From logs to landscapes: determining the scale of ecological processes affecting the incidence of a saproxylic beetle

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Abstract. 1. Species incidence is influenced by environmental and intrinsic factors operating at multiple scales. The incidence of a dispersal-limited beetle, *Odontotaenius disjunctus* (Coleoptera: Passalidae), was surveyed within hierarchically nested organisational levels of its environment (log sections < logs < 10-m radius subplots < 0.66-ha plots) in Louisiana, U.S.A. The finest level was the size of a single territory. Passalid beetles are an ecologically prominent group, but little is known of the factors affecting their incidence.

2. Three scale-sensitive aspects of *O. disjunctus* incidence were evaluated: (i) the extent (52–3600 ha) within which forest cover was most associated with incidence; (ii) the hierarchical level at which environmental variables best predicted incidence; and (iii) the hierarchical level at which incidence exhibited the greatest spatial autocorrelation as a result of intrinsic factors (e.g. dispersal limitation).

3. Forest cover best predicted incidence at 225 ha, but accounted for only 1.2% of variation in incidence. Incidence was most sensitive to environmental factors measured at the finest scale (i.e. territories). Incidence was positively associated with moderately decayed wood and increased surface area of logs (9.9% and 3.1% of variance, respectively). When environmental factors were accounted for, spatial autocorrelation in incidence was greatest within subplots and logs, consistent with the hypothesis that intrinsic autocorrelation is associated with *O. disjunctus* average dispersal distance (<5 m).

4. This study indicates the influences of factors acting at multiple scales, but suggests that environmental conditions at the scale of territories may be most important for species incidence.

Key words. Focal patch, habitat fragmentation, habitat loss, intraclass correlation, saproxylic, scale of effect, xylophagous.

Introduction

Species incidence is influenced by environmental conditions (Hutchinson, 1957), dispersal behaviour (Hanski, 1994), and intra- and interspecific interactions (Connell, 1961; Fretwell, 1972). Determining which factors are most important to incidence is difficult because the multiple processes affecting incidence operate at different spatial scales. Questions on at least three separate issues have guided scale-sensitive empirical investigations of species–environment relationships: (i) the spatial extent at which the structure of the surrounding landscape influences incidence rate (e.g. Holland *et al.*, 2005); (ii) the importance of different levels (e.g. microsite, local, landscape) of environmental organisation to incidence (e.g. Cushman & McGarigal, 2004); and (iii) the spatial scale(s) at which a species is intrinsically organised into neighbourhoods of interacting individuals (e.g. Fraschetti *et al.*, 2005). An empirical study designed to resolve all three issues might provide valuable insight into factors influencing

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the organisation of individuals into neighbourhoods and populations.

The spatial extent at which landscape structure best predicts population responses (sometimes called the 'scale of effect') may be proportional to the extent over which individuals interact with the environment. The scale of effect is commonly measured using a focal patch sampling design (Brennan *et al.*, 2002), in which the response of interest (e.g. incidence) is measured in a focal area and environmental variables are measured at increasing extents surrounding the focal area. The scale of effect tends to be species-specific. For example, the scale of effect of forest cover on 27 wood-boring beetle species varied by two orders of magnitude [20–1600 m (Holland *et al.*, 2005)].

A hierarchical study [e.g. basidiocarp < tree < tree group < forest patch (Rukke & Midtgaard, 1998)] can indicate the scale at which environmental variables exert their greatest influence on incidence. Environmental variables acting at coarse spatial scales are often considered first when predicting variation in incidence, perhaps because they are most easily measured and because of their expected effect on dispersal success and longterm population dynamics. Environmental variables measured at one scale, however, may be important only because of their correlation with variables best measured at a different scale. Cushman and McGarigal (2004), for example, showed that environmental features measured at the stand level were strongly correlated with changes in bird community composition when measured in isolation, but provided little additional information when combined with more important features measured at finer (50-m radius) and coarser (hydrological sub-basin) levels.

Although often considered a nuisance, spatial autocorrelation in incidence is also informative (Peres-Neto & Legendre, 2010). In analyses of hierarchical data, autocorrelation often occurs within each level (e.g. samples from the same tree may be similar). After environmental influences have been taken into account, autocorrelation indicates the effects on distribution of intrinsic species processes (e.g. dispersal) or unmeasured environmental variables (Keitt *et al.*, 2002). A strong autocorrelation at one or more hierarchical levels can indicate the scale at which behavioural mechanisms underlying incidence should be investigated.

We determined the spatial scales at which both environmental variables and intrinsic species processes most influence the incidence of a dispersal-limited beetle, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae). Several characteristics make passalids ideal for a study of incidence at multiple spatial scales. Firstly, *O. disjunctus* movement behaviour suggests a clear hierarchical distinction between daily movements (within logs) and infrequent breeding dispersal. A mark–release study (Jackson, 2010) suggested most individuals (∼ 80%) disperse within 5 m, but rare flight events (Hunter & Jump, 1964) may result in longer distance dispersal, increasing connectivity among habitat fragments. Secondly, passalid habitat is easily defined at multiple spatial scales: passalids live in territories within decayed wood within forests. Thirdly, their distinctive tunnels make passalids easily detectable, allowing high levels of accuracy in estimates of presence or absence. Fourthly, the

subsocial behaviour of *O. disjunctus* makes incidence measured at the level of log sections demographically relevant. The size of our smallest sampling scale (log sections) was selected to approximate the size of a single territory, which *O. disjunctus* adults defend against intruders during the 3-month larval development period (Schuster & Schuster, 1985). Measured at the scale of individual adult females, incidence was a measure of density that has direct relevance to demography and even population persistence (Lande, 1987). These four attributes of *O. disjunctus* allowed us to test the alternative hypotheses that incidence is most associated with environmental factors and intrinsic processes that occur: (i) within logs; (ii) among individual logs; (iii) among subplots (groups of logs); and (iv) among forest plots (distant sampling sites).

Materials and methods

Study system

This is the first landscape-level study of incidence in a member of the Passalidae family [700–1000 species (Boucher, 2006)], a group of saproxylic (decayed wood-dependent) beetles (see also Galindo-Cardona *et al.*, 2007). *Odontotaenius disjunctus* is a large beetle (∼32 mm long), the range of which covers most of eastern North America (Schuster, 1978). Adults and their larvae live in well-defended tunnels within decayed wood (Schuster & Schuster, 1985), in which they consume the wood itself (Pearse *et al.*, 1936). Adult movement outside of the log is largely confined to late spring or early autumn before and after the larval development period (Jackson *et al.*, 2009). Non-forest habitat is avoided [beetles exhibit a strong reflection response to forest boundaries (Jackson *et al.*, 2009)]. The lifespan of adult *O. disjunctus* is unknown, but is probably 2–5 years (Gray, 1946).

Studies of saproxylic (decayed wood-dependent) beetle distribution indicate the importance of log size, position (snag or downed), decay state and insolation for species composition at the scale of logs, and the benefits to species diversity of an increased volume of wood and greater forest amount at the landscape scale (Økland *et al.*, 1996; Rukke & Midtgaard, 1998; Teichert & Bondrup-Nielsen, 2005; Gibb *et al.*, 2006; Buse *et al.*, 2007; Ulyshen & Hanula, 2009). Here, we expand on these studies by: (i) considering four hierarchical levels of organisation (instead of the usual two – logs and among logs); (ii) explicitly considering the relative importance of these features; and (iii) studying a taxon (Passalidae) which has previously received no attention from a landscape perspective.

Study design

We assessed *O. disjunctus* incidence in 22 forested plots in the Mississippi River alluvial floodplain during March–May 2006 (Fig. 1a) [see Jackson (2010) for site information], a time of year when *O. disjunctus* presence is obvious as a result of active tunnel construction. Plot locations were selected to maximise variation in surrounding forest cover (18–96% at a scale of 225 ha) (Table 1). To ensure independence among plots, the
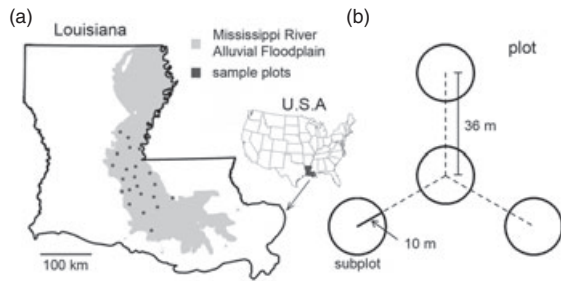
within each plot were separated by 36 m in an arrangement similar to that used in the USDA Forest Inventory and Analysis (Fig. 1b) (USDA Forest Service, 2004). Based on published (Gray, 1946) and our own (H. B. Jackson, personal observation, 2005) data on *O. disjunctus* habitat limits, sampling was restricted to logs that were suitably large (diameter ≥5 cm, length ≥1 m), showed evidence of decay, and were hardwood (i.e. not cypress or pine). We sampled up to three 31.4-dm^2 surface area sections per log (small end, middle, large end). This was the size of the smallest occupied logs in preliminary surveys and was expected to approximate the size of a single territory. We controlled for surface area rather than volume because *O. disjunctus* creates laterally extended tunnels in the outermost layers of wood where decay is advanced (H. B. Jackson, personal observation, 2005). We used a hatchet to sample each section for 2 min, and considered *O. disjunctus* present if individuals or fresh galleries were found.

We measured environmental variables expected to influence *O. disjunctus* incidence (Table 1). At the log section level, we recorded the presence of large wood-boring insects likely to compete with *O. disjunctus* for space. We recorded the presence of ants (in the genera *Camponotus*, *Crematogaster*, *Lasius*, *Myrmecina*, *Pheidole*, *Solenopsis* and *Temnothorax*), termites (*Reticulitermes* spp.) and other large wood-boring beetles (usually Cerambycidae and Buprestidae larvae). Decay stage was classified according to five classes used by the USDA Forest Inventory and Analysis (USDA Forest Service, 2004). Sound, recently fallen logs are in decay class 1 and well-decayed, structurally weak logs are in decay class 5. In addition, the absence of heartwood as a result of heart rot was recorded. Diameter at the centre of each section was measured

Fig. 1. (a) Locations of 22 plots in Louisiana. (b) Arrangement of four 10-m radius subplots within which all logs were surveyed for *Odontotaenius disjunctus*. Dotted lines indicate distances between subplot centres.

minimum distance between plots was 20 km (lack of spatial autocorrelation among plots was confirmed in residual analysis). This area is classified as oak–gum–cypress forest by the U.S. Department of Agriculture (USDA) Forest Service (Smith *et al.*, 2004). Dominant trees in this region include *Nyssa* spp. (tupelo), *Liquidambar styraciflua* L. (sweetgum), *Quercus* spp. (oak) and *Taxodium* spp. (cypress). More than 50% of the bottomland hardwood forest present in the 1930s is gone from this region (McWilliams & Rosson, 1990); most of these areas have been converted to agricultural land (MacDonald *et al.*, 1979). Furthermore, the hydrology of the area has been aggressively altered by over 5900 km of levees built to control the Mississippi River and its tributaries (Interagency Floodplain Management Review Committee, 1994).

Environmental sampling was conducted at four hierarchical organisational levels (Fig. 1b). The centres of four subplots

Table 1. Parameters measured in a multi-scale regional survey of *Odontotaenius disjunctus* occupancy.

Parameter	Abbr.	Mean	SD	Min	Max
(a) Log section (31.4 dm^2 surface area each, $n = 1161$)					
O. disjunctus present	OCC	0.19	0.14	0.00	0.46
Termites present	TRM	0.18	0.10	0.03	0.38
Ants present	ANT	0.47	0.13	0.23	0.71
Other wood-boring beetles present	BTL	0.19	0.12	0.00	0.47
Decay class	DEC 2	0.28	0.10	0.08	0.54
	DEC 3	0.43	0.10	0.31	0.64
	DEC 4	0.26	0.10	0.09	0.42
	DEC 5	0.03	0.05	0.00	0.19
Hollow as a result of heart rot	HOL	0.11	0.08	0.04	0.37
Log diameter, cm	WID	17.13	2.38	12.63	22.70
(b) Log (lengths vary, $n = 629$)					
Number of 31.4-dm^2 sections per log	SZ	7.31	2.02	4.24	10.75
Position (0 = downed, 1 = standing)	SNG	0.07	0.06	0.00	0.21
(c) Subplot (10 m radius each, $n = 88$)					
Canopy closure (proportion)	CAN	0.72	0.10	0.52	0.90
Basal area of hardwood trees, m^2/ha	G	84.50	12.08	60.68	105.80
(d) Plot (four subplots each, $n = 22$)					
Number of 31.4-dm^2 sections per plot	CWD	2999	1111	943	4724
Levee-protected	LEV	0.86	0.01	—	—
Proportion of surrounding 225 ha forested	FOR	0.65	0.25	0.18	0.96
Aggregation of forest cover within 225 ha	AGG	0.73	0.85	0.35	0.98

Continuous and categorical data are summarised by plot (e.g. mean proportion of log sections in a category per plot).
SD, standard deviation.

to the nearest cm. For each log we recorded the number of 31.4-dm^2 sections in the log and the position of the log (downed or standing). *Odontaenius disjunctus* is found in most, if not all, hardwood species in the southeastern U.S.A. (Gray, 1946). We omitted tree species from our analysis because moderately to well-decayed logs (most logs) could not be accurately identified to species. At the subplot scale, the percentage of canopy cover was estimated from the centre of each subplot based on visual inspection according to Forest Inventory Analysis guidelines (USDA Forest Service, 2004). As a rough estimate of stand age, basal area (m^2/ha) of hardwoods, a measure of the volume of live trees with a diameter greater than a preset cut-off, was estimated using angle-count sampling which involves a count of trees surrounding a fixed point that are larger than an object (basal area factor = 10) held at arm's length from the eye (Bay, 1960). We recorded flood history at the plot level because flooding is expected to disrupt passalid beetle populations (Mouzinho *et al.*, 2010). Limited USDA historical gage height data (http://ngmdb.usgs.gov) augmented by personal interviews with each land manager clarified that flood history was best described categorically rather than continuously, as heavy (unleveed area subject to multiple months of deep standing water in most years) or light (leveed area subject to rare, fleeting and shallow standing water). As a measure of habitat availability within plots, the total number of log sections of decay class 2 or greater in each plot was estimated.

To quantify landscape-level habitat amount, we quantified the amount of suitable forest habitat surrounding each plot. Land use data at a resolution of 30 × 30 m were obtained from the United States Geological Survey (USGS) online database [sabdata.cr.usgs.gov (USGS, 1998)]. We simplified land use data into two classes: forested and non-forested. Most of the non-forested areas were areas of either water or agriculture. Jackson *et al.* (2009) demonstrated that passalids are unlikely to disperse through open habitats and thus the amount of non-forested habitat was expected to influence movement and incidence. We considered land use patterns in four increasingly larger square regions around each plot (52 ha, 225 ha, 900 ha and 3600 ha, measuring 0.75 km, 1.5 km, 3.0 km and 6.0 km, respectively, per side). Land use information was converted into grid format in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California). Proportion forested ('PLAND' in FRAGSTATS) and aggregation of forest ('CLUMPY' in FRAGSTATS) were measured using FRAGSTATS 3.3 (McGarigal *et al.*, 2002). Forest aggregation was not measured for the smallest scale (52 ha) because aggregation cannot be calculated for areas with 100% cover (three landscapes).

Statistical methods

Statistical analyses focused on: (i) determining the scale of effect for landscape structure; (ii) comparing the relative importance of environmental factors across multiple hierarchical levels; and (iii) assessing the spatial autocorrelation of incidence within each hierarchical level. We used multiple steps to understand these scale-sensitive aspects of incidence.

Step 1: determining the best scale for measurement of landscape context. We evaluated the scale of effect of forest cover and aggregation on incidence by finding the spatial extent at which these variables best predicted incidence. Four logistic mixed-effects regression models relating forest cover, forest aggregation, the presence of levees, and the amount of coarse woody debris to the incidence of *O. disjunctus* within sections were created, one for each spatial extent at which the surrounding landscape variables were measured (note that presence of levees and amount of coarse woody debris were scale-invariant). Forest cover required a logit transformation to achieve normality in residuals. The correlation between forest cover and aggregation ($r = 0.01$, $r = -0.29$, $r = -0.28$ at 225 ha, 900 ha and 3600 ha, respectively) was statistically removed before analysis by using residuals of the regression of forest cover on forest aggregation instead of raw values. Plot, subplot and log were included as nested random effects to factor out autocorrelation within hierarchical levels [lme4 package in R (Bates *et al.*, 2008)]. The scale that produced a model with the lowest Akaike information criterion value adjusted for small sample size (AIC_c) was considered the best scale.

Step 2: selecting the most important predictors for each hierarchical level. In order to make hierarchical analysis more manageable, we reduced the number of predictors by separately considering environmental factors at each sampling level (section, log, subplot and plot). The response and random-effects variables were the same as those in Step 1, but predictors from each level were considered in separate models. Analysis at the plot level included forest cover and aggregation measured at the best scale determined in Step 1. Diameter of log sections and number of sections per log required an ln transformation. Predictors were retained for multi-level analysis if their summed Akaike weight [$\sum w_i$, interpreted as the probability that a predictor is in the true model (Burnham & Anderson, 2004)] was ≥ 0.5.

Step 3: combining important environmental predictors from each hierarchical level in one analysis. Using the same model structure as in the previous two steps, we combined the best predictors (nine in total) from the single-level analyses into one logistic mixed-effects analysis. Canopy cover was moderately collinear with all three significant variables measured at the plot level ($r = -0.18$, $r = 0.43$ and $r = 0.33$ for levees, forest cover and forest aggregation, respectively). Thus, we used the residuals of the regression of canopy cover on plot-level variables instead of raw canopy values. Pearson's correlation statistics among other independent variables used in the multi-level analysis did not exceed an absolute value of $r = 0.14$. Models with all possible combinations of fixed effects were considered (512 models in total). Model fit was assessed using the area under the receiver operating characteristic curve (AUC). The AUC indicates predictive accuracy where 0.5 indicates prediction as good as random and 1 indicates perfect prediction.

Step 4: accounting for model uncertainty. Models with AIC_c scores similar to the best model ($\Delta AIC_c < 2$) were considered equally informative and were therefore averaged together following the methods of Burnham and Anderson (2004). Model averaging tends to result in greater predictive accuracy (Madigan & Raftery, 1994). The averaged estimates for means and standard errors were calculated using estimates weighted by Akaike weights from each model.

Step 5: evaluating variance explained by each environmental predictor. We next compared the relative importance of environmental predictors (those determined to be important in Step 3) using hierarchical variance partitioning. The variation explained independently by each predictor variable included in the full multi-scale model was assessed using the algorithm outlined by Chevan and Sutherland (1991) [hier.part package in R (Walsh & MacNally, 2008)], which averages the change in R^2 when the variable in question is dropped from all nested models of the full model. We used the pseudo-R^2 (R_N^2) of Nagelkerke (1991) as an estimate of goodness of fit that is appropriate for general linear models. We used the intercept-only model (no random effects) as the null model for R_N^2 because it provides a better estimate of the significance of fixed effects than a random-effects only model (Orelien & Edwards, 2008).

Step 6: comparing the relative importance of environmental predictors using standardised coefficients. To compare the relative importance of environmental predictors using effect size, we standardised each input variable by subtracting the mean and dividing by the standard deviation (SD) before analysis. The resulting standardised coefficient is interpreted as the change in incidence associated with a change of 1 SD in a given independent variable (Menard, 2004) and provides an estimate of relative importance that is less sensitive to collinearity than variance partitioning (Smith *et al.*, 2009).

Step 7: identifying the hierarchical level at which spatial autocorrelation is greatest. We identified the hierarchical level at which the greatest spatial autocorrelation in incidence occurred (i.e. highest intraclass correlation) after underlying environmental filters were taken into account. We estimated

confidence intervals (CIs) for the random effects in our full hierarchical model (Step 3) using 1000 posterior simulations ['arm' package (Gelman & Hill, 2006)]. A large random effect estimate indicates greater spatial autocorrelation in incidence which is caused by intrinsic species processes (e.g. dispersal), assuming that environmental influences have been taken into account. All analyses were performed in R (R Development Core Team, 2010).

Results

Odontotaenius disjunctus was common, occurring in all but one forest plot and occupying an average proportion of 0.19 (95% parametric CI 0.17–0.21) suitable log sections, 0.26 (95% CI 0.22–0.29) logs, 0.73 (95% CI 0.62–0.81) subplots, and 0.95 (95% CI 0.75–1.00) plots. Forest cover and forest aggregation had greater effect sizes and were more informative when measured at 225 ha than at 52 ha, 900 ha or 3600 ha (Table 2). For the subsequent multi-scale analysis, we considered the scale of effect for landscape-scale parameters to be 225 ha.

The most informative predictors ($\sum w_i = 1$) in the full multi-scale model included the log section-level variables decay class, presence of heart rot and presence of ants, the log-level variables log size and log position, and the plot-level variables presence of levees and forest cover (Table 3). The presence of other wood-boring beetles ($\sum w_i = 0.33$, log section level) and canopy cover ($\sum w_i = 0.81$, subplot level) were less informative. The presence of termites, log diameter, basal area of standing hardwood, and amount of coarse woody debris within plots were eliminated from the analysis because single-level analyses gave low information values ($\sum w_i < 0.5$). Although informative in the single-level plot analysis, forest aggregation was not informative in the multi-scale analysis.

The best model provided good fit to the data ($R_N^2 = 30.0\%$, AUC $= 0.92$) (Table 3). Two predictors, measured at the log section level and the log level, respectively, explained passalid incidence particularly well: decay class ($iR_N^2 = 9.9\%$) and log size ($iR_N^2 = 3.1\%$) (Table 3, Fig. 2). Other predictors, among which the presence of levees (measured at the plot level) was the most prominent ($iR_N^2 = 1.7\%$), each explained <2% of the variance (Table 3).

Table 2. Spatial scale at which incidence within a log section responds to forest cover and aggregation measured at four spatial extents ($n = 22$ forest plots).

	$\hat{z}$				Comparison of full models			
Spatial extent, ha	FOR	AGG	LEV	CWD	k	ΔAIC_c	w_i	$R_N^2\%$,
3600.0	0.18 (0.20)	−0.11 (0.20)	0.90 (0.26)	−0.05 (0.20)	8	6.14	0.04	2.0
900.0	0.24 (0.20)	−0.12 (0.20)	0.89 (0.26)	−0.04 (0.19)	8	5.33	0.06	2.1
225.0	**0.42 (0.19)**	**−0.24 (0.16)**	**0.90 (0.25)**	**−0.05 (0.17)**	**8**	**0.00**	**0.80**	**2.9**
51.8	0.24 (0.21)	—	0.93 (0.27)	0.01 (0.20)	7	4.05	0.10	2.0

The best model is in bold. R_N^2, Nagelkerke's pseudo-R^2; $\hat{z}$, standardised regression coefficient (SE); ΔAIC_c, change in Akaike information criterion adjusted for small sample sizes; AGG, residuals of the regression of aggregation on forest cover; FOR, proportion forest cover (logit-transformed); k, number of parameters; LEV, levees (present/absent); w_i, Akaike weight indicating probability that a model is the 'true' one.
Linear regression models also included plot, subplot and log as nested random effects.

Table 3. Test of the relative importance of environmental variables measured at multiple organisational levels when predicting the incidence of *Odontotaenius disjunctus* in log sections ($n_{plot} = 22$, $n_{subplot} = 88$, $n_{log} = 629$, $n_{sections} = 1161$).

(a) Model-averaged fixed-effect estimates

Predictor			$\bar{b}$	$\hat{z}$	$\sum w_i$	iR_N^2	jR_N^2
	Intercept	—	−7.11 (0.81)	—	1.00	—	—
	DEC	3	2.21 (0.34)	1.09	1.00	9.9%	−0.1%
		4	2.51 (0.36)	1.10	1.00	—	—
		5	1.27 (0.74)	0.22	1.00	—	—
Section	HOL	—	−1.04 (0.39)	−0.33	1.00	1.1%	0.2%
	ANT	—	−0.61 (0.20)	−0.31	1.00	0.8%	0.3%
	BTL	—	0.09 (0.08)	0.04	0.33	0.4%	0.2%
	SZ	—	0.55 (0.10)	0.54	1.00	3.1%	0.0%
Log	SNG	—	−0.93 (0.45)	−0.24	1.00	0.2%	0.1%
Subplot	CAN	—	−2.87 (1.41)	−0.27	0.81	0.3%	−0.2%
Plot	LEV	—	2.85 (0.71)	1.03	1.00	1.7%	0.1%
	FOR	—	0.33 (0.16)	0.42	1.00	1.2%	1.9%

(b) Random-effect estimates

Level	σ_R (95 CI)
Log	0.73 (0.69–0.77)
Subplot	0.84 (0.73–0.96)
Plot	0.61 (0.44–0.80)

(c) Best model set

Model	k	ΔAIC_c	w_i	R_N^2%,	AUC
DEC + ANT + HOL + SZ + SNG + CAN + LEV + FOR	14	0.00	0.48	30.0	0.92
DEC + ANT + HOL + BTL + SZ + SNG + CAN + LEV + FOR	15	0.77	0.33	30.1	0.92
DEC + ANT + HOL + SZ + SNG + LEV + FOR	13	1.86	0.19	29.6	0.91

Key to predictor abbreviations in Table 1. $\hat{z}$, model-averaged coefficient based on standardised data (= change in incidence associated with a change in one standard deviation in x); $\bar{b}$, model-averaged coefficient based on unstandardised data; $\sum w_i$, summed Akaike weight indicating probability that a predictor is in the 'true' model; iR_N^2, variation independently explained by a predictor; jR_N^2, variation jointly explained by predictor; σ_R, median random effect and 95% confidence interval estimated using 1000 posterior simulations; R_N^2, marginal Nagelkerke pseudo-R^2; ΔAIC_c, change in Akaike information criterion adjusted for small sample sizes; AUC, area under the receiver operating characteristic curve indicating the predictive accuracy of the model; w_i, Akaike weight indicating probability that a model is the 'true' one.

Decay class and presence of levees had large effects on incidence (Table 3, Fig. 3). The relative importance of log size depends on how effect size is measured: the expected change in incidence associated with a change of 1 SD in log size ($\hat{z} = 0.54$) is less than a comparable change in levees ($\hat{z} = 1.03$). However, over the full range of these predictor variables, the expected change in incidence is much greater for log size than for levees (Fig. 3). As determined by standardised coefficients, the relative importance of other predictors was generally consistent with their explained variance (Table 3, Figs 2 and 3).

Small but significant spatial autocorrelation in incidence occurred at the log, subplot and plot levels (Table 3). Autocorrelation in incidence was greatest at the subplot level and least at the plot level.

Discussion

This study is one of only a few to demonstrate the importance of both environmental and intrinsic factors affecting species incidence at multiple scales (see also de Juan & Hewitt, 2011) and is the first to document the importance of these factors for one of the 700–1000 species of Passalidae. Given the well-documented negative effects of habitat loss on populations (reviewed in Fahrig, 2003), the pattern of *O. disjunctus* incidence indicates a surprisingly small effect of landscape-level habitat loss and fragmentation within the surrounding 225 ha. Instead, the environmental factors acting at the scale of territories (within log sections) were much stronger predictors of incidence, and autocorrelation in incidence was most evident at the scale of groups of logs (subplots). These data indicate the importance of fine-scale (i.e. territory level) environmental variables when predicting the scale at which patterns in distribution are most pronounced.

Scale of effect of landscape structure

The small scale of effect of forest cover on *O. disjunctus* incidence is consistent with its greater dispersal limitation relative to those of saproxylic beetles of similar size. In previous studies, the radius of the scale of effect of forest amount on saproxylic beetle occupancy (Ranius *et al.*, 2010) or abundance (Holland *et al.*, 2005) ranged between 20 m and 2250 m. Body size may positively predict scale of effect. For 12 cerambycid beetle species (also saproxylic), the scale of effect of forest cover varied from a radius of 20 m for the
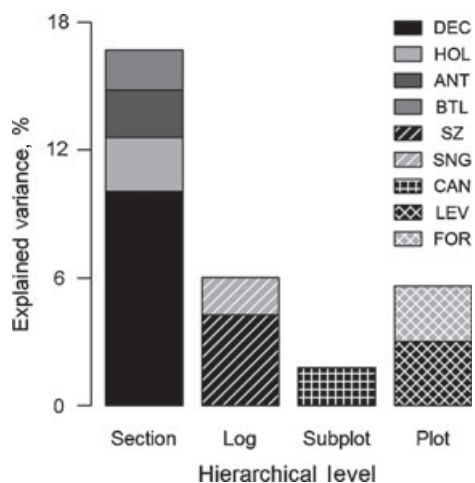
Fig. 2. Relative importance of environmental factors predicting *Odontotaenius disjunctus* incidence as estimated by the amount of variation independently explained (iR_N^2; total $R_N^2 = 30.1\%$). Environmental factors are organised by the hierarchical level at which they were measured. DEC, decay class; HOL, hollow centre caused by heart rot; ANT, ants present; BTL, other wood-boring beetles present; SZ, number of 31.4-dm^2 sections per log; SNG, standing logs; CAN, canopy cover; LEV, levee-protected; FOR, proportion of surrounding 225 ha forested.

smallest species (6.5 mm long) to a radius of 1000 m for the largest (21.5 mm long) (Holland *et al.*, 2005). Although *O. disjunctus* is 50% larger (32 mm long) than the largest cerambycid in the study by Holland *et al.* (2005), our findings show a smaller scale of effect (225 ha, ≈750-m radius). This disparity probably reflects differences in dispersal mode: cerambycids rely on flight, whereas *O. disjunctus* primarily disperses via walking (Hunter & Jump, 1964; Jackson *et al.*, 2009). The dispersal distance of saproxylic beetles (and potentially the scale of effect) may also be affected by other life-history traits such as whether larval and adult hosts differ (Hanks, 1999) and the ephemerality of the decay state to which they are best adapted (Travis & Dytham, 1999).

Hierarchy of environmental filters

Odontotaenius disjunctus incidence was most strongly related to environmental characteristics measured at the finest scale (log sections). There are some indications that pronounced structure in fine-scale (i.e. individual level) distribution is a general rule (e.g. Fraschetti *et al.*, 2005) for the simple reason that organisms are better able to reach the most ideal habitat that is within their perceptual or dispersal range (e.g. Pinto & MacDougall, 2010).

This is the first study of saproxylic beetles to directly compare the importance of within-log characteristics with whole log characteristics and shows the interesting result that within-log characteristics are more important. A few studies of saproxylic beetles have measured within-log characteristics, such as sporophores (Rukke & Midtgaard, 1998; Teichert & Bondrup-Nielsen, 2005), but because they did not compare

environmental variables directly in a hierarchical statistical test the relative importance of these variables is difficult to infer. Our study indicated a response on the part of *O. disjunctus* to decay and competitors at the log section level. Most researchers estimate the average decay of an entire log, a reasonable approach considering that decay within a log is correlated. Even so, decay can vary widely within a log (Saint-Germain *et al.*, 2010). When more than one section in a log was sampled in our survey, there was a 50% probability that sections would be in different stages of decay. Furthermore, a log-level perspective is not precise enough to show potentially important interspecific relationships, such as the negative relationship between *O. disjunctus* incidence and ants. The two taxa actually show a positive correlation in incidence when analysed at the log level (data not shown).

Consistent with findings from two previous studies of saproxylic beetle abundance (Buse *et al.*, 2007) and richness (Ulyshen & Hanula, 2009), log characteristics were more important to *O. disjunctus* incidence than subplot (or stand) characteristics. Log size may be the most important environmental variable at the log level for saproxylic beetles (reviewed in Grove, 2002; Ferro *et al.*, 2009). When the effect of log size is removed (i.e. by experimentally controlling log size), stand-level environmental variables are often more important than other log-level variables (e.g. Gibb *et al.*, 2006). The pattern of greater incidence of *O. disjunctus* in large logs is consistent with space limitations suggested by performance experiments in which *O. disjunctus* population growth rate was negative in logs smaller than a certain size [28 dm^2 surface area (Jackson, 2010)]. Large logs may provide advantages beyond adequate space; thicker walls in large logs provide improved microclimate stability, and large diameter is associated with longer persistence times (Harmon *et al.*, 1986; Zell *et al.*, 2009). Furthermore, decay properties are especially variable within large logs (Allen *et al.*, 2000) and therefore currently undecayed sections may represent potential territories for future breeding seasons.

Landscape-level factors more strongly predicted *O. disjunctus* incidence than subplot-level factors. Franc *et al.* (2007) argue that the greater importance of forest amount at large scales over dead wood amount at middle scales suggests not that forest is more important than dead wood for saproxylic insects (dead wood is clearly essential), but, rather, that the scale at which habitat availability should be measured is much greater than the scale of most woody debris surveys.

Given the limited dispersal ability of *O. disjunctus*, we had expected the explanatory value of forest amount at the landscape level to be greater than that found in our study. A common expectation among researchers is that habitat loss will negatively influence dispersal-limited taxa more than highly vagile taxa. In Europe, for example, landscape-scale habitat loss and fragmentation were negatively associated with the species richness of dispersal-limited carabid beetle species, but positively associated with the richness of more dispersive carabids (Hendrickx *et al.*, 2009). By contrast, if the costs of dispersal outweigh the benefits of immigration, then less dispersive species may fare better than more dispersive species in the presence of habitat loss (Fahrig, 2001). *Odontotaenius*
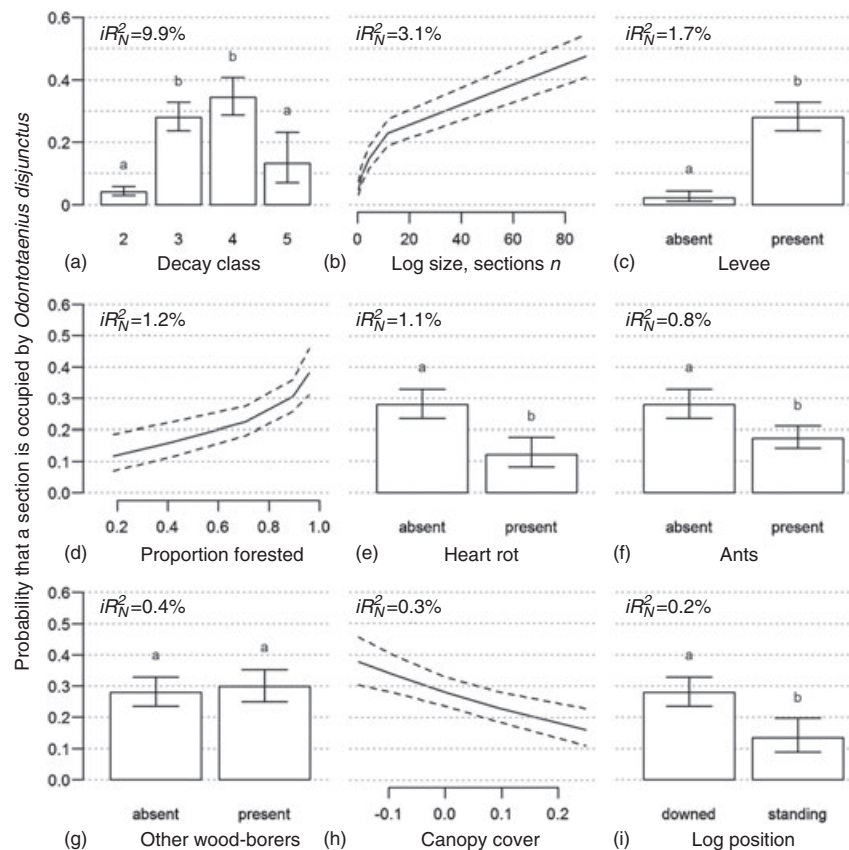
Fig. 3. The probability that a section (31.4 dm^2 surface area) of log located in one of 22 replicate landscapes was occupied by *Odontotaenius disjunctus* was dependent on (in order of independently explained variation): (a) moderate decay class; (b) large log size; (c) presence of a levee; (d) proportion of landscape within 225 ha that was forested; (e) absence of heart rot; (f) absence of ants; (g) presence of other wood-borers (mostly cerambycid beetles); (h) decreased canopy cover; and (i) downed position (not a snag). Values are back-transformed model-averaged estimates of least square means and standard errors. Different letters indicate significant least square differences among model-averaged means ($\alpha = 0.05$). Predictors are those deemed informative by model selection based on AIC$_c$ values (Table 3). Estimates are those predicted when all other predictors are held constant at: DEC = 3; SZ = 4.36 sections; LEV = present; FOR = 0.71; ROT = absent; ANT = absent; BTL = absent; CAN = 0; and SNG = downed. iR_N^2 is the variance independently explained by a predictor.

disjunctus moves short distances and avoids crossing forest boundaries (Jackson *et al.*, 2009). Multiple simulation studies have shown that a low probability for crossing boundaries can have a strong positive effect on population density and incidence (Tischendorf *et al.*, 2005; Jackson, 2010). Even so, the cost of isolation may catch up with otherwise stable populations in the long run. Komonen *et al.* (2000) showed that the negative effects of isolation on incidence became more apparent as time since isolation increased. Species with stable population dynamics may take even longer than other species to respond to habitat loss [e.g. several decades for a ground beetle (Petit & Burel, 1998)]. An alternative explanation for the small effect of forest loss on *O. disjunctus* is that the negative effect of forest loss has been mitigated by the concurrent release from important predators (Ryall & Fahrig, 2006). *Odontotaenius disjunctus* predators include multiple vertebrate and invertebrate species, some of which are threatened by habitat loss [e.g. Louisiana black bear (U.S. Department of the Interior, 1992)], but unfortunately their effects on *O. disjunctus* populations are unknown.

Flood history was the strongest predictor of incidence rate at the plot level such that incidence rates in heavily flooded areas were low. Like decay, flood severity is a strong force structuring communities of saproxylic beetles (Ballinger *et al.*, 2010) and other forest arthropods, such as carabid beetles and spiders (Lambeets *et al.*, 2008).

Scale of autocorrelation

Although some authors have hypothesised that limited dispersal will result in strong variation in density across sampling sites (Taylor *et al.*, 1983), *O. disjunctus* exhibits surprisingly little spatial autocorrelation in incidence, suggesting that spatial autocorrelation in incidence is smoothed out either by infrequent long-distance dispersal or by the cumulative effect of frequent short-distance dispersal events among nearby logs [e.g. as stepping stones (Ibrahim *et al.*, 1996)], or both. The patchiness that does exist is strongest at the subplot and log levels, a pattern consistent with the hypothesis that autocorrelation is associated with average dispersal distance

[dispersal is usually <5 m but a small number of beetles move >30 m (Jackson, 2010)]. Logs were separated by an average of 2.74 m (95% CI 0.24–11.6); subplots were 20 m in diameter and were separated by >16 m. Although we measured all of the environmental factors that the literature led us to believe might be important, we cannot rule out the possibility that part of the remaining autocorrelation in incidence is associated with unmeasured environmental variables.

Conclusions

Although sensitivity to large-scale environmental phenomena (e.g. habitat loss) is a consistent pattern across taxa (reviewed in Fahrig, 2003), this study emphasises the importance of fine-scale environmental variation for distribution. Landscape-level factors have shown significant correlation with distributions of other saproxylic beetles (e.g. Franc *et al.*, 2007; Laaksonen *et al.*, 2008), but landscape-level factors (e.g. forest amount) are rarely measured concurrently with fine-scale patterns (e.g. territory quality). We cannot discount the importance of landscape-level factors for other taxa, but, rather, suggest that concurrent measurement of fine-scale factors can help to determine the scale at which the most important processes influencing a species occur. For example, our study suggests that effective management and prediction of *O. disjunctus* distribution should focus on the size and quality of wood at fine scales more than on connectivity among forested areas at landscape scales.

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