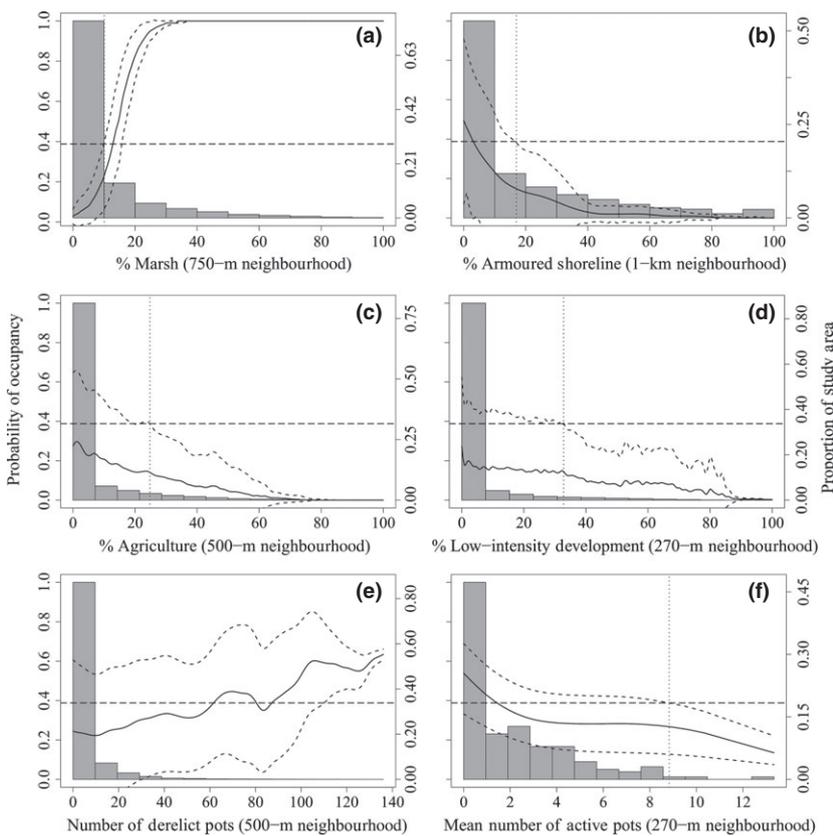
study documents a strong association with marsh and identified a 10% threshold within a neighbourhood of 750 m, which suggests that the terrapin is an area-sensitive species. As such, we attribute the negative associations of terrapin with the terrestrial–aquatic modifications examined in this study to the effects of marsh fragmentation and subsequent altered connectivity. Further, our work suggests that terrapins respond in predictable ways to alterations to the aquatic–terrestrial ecotone.

Our study suggests that terrestrial–aquatic connectivity is influenced at multiple scales, as has been well established separately for both terrestrial (Bergin *et al.*, 2000; Hanser *et al.*, 2011; Martin & Fahrig, 2012; Soranno *et al.*, 2014) and aquatic systems (Boström *et al.*, 2011; Hitt *et al.*, 2011; Wedding *et al.*, 2011). We identified a number of spatial scale-dependent factors that were associated with the distribution of terrapin. Both the proportion of armoured shoreline within a 1-km neighbourhood and the proportion of marsh within a 750-m neighbourhood explained heterogeneity of terrapin occupancy at or just beyond the home range scale. Important variables within the home range scale are agricultural land cover and derelict crab pots within a 500-m neighbourhood. Proportion of low-intensity development within a 270-m neighbourhood was associated with local distribution of terrapin, likely determining whether a section of shoreline within a terrapin's home range was unsuitable. These results are consistent with the results of other studies of turtles where habitat variables were most important at the home range scale (Rasmussen & Litzgus, 2010).

Our study suggests that terrapins are area sensitive to marsh and that marshes in excess of 17.6 ha within a 750-m neighbourhood are most suitable. While not a focus of our study, the effect of marsh configuration on terrapin occupancy is an important consideration and worthy of future investigation. For example, the total area of fringing marshes along a convoluted shoreline may exceed the above threshold and even support 'robust terrapin populations', as observed in Maryland (W. M. Roosenburg pers. comm.). Smaller total areas of narrow, disjunct fringing marshes, however, may not be sufficient for core terrapin habitat, but may still provide food and shelter for dispersing individuals or females on long-distance nesting forays. In this sense, the connectivity



**Figure 2** Predicted probability of occupancy ( $\Psi$ ) of diamondback terrapin in the Chesapeake Bay, Virginia, and illustrative sections of shoreline with high (a) and low (b) probabilities of occupancy.



**Figure 3** Dose–response relationship for variables associated strongly with probability of terrapin occurrence. Solid black lines represent predicted probability of occurrence; short-dashed lines delineate upper and lower 95% confidence intervals; dotted lines indicate intersection between the upper 95% confidence interval and the predicted occupancy threshold value; and horizontal long-dashed lines represent predicted occupancy threshold value. Grey bars indicate the proportion of the study area in each bin. Note that the right axis on panel (f) is proportion of study sites rather than proportion of study area. Panels a–e represent % marsh, % armoured shoreline, % agriculture, % low-intensity development, and number of derelict pots, respectively.

between core terrapin habitat may be mediated by narrow fringing marshes.

Contrary to our hypothesis, we found a strong, negative association between per cent cover of agricultural land and terrapin occupancy. Although no studies have demonstrated that agriculture is the mechanism for decreased terrapin

occurrence, synanthropic predators including the American crow (*Corvus brachyrhynchos*), fish crow (*Corvus ossifragus*), raccoon and red fox (*Vulpes vulpes*) thrive in landscapes dominated by agriculture (Johnston, 2001; Graser *et al.*, 2012) and in urban areas (Marzluff *et al.*, 2001). Many agricultural fields are ploughed in spring, which provides open,

loose soil near the beginning of the nesting season. However, as crops grow, roots (a common source of nest mortality on beaches (Brennessel, 2006)) and agricultural activities (e.g. application of biocides and cultivation) may destroy nests. Agricultural lands are ecological traps for other species (Hiron *et al.*, 2012; Northrup *et al.*, 2012), and some species of turtles avoid agricultural lands (Bodie & Semlitsch, 2000; Rizkalla & Swihart, 2006). Although agricultural run-off is often cited as a cause of estuarine eutrophication (Kemp *et al.*, 2005), the effects of eutrophication on terrapin distribution are unclear.

Other studies have demonstrated reductions in estuarine integrity when 10–25% of the shoreline is armoured (Silliman & Bertness, 2004; Bilkovic *et al.*, 2006; Bilkovic & Roggero, 2008; DeLuca *et al.*, 2008). Our threshold of 17% (Fig. 3b) falls within the ranges documented by these other studies. Although shoreline armouring prevents terrapin from accessing a given location (Roosenburg, 1991; Wnek, 2010), the effect of armouring on terrapin distribution is likely from a reduction in habitat quality across extensive areas rather than a local nesting effect. Other studies have indicated that shoreline armouring is increasing rapidly (Isdell, 2014) and will continue to increase in the future (Woth *et al.*, 2006). As more of the shoreline becomes armoured, terrapin habitat will become increasingly fragmented, and ecosystem connectivity will be diminished. Fortunately, this is a recognized problem in the Chesapeake Bay, and for the last 20+ years, there has been a concerted effort by local institutions, agencies and private groups to restore wetlands, reduce or replace armouring with nature-based shoreline protection designs (or living shorelines), and to encourage best management practices for shoreline stabilization (Koslow *et al.*, 2006). Living shorelines prevent erosion by providing protection, restoration, or enhancement of wetland habitats through strategic placement of plants, stone, and sand while maintaining natural coastal processes (Bilkovic & Mitchell, 2013). Many US states, including Maryland, Virginia and North Carolina, have enacted regulations to encourage or require the use of living shorelines instead of traditional armouring, such as bulkheads, for shoreline erosion control. Preferentially selecting a living shoreline approach over armouring to stabilize a shore may help to maintain or even enhance terrestrial–aquatic connectivity for terrapin throughout its range. Our study adds to the growing body of evidence for the importance of maintaining shoreline integrity over a large spatial extent.

Low-intensity development may have many of the same effects on terrapin distribution as agriculture. The density of synanthropic predators can be relatively high in these areas (Neatherlin & Marzluff, 2004), and terrapins lay their eggs in the low-quality habitat around houses (R. E. Isdell pers. obs.). Urban areas also have relatively high densities of recreational docks and piers (Isdell, 2014). Several studies have demonstrated that near docks, diversity of nekton is relatively low (Scheuerell & Schindler, 2004; Able & Duffy-Anderson, 2006), submerged aquatic vegetation is limited

(Burdick & Short, 1999; Shafer, 1999), and boat traffic is high (Liddle & Scorgie, 1980; Asplund & Cook, 1997), all of which may negatively affect terrapin occupancy. Many waterfront property owners also deploy recreational crab pots, which are identical to commercial pots, from their docks. Virginia law allows two pots per person per household (VA §28.2–262). More than 47,000 docks are along Virginia's coastline, and recreational pots may be a substantial source of terrapin mortality. Additionally, because most docks occur in the relatively shallow waters that are inhabited by terrapins, many more recreational pots than commercial pots may overlap with terrapin habitat (Harden & Williard, 2012).

The strong, negative association of active crab pots with terrapin occupancy is in line with our hypothesis and other studies that have demonstrated the detrimental effects of crab pots on terrapins (Roosenburg *et al.*, 1997; Dorcas *et al.*, 2007; Wolak *et al.*, 2010). Our threshold of  $\geq 9$  active pots within a 270-m neighbourhood indicates that a relatively high crabbing pressure is required to affect terrapin occupancy. Local terrapin abundance, however, may be affected by lower levels of crabbing pressure. Some locations with lower crabbing pressure could be occupied by a declining population, possibly resulting in a lag effect on terrapin occupancy. We suspect that crab pots affect terrapin connectivity in much the same way as a gill net catches fish. With a set mesh size, gill nets passively capture those animals that are the correct size to be caught and those unlucky enough to become entangled. Crab pots may act similarly as a filter to connectivity. Of the adults, crab pots primarily catch male terrapin as they are small enough to fit through the openings in the crab pots (Roosenburg *et al.*, 1997). Some juveniles are small enough to escape, and mature females are often too large to fit. Thus, as male terrapin have been documented as the most important for dispersal (Sheridan *et al.*, 2010), crab pots may reduce immigration/emigration success among habitat patches.

One contradictory result was the positive relationship of derelict crab pots to terrapin occurrence. This variable had the smallest relative effect of all variables. One possible explanation for this result is that for each pot removed from the water, there may be a slight increase in terrapin survival due to the removal of those potentially deadly traps. The small positive result could also be a statistical anomaly. Derelict crab pots were recovered with the use of larger, deeper-hulled boats than are typically used by crabbers when they set and retrieve pots. This led to an undersampling of the shallow waters where terrapins and crab pots are more likely to overlap. An alternative hypothesis is that high-quality terrapin habitat overlaps with high-quality blue crab habitat, and therefore, we see an increased fishing effort in those areas. However, this seems unlikely as we have found a strong negative association between active crab pots and terrapin occupancy. The active pots that were counted at each site are, therefore, more likely to accurately reflect the negative impact that crab pots are known to have on terrapins.

When examined together, the variables identified by this study significantly affect terrestrial–aquatic connectivity in the region. Although we cannot assess the likelihood of gene flow among meta-populations of terrapin, as our study focused on local factors associated with terrapin occurrence, one could imagine a dramatic reduction in gene flow among meta-populations where the terrestrial–aquatic connectivity was impaired. The dispersal of male terrapin between meta-populations, for example, would be reduced by high numbers of crab pots in which terrapin drown. In addition to reduced gene flow, Wolak *et al.* (2010) found that terrapin in the Chesapeake Bay are significantly larger and mature faster than other populations in the Mid-Atlantic, indicating that crab pot-related mortality may have resulted in directional selection in local populations. Because of the spatial overlap between terrapin habitat, some commercial crabbing, and most recreational crabbing, implementation of measures to reduce crab pot-related terrapin mortality would be recommended.

The results of this study have direct implications for management throughout the terrapin's range. Salt marsh conservation, the expansion of shoreline armouring and coastal development, and bycatch in fishing gear are important issues not only from Cape Cod, Massachusetts to Corpus Christi, Texas, but throughout coastal regions of the world. Additionally, all of these factors are likely to be affected by rising sea level. As sea level continues to rise, the extent of salt marshes along the Atlantic coast is likely to decrease substantially (Titus *et al.*, 2009). Much of this loss will be due to interactions between rising sea level and the prevention of inland migration of marshes by topography, including embankments with steep slopes and shoreline armouring. In regions where subsidence is occurring, such as the Chesapeake Bay, marshes likely will be unable to accrete vertically to keep pace of anticipated accelerated sea level rise without a significant sediment source (Craft *et al.*, 2009). Although we do not know how other factors such as bank erosion might provide sediment to sustain marshes (Bozek & Burdick, 2005), the cumulative effects of sea level rise, the human response to protect personal property and subsequent loss of marshes would exacerbate terrapin habitat loss and result in further decreased terrestrial–aquatic connectivity.

We are the first to identify numerous spatial scales of effect and to quantify ecological occupancy thresholds based on field observations and models evaluated with independent data for terrapins in any segment of their range. The methods developed for this study also provide an inexpensive and effective tool for monitoring terrapins. If applied over a longer time, the approach may also afford scientists the ability to identify and assess the factors that lead to site-level colonization and extinction (MacKenzie *et al.*, 2006). Our methods may also be applicable to study other aquatic turtle distributions in riverine systems that flow through complex, heterogeneous landscapes. In the Chesapeake Bay, conservation efforts could include increasing the riparian buffer of

agricultural fields, limiting future shoreline armouring in areas below the 17% threshold, requiring turtle excluder devices (TEDs) on those crab pots that overlap with terrapin habitat, and a strong effort to maintain extensive salt marshes. Improving terrapin habitat quality would also have positive effects on other estuarine species, as demonstrated by Roosenburg *et al.* (2003). The thresholds identified in this study provide spatially explicit, data-driven conservation and restoration targets for the Chesapeake Bay, while the methods provide a cost-effective and efficient way to establish those targets in other systems.

## ACKNOWLEDGEMENTS

We thank Bruce Pfirrmann and Mary Isdell for help in the field. Timothy Russell helped with spatial shoreline delineations, and John Swaddle, Cheryl Leu and Erica Fleishman provided helpful editorial comments. This study was funded by the Commonwealth of Virginia (ML), the College of William & Mary (RI), Virginia Sea Grant (DB, RC, and ML) and NOAA (DB and RC). This paper is Contribution No. 3421 of the Virginia Institute of Marine Science, College of William & Mary.

## REFERENCES

- Able, K.W. & Duffy-Anderson, J.T. (2006) Impacts of piers in the lower Hudson River. *The Hudson River estuary* (ed. by J.S. Levinton and J.R. Waldman), pp. 428–440. Cambridge University Press, New York, NY.
- Asplund, T.R. & Cook, C.M. (1997) Effects of motor boats on submerged aquatic macrophytes. *Lake and Reservoir Management*, **13**, 1–12.
- Baker, P.J., Thomson, A., Vatnick, I. & Wood, R.C. (2013) Estimating survival times for northern diamondback terrapins, *Malaclemys terrapin terrapin*, in submerged crab pots. *Herpetological Conservation and Biology*, **8**, 667–680.
- Bergin, T.M., Best, L.B., Freemark, K.E. & Koehler, K.J. (2000) Effects of landscape structure on nest predation in roadsides of a midwestern agroecosystem: a multiscale analysis. *Landscape Ecology*, **15**, 131–143.
- Bilkovic, D.M., Chambers, R.M., Leu, M. & Russell, T. (2012) Diamondback terrapin bycatch reduction strategies for commercial and recreational blue crab fisheries. Final Report to Virginia Sea Grant, National Oceanic and Atmospheric Administration. Report NA10OAR4170085. 21.
- Bilkovic, D.M. & Mitchell, M.M. (2013) Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages. *Ecological Engineering*, **61**, Part A, 469–481.
- Bilkovic, D.M. & Roggero, M.M. (2008) Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology Progress Series*, **358**, 27–39.
- Bilkovic, D.M., Roggero, M., Hershner, C.H. & Havens, K.H. (2006) Influence of land use on macrobenthic communities in nearshore estuarine habitats. *Estuaries and Coasts*, **29**, 1185–1195.

- Bilkovic, D.M., Havens, K., Stanhope, D. & Angstadt, K. (2014) Derelict fishing gear in Chesapeake Bay, Virginia: spatial patterns and implications for marine fauna. *Marine Pollution Bulletin*, **80**, 114–123.
- Biodiversity and Spatial Information Center (2010) SEGAP. Available at: <http://www.basic.ncsu.edu/segap/> (accessed 18 November 2013).
- Bodie, J.R. & Semlitsch, R.D. (2000) Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia*, **122**, 138–146.
- Boström, C., Pittman, S., Simenstad, C. & Kneib, R. (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series*, **427**, 191–217.
- Bouchard, S.S. & Bjorndal, K.A. (2000) Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology*, **81**, 2305–2313.
- Bozek, C.M. & Burdick, D.M. (2005) Impacts of seawalls on saltmarsh plant communities in the Great Bay Estuary, New Hampshire, USA. *Wetlands Ecology and Management*, **13**, 553–568.
- Bradley, C. (2011) *The impacts of shoreline development on shallow-water benthic communities in the Patuxent River, MD*. Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA. PhD Dissertation.
- Brennessel, B. (2006) *Diamonds in the marsh: a natural history of the diamondback terrapin*. UPNE, Lebanon, NH.
- Burdick, D.M. & Short, F.T. (1999) The effects of boat docks on eelgrass beds in coastal waters of Massachusetts. *Environmental Management*, **23**, 231–240.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York, NY.
- Butler, J.A., Seigel, R.A. & Mealey, B.K. (2006) *Malaclemys terrapin* – diamondback terrapin. *Chelonian Research Monographs*, **3**, 279–295.
- Carpenter, S.R., Ludwig, D. & Brock, W.A. (1999) Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications*, **9**, 751–771.
- Center for Coastal Resources Management (2011) Comprehensive Coastal Inventory. Available at: [http://ccrm.vims.edu/gis\\_data\\_maps/shoreline\\_inventories/index.html](http://ccrm.vims.edu/gis_data_maps/shoreline_inventories/index.html) (accessed 18 November 2013).
- Chambers, R.M., Meyerson, L.A. & Dibble, K.L. (2012) Ecology of *Phragmites australis* and responses to tidal restoration. *Tidal marsh restoration* (ed. by C.T. Roman and D.M. Burdick), pp. 81–96. Island Press/Center for Resource Economics, Washington, D.C., USA.
- Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H. & Machmuller, M. (2009) Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment*, **7**, 73–78.
- Cristol, D.A., Brasso, R.L., Condon, A.M., Fovargue, R.E., Friedman, S.L., Hallinger, K.K., Monroe, A.P. & White, A.E. (2008) The movement of aquatic mercury through terrestrial food webs. *Science*, **320**, 335.
- DeLuca, W.V., Studds, C.E., King, R.S. & Marra, P.P. (2008) Coastal urbanization and the integrity of estuarine waterbird communities: threshold responses and the importance of scale. *Biological Conservation*, **141**, 2669–2678.
- Doherty, P.F., White, G.C. & Burnham, K.P. (2012) Comparison of model building and selection strategies. *Journal of Ornithology*, **152**, 317–323.
- Dorcas, M.E., Willson, J.D. & Gibbons, J.W. (2007) Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. *Biological Conservation*, **137**, 334–340.
- Ells, K. & Murray, A.B. (2012) Long-term, non-local coastline responses to local shoreline stabilization. *Geophysical Research Letters*, **39**, 1–7.
- Ernst, C.H. & Lovich, J.E. (2009) *Turtles of the United States and Canada*. Johns Hopkins University Press, Baltimore, MD.
- ESRI (2011) *ArcMap*. Environmental Systems Research Institute, Redlands, CA.
- Feinberg, J. & Burke, R. (2003) Nesting ecology and predation of diamondback terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. *Journal of Herpetology*, **37**, 517–526.
- Fiske, I. & Chandler, R. (2011) unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1–23.
- Graser, W.H., Gehrt, S.D., Hungerford, L.L. & Anchor, C. (2012) Variation in demographic patterns and population structure of raccoons across an urban landscape. *The Journal of Wildlife Management*, **76**, 976–986.
- Grosse, A.M., Maerz, J.C., Hepinstall-Cymerman, J. & Dorcas, M.E. (2011) Effects of roads and crabbing pressures on diamondback terrapin populations in coastal Georgia. *The Journal of Wildlife Management*, **75**, 762–770.
- Hanser, S.E., Leu, M., Knick, S.T. & Aldridge, C.L. (2011) *Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins*. Allen Press, Lawrence, KS.
- Harden, L.A. & Williard, A.S. (2012) Using spatial and behavioral data to evaluate the seasonal bycatch risk of diamondback terrapins, *Malaclemys terrapin*, in crab pots. *Marine Ecology Progress Series*, **467**, 207–217.
- Hart, K.M. & Lee, D.S. (2006) The diamondback terrapin: the biology, ecology, cultural history, and conservation status of an obligate estuarine turtle. *Terrestrial vertebrates of tidal marshes: evolution, ecology and conservation* (ed. by R. Greenberg, J. Maldonado, S. Droege and M.V. McDonald), pp. 206–213. Cooper Ornithological Society, Ephrata, PA.
- Havens, K.J., Bilkovic, D.M., Stanhope, D., Angstadt, K. & Hershner, C. (2008) The effects of derelict blue crab traps on marine organisms in the lower York River, Virginia. *North American Journal of Fisheries Management*, **28**, 1194–1200.
- Hiron, M., Berg, Å. & Pärt, T. (2012) Do skylarks prefer autumn sown cereals? Effects of agricultural land use, region and time in the breeding season on density. *Agriculture, Ecosystems & Environment*, **150**, 82–90.

- Hitt, S., Pittman, S. & Nemeth, R. (2011) Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series*, **427**, 275–291.
- Isdell, R.E. (2014) *Anthropogenic modifications of connectivity at the aquatic-terrestrial ecotone in the Chesapeake Bay*. Master's Thesis, College of William and Mary, Williamsburg, Virginia, USA.
- Jantz, P., Goetz, S. & Jantz, C. (2005) Urbanization and the loss of resource lands in the Chesapeake Bay watershed. *Environmental Management*, **36**, 808–825.
- Johnston, R.F. (2001) Synanthropic birds of North America. *Avian ecology and conservation in an urbanizing world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 49–67. Springer US, New York, USA.
- Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G., Cornwell, J.C., Fisher, T.R., Glibert, P.M., Hagy, J.D., Harding, L.W., Houde, E.D., Kimmel, D.G., Miller, W.D., Newell, R.I.E., Roman, M.R., Smith, E.M. & Stevenson, J.C. (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, **303**, 1–29.
- King, R.S., Hines, A.H., Craige, F.D. & Grap, S. (2005) Regional, watershed and local correlates of blue crab and bivalve abundances in subestuaries of Chesapeake Bay, USA. *Journal of Experimental Marine Biology and Ecology*, **319**, 101–116.
- Koslow, D., Register, K., Burton, B., Priest III, W.I. & Luscher, A.E. (2006) Living shoreline case studies. *Management, policy, science, and engineering of nonstructural erosion control in the Chesapeake Bay* (ed. by S.Y. Erdle, J.L.D. Davis and K.G. Sellner), pp. 117–121. CRC Publication No. 08-164, Gloucester Point, VA.
- Leu, M., Hanser, S.E., Aldridge, C.L., Cade, B.S. & Knick, S.T. (2011) A sampling and analytical approach to develop spatial distribution models for sagebrush-associated species. *Sagebrush ecosystem conservation and management: coregional assessment tools and models for the Wyoming Basins* (ed. by S.E. Hanser, M. Leu, S.T. Knick and C.L. Aldridge), pp. 387–409. Allen Press, Lawrence, KS.
- Liddle, M.J. & Scorgie, H.R.A. (1980) The effects of recreation on freshwater plants and animals: a review. *Biological Conservation*, **17**, 183–206.
- Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, Burlington, Massachusetts, USA.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- Martin, A.E. & Fahrig, L. (2012) Measuring and selecting scales of effect for landscape predictors in species–habitat models. *Ecological Applications*, **22**, 2277–2292.
- Marzluff, J.M., McGowan, K.J., Donnelly, R. & Knight, R.L. (2001) Causes and consequences of expanding American Crow populations. *Avian ecology and conservation in an urbanizing world* (ed. by J.M. Marzluff, R. Bowman and R. Donnelly), pp. 331–363. Springer US, New York, NY.
- Metz, C.E. (1978) Basic principles of ROC analysis. *Seminars in Nuclear Medicine*, **8**, 283–298.
- Morley, S.A., Toft, J.D. & Hanson, K.M. (2012) Ecological effects of shoreline armoring on intertidal habitats of a Puget Sound urban estuary. *Estuaries and Coasts*, **35**, 774–784.
- Morris, A.S., Wilson, S.M., Dever, E.F. & Chambers, R.M. (2011) A test of bycatch reduction devices on commercial crab pots in a tidal marsh creek in Virginia. *Estuaries and Coasts*, **34**, 386–390.
- Nakano, S. & Murakami, M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences USA*, **98**, 166–170.
- Neatherlin, E.A. & Marzluff, J.M. (2004) Responses of American Crow populations to campgrounds in remote native forest landscapes. *Journal of Wildlife Management*, **68**, 708–718.
- NOAA NGDC (2000) Medium Resolution Digital Vector Shoreline Digital Geography. Available at: <http://www.ngdc.noaa.gov/mgg/shorelines/data/gshhg/latest/> (accessed 01 April 2013).
- Northrup, J.M., Stenhouse, G.B. & Boyce, M.S. (2012) Agricultural lands as ecological traps for grizzly bears. *Animal Conservation*, **15**, 369–377.
- R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rasmussen, M.L. & Litzgus, J.D. (2010) Habitat selection and movement patterns of Spotted Turtles (*Clemmys guttata*): effects of spatial and temporal scales of analyses. *Copeia*, **2010**, 86–96.
- Rizkalla, C.E. & Swihart, R.K. (2006) Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation. *Landscape Ecology*, **21**, 1361–1375.
- Rook, M.A., Lipcius, R.N., Bronner, B.M. & Chambers, R.M. (2010) Bycatch reduction device conserves diamondback terrapin without affecting catch of blue crab. *Marine Ecology Progress Series*, **409**, 171–179.
- Roosenburg, W.M. (1991) The diamondback terrapin: population dynamics, habitat requirements, and opportunities for conservation. *New Perspectives in the Chesapeake System: A Research and Management Partnership. Proceedings of a Conference*, 227–234.
- Roosenburg, W.M. (1994) Nesting habitat requirements of the diamondback terrapin: a geographic comparison. *Wetland Journal*, **6**, 8–11.
- Roosenburg, W.M., Cresko, W., Modesitte, M. & Robbins, M.B. (1997) Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. *Conservation Biology*, **11**, 1166–1172.
- Roosenburg, W.M., Haley, K.L. & McGuire, S. (1999) Habitat selection and movements of diamondback terrapins,

- Malaclemys terrapin*, in a Maryland estuary. *Chelonian Conservation and Biology*, **3**, 425–429.
- Roosenburg, W.M., Allman, P.E. & Fruh, B.J. (2003) Diamondback terrapin nesting on the Poplar Island environmental restoration project. 13th Biennial Coastal Zone Conference, Baltimore, MD, July 13–17. 2003. NOAA/CS/20322-CD. CD-ROM. Charleston, SC: NOAA Coastal Services Center.
- Scheuerell, M.D. & Schindler, D.E. (2004) Changes in the spatial distribution of fishes in lakes along a residential development gradient. *Ecosystems*, **7**, 98–106.
- Seitz, R.D., Lipcius, R.N., Olmstead, N.H., Seebo, M.S. & Lambert, D.M. (2006) Influence of shallow-water habitats and shoreline development on abundance, biomass, and diversity of benthic prey and predators in Chesapeake Bay. *Marine Ecology Progress Series*, **326**, 11–27.
- Shafer, D.J. (1999) The effects of dock shading on the seagrass *Halodule wrightii* in Perdido Bay, Alabama. *Estuaries*, **22**, 936–943.
- Sheridan, C.M., Spotila, J.R., Bien, W.F. & Avery, H.W. (2010) Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*. *Molecular Ecology*, **19**, 5497–5510.
- Silliman, B.R. & Bertness, M.D. (2004) Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. *Conservation Biology*, **18**, 1424–1434.
- Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. (2013) *Visualizing the performance of scoring classifiers*, Version 1.0-5. Available at: <http://rocr.bioinf.mpi-sb.mpg.de/> (accessed 01 September 2013).
- Soranno, P.A., Cheruvilil, K.S., Bissell, E.G., Bremigan, M.T., Downing, J.A., Fergus, C.E., Filstrup, C.T., Henry, E.N., Lottig, N.R., Stanley, E.H., Stow, C.A., Tan, P.-N., Wagner, T. & Webster, K.E. (2014) Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems. *Frontiers in Ecology and the Environment*, **12**, 65–73.
- Talley, D.M., Huxel, G.R. & Holyoak, M. (2006) Connectivity at the land–water interface. *Connectivity conservation* (ed. by K.R. Crooks and M. Sanjayan), pp. 97–129. Cambridge University Press, New York, NY.
- Titus, J., Hudgens, D., Trescott, D.L., Craghan, M., Nuckols, W.H., Hershner, C.H., Kassakian, J.M., Linn, C.J., Merritt, P.G., McCue, T.M., O’Connell, J.F., Tanski, J. & Wang, J. (2009) State and local governments plan for development of most land vulnerable to rising sea level along the US Atlantic coast. *Environmental Research Letters*, **4**, 1–7.
- Tulipani, D.C. (2013) Foraging ecology and habitat use of the northern diamondback terrapin (*Malaclemys terrapin*) in southern Chesapeake Bay. College of William and Mary - School of Marine Science, PhD Dissertation. 238.
- Wedding, L., Lepczyk, C., Pittman, S., Friedlander, A. & Jorgensen, S. (2011) Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. *Marine Ecology Progress Series*, **427**, 219–232.
- Wnek, J.P. (2010) Anthropogenic impacts on the reproductive ecology of the diamondback terrapin, *Malaclemys terrapin*. Doctoral Thesis submitted to Drexel University, Philadelphia, Pennsylvania, USA.
- Wolak, M.E., Gilchrist, G.W., Ruzicka, V.A., Nally, D.M. & Chambers, R.M. (2010) A contemporary, sex-limited change in body size of an estuarine turtle in response to commercial fishing. *Conservation Biology*, **24**, 1268–1277.
- Worm, B. & Lotze, H.K. (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnology and Oceanography*, **51**, 569–579.
- Woth, K., Weisse, R. & von Storch, H. (2006) Climate change and North Sea storm surge extremes: an ensemble study of storm surge extremes expected in a changed climate projected by four different regional climate models. *Ocean Dynamics*, **56**, 3–15.
- Wu, J. (2013) Landscape ecology. *Ecological systems* (ed. by R. Leemans), pp. 179–200. Springer, New York, NY.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Detailed methodology.

**Table S1** Full list of statistical models and rankings.

**Table S2** Site-specific covariate selection.

**Table S3** Top models and parameter estimates for model averaging.

## BIOSKETCH

**Robert E. Isdell** is a PhD student with the Center for Coastal Resources Management at the Virginia Institute of Marine Science, College of William & Mary, and is studying interactions between humans and the environment at multiple scales throughout the Chesapeake Bay. His interests include spatial ecology, coastal resource conservation and management, and the impacts of climate change.

As a group, we are interested in combining principles and techniques of terrestrial and marine ecology to study the aquatic–terrestrial ecotone. Previous research efforts have involved marine debris impacts, bycatch reduction and species distribution models.

Author contributions: R.E.I., R.M.C., D.M.B. and M.L. conceived the ideas; R.E.I. collected the data; R.E.I. and M.L. analysed the data; and R.E.I., R.M.C., D.M.B. and M.L. contributed to the writing.

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Editor: David Richardson