

Can coarse-grain patterns in insect atlas data predict local occupancy?

Louise J. Barwell^{1,2*}, Sandro Azaele³, William E. Kunin² and Nick J. B. Isaac¹

¹NERC Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK, ²School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK, ³School of Mathematics, Faculty of Mathematics and Physical Sciences, University of Leeds, Leeds, LS2 9JT, UK

ABSTRACT

Aim Species atlases provide an economical way to collect data with national coverage, but are typically too coarse-grained to monitor fine-grain patterns in rarity, distribution and abundance. We test the performance of ten downscaling models in extrapolating occupancy across two orders of magnitude. To provide a greater challenge to downscaling models, we extend previous downscaling tests with plants to highly mobile insect taxa (Odonata) with a life history that is tied to freshwater bodies for reproduction. We investigate the species-level correlates of predictive accuracy for the best performing model to understand whether traits driving spatial structure can cause interspecific variation in downscaling success.

Location Mainland Britain.

Methods Occupancy data for 38 British Odonata species were extracted from the Dragonfly Recording Network (DRN). Occupancy at grains ≥ 100 km² was used as training data to parameterize ten downscaling models. Predicted occupancy at the 25, 4 and 1 km² grains was compared to observed data at corresponding grains. Model predictive error was evaluated across species and grains.

Main conclusions The Hui model gave the most accurate downscaling predictions across 114 species:grain combinations and the best predictions for 14 of the 38 species, despite being the only model using information at a single spatial grain. The occupancy–area relationship was sigmoidal in shape for most species. Species' distribution type and dispersal ability explained over half of the variation in downscaling predictive error at the species level. Species with a climatic range limit in Britain were poorly predicted compared with other distribution types, and high dispersal ability was associated with relatively poor downscaling predictions. Our results suggest that downscaling models, using widely available coarse-grain atlas data, provide reasonable estimates of fine-grain occupancy, even for insect taxa with strong spatial structure. Linking species-level traits with predictive accuracy reveals general principles about when downscaling will be successful.

Keywords

Aggregation, biodiversity monitoring, distribution, occurrence, spatial scale.

*Correspondence: Louise J. Barwell, NERC Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK. E-mail: loubar@nerc.ac.uk

INTRODUCTION

The lack of fine-grain data over large spatial extents is problematic for accurate monitoring of threatened species and limits our theoretical understanding of biodiversity patterns

(McGill, 2010a, b; Beck *et al.*, 2012; Jetz *et al.*, 2012; Keith *et al.*, 2012). Species' distributions are typically mapped in the form of atlases derived from spatially explicit, opportunistic occurrence records for a specific taxonomic group within a defined geographical extent and time period (Rob-

ertson *et al.*, 2010). Atlases use coarse-grain sizes to minimize pseudo-absences (false absences or omission errors), at a cost of including large areas where the species is actually absent (commission errors: Boitani *et al.*, 2011). However, distribution size is highly scale dependent (Kunin, 1998), such that coarse-grain occupancy is a poor predictor of abundance (Hartley & Kunin, 2003).

Recently, ecologists have begun to realize that the scale dependency of species distributions can be described statistically and even extrapolated across scales (He & Gaston, 2000; Kunin *et al.*, 2000; He *et al.*, 2002; Hui *et al.*, 2006; He & Condit, 2007), thus helping to address this fine-grain data deficit and improve our assessment of rarity and extinction risk (Mace *et al.*, 2008). Specifically, the occupancy–area relationship (OAR, following the terminology in McGill, 2010b) describes how occupancy (the proportion of grid cells where a species is present) increases with grain size (the area of each grid cell). Elsewhere, closely related relationships are the scale–area curve (Kunin, 1998; Veldtman *et al.*, 2010), area–area curve (He & Gaston, 2000), range–area curve (Green *et al.*, 2003), scaling pattern of occupancy (Hui *et al.*, 2006; Hui, 2009) and p-area curve (Storch *et al.*, 2008). As the grain used to record species' presences becomes coarser, empty fine-grain cells merge with neighbouring occupied cells and a greater proportion of the study region appears occupied. There is considerable variation in the shape and slope of the OAR among species, driven by species' overall abundances, patterns of intraspecific aggregation (Cowley *et al.*, 2001; Storch *et al.*, 2008; Conlisk *et al.*, 2009; Gaston & He, 2011) and the logical constraint that no fewer than one cell can be occupied at a given scale (Fig. 1). The local slope of the OAR contains information about intraspecific aggregation: a steep local slope between two spatial grains indicates a species occurs in few fine-grain cells within each occupied coarse-grain cell (a sparse, fragmented distribution). A shallow local slope indicates that the species is present in many fine-grain cells within each coarse-grain cell (an aggregated, contiguous distribution) (Wilson *et al.*, 2004; Veldtman *et al.*, 2010). Although downscaling models do not describe the processes shaping aggregation patterns, they are nonetheless able to capture interspecific variation in the shape of the OAR (Azaele *et al.*, 2012).

Downscaling models have been tested (using training data at coarse grains and a test data set at fine grains) for 73 species of rare plants in mainland Britain (Kunin, 1998; Kunin *et al.*, 2000), 92 species of grasses in mainland Britain (Kunin *et al.*, 2000), 301 tree species in a 0.5 km² tropical rainforest plot in Barro Colorado Island, Panama (He & Condit, 2007), 824 tree species in 0.5 km² tropical rainforest plot in Pasoh, Malaysia (He & Gaston, 2000), passerine birds in Bedfordshire (He & Gaston, 2000), six large mammalian herbivores in the 13912 km² Kruger National Park (Tosh *et al.*, 2004) and southern African bird species (Lennon *et al.*, 2007; Hui *et al.*, 2009). Azaele *et al.* (2012) tested the performance of nine downscaling models across several orders of magnitude in grain size using multi-scale occupancy data for 16 rare British plant species. The Thomas model, derived from a clustered

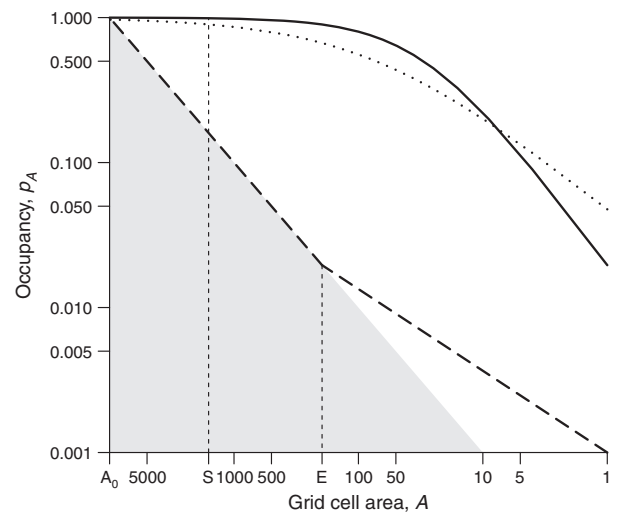


Figure 1 The occupancy–area relationship (OAR) for three hypothetical species (adapted from Azaele *et al.*, 2012). There are a wide variety of shapes and slopes of the OAR among species, reflecting both the extent of a species' distribution within the study region and the intensity of intraspecific aggregation. Here, the differences in slopes cause the species' curves represented by the solid black line and the dotted black line to cross over, demonstrating that the grain at which occupancy is measured can change our perception of which species is rarest. For widespread species (solid black line) within the study region, the curve becomes shallower as the sampling grain approaches the extent of the study region, A_0 . At grains coarser than the point of saturation, S , the species represented by the solid black line occurs in all cells (e.g. occupancy = 1). For a species that is restricted to some portion of the study region (dashed line), an inflection point will be seen at the finest grain to contain the entire distribution within a single grid cell (the point of endemism, E). Saturated and endemic grains add no information about the scaling of occupancy for the purposes of downscaling. Occupancy cannot fall within the shaded grey area, which represents the region where occupancy $< A/A_0$ and equates to a species occurring in less than one cell in the study region.

Poisson point process, provided the most accurate and unbiased estimates of fine-grain occupancy across the 16 species, despite the absence of information about the spatial positions of occupied cells. Virtually all of these tests are for plants, and in most cases, three or fewer of the available downscaling methods were applied to the data. The range of extrapolation varies greatly among studies from 25-fold (Kunin, 1998) to four orders of magnitude (Azaele *et al.*, 2012). In the absence of a mechanistic understanding of the OAR (but see McGill & Nekola, 2010; McGill, 2011), it is important to establish whether downscaling models are general enough to describe all observed forms of the OAR and to extend comparative tests of model performance to taxa with a very different set of dispersal abilities, habitat requirements and spatial structures.

We identify four traits, measured at the level of the species, which we predict will lead to interspecific variation in the shape of the OAR (and therefore downscaling success). A spe-

cies' distribution type (widespread, range limited, local-sparse or local-aggregated) is a broad descriptor of interspecific variation in the number and spatial arrangement of occupied cells (see Appendix S2d in Supporting Information). On a more mechanistic level, patterns of intraspecific aggregation depend on the interplay between dispersal ability and the patchy distribution of suitable (micro)climate and habitat (Hubbell, 2001; Green & Plotkin, 2007; Storch *et al.*, 2008; McGill, 2010b). The other three traits (dispersal ability, habitat breadth and range change) are chosen for their relationship to those processes influencing intraspecific aggregation and variation in the shape and slope of the OAR (Fig. 1).

Here, we present a comparison of downscaling methods applied to coarse-grain records of British Odonata and extrapolate occupancy through two orders of magnitude in spatial grain. These distribution data are used to investigate (1) which downscaling models perform best in predicting fine-grain occupancy from coarse-grain atlas data and (2) whether species traits can explain interspecific variation in predictive success. Our analyses extend knowledge gained in previous downscaling studies by testing for general principles in our ability to predict occupancy at fine-spatial grains.

METHODS

Odonata distribution data

Occupancy data for British Odonata were extracted from the Dragonfly Recording Network (DRN) held by the British Dragonfly Society (BDS). The DRN data comprise over 1 million records on 34 510 spatially referenced 1 km² cells in mainland Britain. OARs based on eight spatial grains were estimated for a total of 38 species, comprising the resident breeding Odonata species in the UK (Appendix S1). Spatial variation in recording intensity, geographical biases and pseudo-absences must be acknowledged when estimating species occupancies from presence-only, opportunistic occurrence records (Van Strien *et al.*, 2013). To address the issue of pseudo-absences, we included only cells in which at least one species had been recorded (as evidence of a visit), and assumed species not recorded in a grid cell were absent. This threshold is intended to address the trade-off between the number of false absences and the exclusion of large amounts of fine-grain data (Appendix S2a). Cells with < 30% land cover ($\geq 70\%$ sea) were excluded at each spatial grain as a trade-off between the total amount of land represented by cells in the analysis and the total number of cells available for analysis at coarse grains (Appendix S2b). The spatial references of occupied grid cells at 1 km² were coarsened to obtain species' occupancies at the 4, 25, 100, 144, 400, 1600, 6400 km² grains to estimate the OAR for each species. A species' occupancy was calculated as the proportion of the total number of sampled grid cells in which the focal species occurs. Data cleaning, manipulation and calculation of species occupancies at multiple scales were performed in R version 2.15.1 (R Development Core Team, 2012).

Downscaling

Ten downscaling models (Table 1) were fitted to occupancy data at coarse grains (≥ 100 km²) for the 38 British Odonata species. This reflects the typical 100 km² grain of atlas data in the UK. Models 2–9 (Table 1; Appendix S2c) use the shape of the OAR at multiple grains to extrapolate to finer grains (reviewed in Azae *et al.*, 2012). The term Thomas model, as used here, refers to the downscaling formula in Appendix S2c, rather than the spatially explicit Thomas point process from which it was derived by Azae *et al.* (2012). We parameterized these models using occupancy at five coarse-spatial grains (100, 144, 400, 1600 and 6400 km²) (Appendix S2c). Saturated grains contain no information for downscaling purposes (Fig. 1). For seven widespread species, the OAR was saturated (i.e. reached 100% occupancy) at the coarsest (*Enallagma cyathigerum*, *Sympetrum striolatum*, *Pyrrosoma nymphula*, *Libellula quadrimaculata* and *Sympetrum danae*) or two coarsest (*Lestes sponsa*, *Ischura elegans*) grains, and so these grains were excluded when parameterizing models. Model 1, the Hui model (Hui *et al.*, 2006; Hui, 2009; Table 1), uses spatially referenced data from one reference grain size to estimate occupancy at others based on just two pieces of information: the probability that a cell is occupied, P_{+} , and the conditional probability that neighbouring cells are occupied, $Q_{+/+}$ (an index of spatial aggregation). Bayes' theorem can be used to express all conditional probabilities of occupancy in terms of P_{+} and $Q_{+/+}$ and to derive the OAR. We implemented the formulae in Hui (2009), using 100 km² as our reference grain size (Appendix S2c).

Mathematica 9.0 Student Edition (Wolfram Research, Inc. 2012) was used for optimization of parameter estimates for all models.

The parameterized models were used to predict occupancy at 25, 4 and 1 km² grains. Model predictions were obtained at three grains (25, 4 and 1 km²) for the 38 species, giving a total of 114 predictions for each model. Model predictions were evaluated as the absolute value of the percentage error $\frac{|p_{A,i}^{\text{pred}} - p_{A,i}^{\text{ob}}|}{p_{A,i}^{\text{ob}}} \cdot 100$, where $p_{A,i}^{\text{ob}}$ and $p_{A,i}^{\text{pred}}$ are the observed and predicted occupancies at grain A for species i . We assessed model performance on a species-by-species basis, as well as across all 114 species:grain combinations. Species-level performance was evaluated as the number of species for which each model gave the best overall predictions (the mean absolute value of percentage error across the three predicted grains). The median, minimum and maximum of absolute values of percentage errors were used to evaluate model performance across all 114 species:grain combinations.

Odonata traits

Downscaling errors are most extreme when extrapolated furthest from the fitted region of the OAR. Therefore, the percentage errors at 1 km² (including the direction of error, + or –) for the overall best performing model were used as the

Table 1 Summary of performance for ten downscaling models.

Model	# Params	Best	Median	Min	Max	References
Hui	2	14	16.594	0.313	102.467	(Hui <i>et al.</i> , 2006; Hui, 2009)
Nachman	2	12	19.480	0.119	85.121	(Nachman, 1981)
Power Law	2	5	25.196	0.202	126.543	(Kunin, 1998)
Logistic	2	5	30.107	0.548	93.259	(Hanski & Gyllenberg, 1997)
Thomas	3	1	59.795	0.457	98.518	(Azaele <i>et al.</i> , 2012)
Finite negative binomial	2	1	73.946	0.835	97.591	(Zillio & He, 2010)
Generalized negative binomial	3	0	32.561	0.209	99.515	(He <i>et al.</i> , 2002)
Improved negative binomial	3	0	35.009	0.080	89.026	(He & Gaston, 2003)
Negative binomial	2	0	72.046	0.473	97.863	(He & Gaston, 2000)
Poisson	1	0	91.111	46.648	99.132	(Wright, 1991)

For model formulae and notation, see Appendix S2c. # Params is the number of free parameters. Best is the number of species for which each model gave the best downscaling predictions (the lowest mean percentage error for each species across the three predicted grains). Median, Min and Max are the median, minimum and maximum absolute value of percentage error of downscaling predictions across 114 species: grain combinations, $\frac{|p_{A,i}^{\text{pred}} - p_{A,i}^{\text{ob}}|}{p_{A,i}^{\text{ob}}} \cdot 100$, where $p_{A,i}^{\text{pred}}$ and $p_{A,i}^{\text{ob}}$ are the predicted and observed occupancy at grain *A* for species *i*.

response variable in a species-level trait analysis calculated as $\frac{|p_{1,i}^{\text{pred}} - p_{1,i}^{\text{ob}}|}{p_{1,i}^{\text{ob}}} \cdot 100$, where $p_{1,i}^{\text{ob}}$ and $p_{1,i}^{\text{pred}}$ are the observed and predicted occupancies at the 1 km² grain for species *i*. Data on two distributional traits (distribution type, range change) and two life-history traits (habitat breadth, dispersal ability) were obtained for the 38 British Odonata species. Distribution type was classified as widespread, range limited, local-aggregated or local-sparse, based on the number and spatial arrangement of occupied cells (Appendix S2d). Habitat breadth (1–6) was obtained from Powney *et al.* (2014). Data for British Odonata range change between 1970 and 2012 were taken from NJB Isaac (unpublished data) as the annual linear trend in the probability of occupancy on a logit scale using a generalized linear mixed-effect model (Roy *et al.*, 2012). We obtained dispersal ability estimates from Fitt (2013), who inferred dispersal distances from the positions of newly colonized 1 km² cells in each year from 1991 to 2012 (2000–2012 for the recent colonist *Erythromma viridulum*). Distances of newly colonized cells from the nearest previously occupied 1 km² cell were weighted by the probability of a species being previously missed in that cell, given the number of times the newly colonized cell was surveyed prior to the first recording of the species (using the list length model; Szabo *et al.*, 2010). This method is intended to reduce the error in dispersal distance estimates driven by cells that appear newly colonized, but were in fact merely unrecorded due to low sampling intensity. The 75th percentile of dispersal distances was used as the measure of dispersal ability in the trait analysis (Appendix S2e).

Statistical analyses

We fitted a phylogenetic generalized least squares model (Appendix S2f) with normally distributed errors using function *ppls* in R package *caper* (Orme *et al.*, 2013). The dependent variable was the percentage error of downscaling

predictions at the 1 km² grain. In the global model, predictor variables were the dispersal ability (measured as the upper quartile of dispersal distances), habitat breadth, range change and distribution type. Residuals of the model were improved by log₁₀ transformation of dispersal ability. Models were ranked by Akaike information criterion with a small sample size correction (AIC_c) using the function *dredge* in R package *MuMIn* (Barton, 2013). Models with Δ(AIC_c difference) < 4 were selected, and weighted model averaging across this subset of models was used to estimate the parameters (Burnham & Anderson, 2002). Standardized model parameter estimates were used to compare effect sizes between traits. We tested for collinearity between predictor variables using both correlation coefficients between pairs of predictors and variance inflation factors (Appendix S3b), but found collinearity was not sufficient to warrant exclusion of predictors from the global model. All statistical analyses were performed in R version 2.15.1 (R Development Core Team, 2012).

RESULTS

Observed OARs generally became shallower at the finest grains, resulting in a concave or sigmoidal OAR for many of the 38 Odonata species. The Hui model predictions were also of this shape (Fig. 2). The Hui and Power Law models were the only models biased towards over-prediction of occupancy (see Fig. 2; Appendix S3b), as indicated by the positive median value of percentage errors (Fig. 3). All other models tended to under-predict occupancy. This was particularly severe for the Poisson model, which systematically under-predicted occupancy at all predicted grains for all species (Fig. 3). The Hui model had the highest peak in percentage errors surrounding zero, followed by the Nachman and Power Law models. The Hui model also had a lower range of percentage errors (141.6) than either the Nachman (151.3) or Power Law (210.2) models (Fig. 3). Half the Hui model

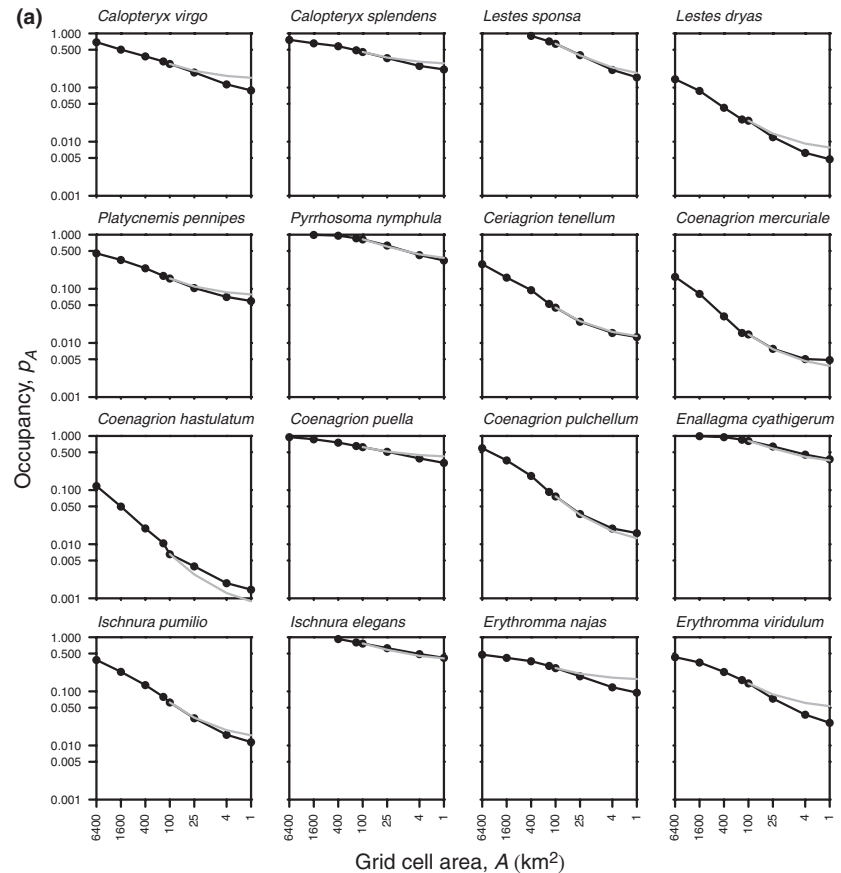


Figure 2 Hui model downscaling predictions for (a) 14 species of British Zygoptera (damselflies) and (b) 24 species of British Anisoptera (dragonflies). The Hui model gave the best overall predictions of the ten downscaling models tested. Black lines and points are the observed occupancies at each spatial grain. Grey lines are the Hui downscaling predictions at the 25, 4 and 1 km² grains.

predictions were within 16.6% of the observed occupancy (Table 1): the next two best models were the Nachman and Power Law, with comparable figures of 19.5% and 25.2%, respectively. The Hui model had the lowest median absolute percentage error across species and gave the best predictions for 14 of the 38 species (Fig. 4; Table 1). The Hui model was never worse than the seventh best model for any species. The relative performance of the Hui model was retained when only predictions at the finest grain were considered; at the 1 km² grain, the Hui model gave the best predictions for 15 of the 38 species, with 50% of predictions within 36.2% of observed occupancy. By comparison, the Nachman model gave the best predictions for 10 species at the 1 km² grain with 50% of predictions within 41.1% of observed occupancy, and the Power Law model was best for 5 of the 38 species with 50% of predictions within 42.6% of observed occupancy.

The percentage errors of Hui model downscaling predictions at the 1 km² grain were used to investigate species-level trait correlates of downscaling predictive accuracy. The estimate of lambda from the phylogenetically controlled analysis was zero, implying no tendency for closely related species to have similar downscaling error at the 1 km² grain. Therefore, we proceeded with model averaging of linear models. The top three models, ranked by AIC_c, explained between 0.590 and 0.596 of the variation in downscaling predictions among species (Table 2). Distribution type and dispersal ability were

the most important predictors of Hui model downscaling error and were present in all three models with $\Delta\text{AIC}_c < 4$ (Table 2). Percentage error for species with local-aggregated distributions, local-sparse distributions and widespread distributions was, on average, 35.6, 52.8 and 36.8 lower than climatic range limited species, respectively. The 95% confidence intervals of the parameter estimates for these three distribution types did not incorporate zero (Fig. 5). A unit increase in a species' log₁₀ dispersal ability increased percentage error of downscaling predictions by, on average, 89.8 (see Appendix S3b). The 95% confidence intervals for the dispersal ability parameter estimate did not incorporate zero (Fig. 5). Habitat breadth was present in two of the four best models and had lower relative importance in predicting downscaling error. Range change was present in one of the top three ranked models (Table 2), increasing the amount of variation in error explained by less than one per cent. There was a weak positive effect of range change on the percentage error of downscaling predictions but the 95% confidence intervals for this parameter incorporated zero. Habitat breadth had the lowest relative importance, and the effect size was close to zero (Table 2; Fig. 5).

DISCUSSION

Our comparison of methods for downscaling coarse-grain atlas data has produced four notable results. First, we have

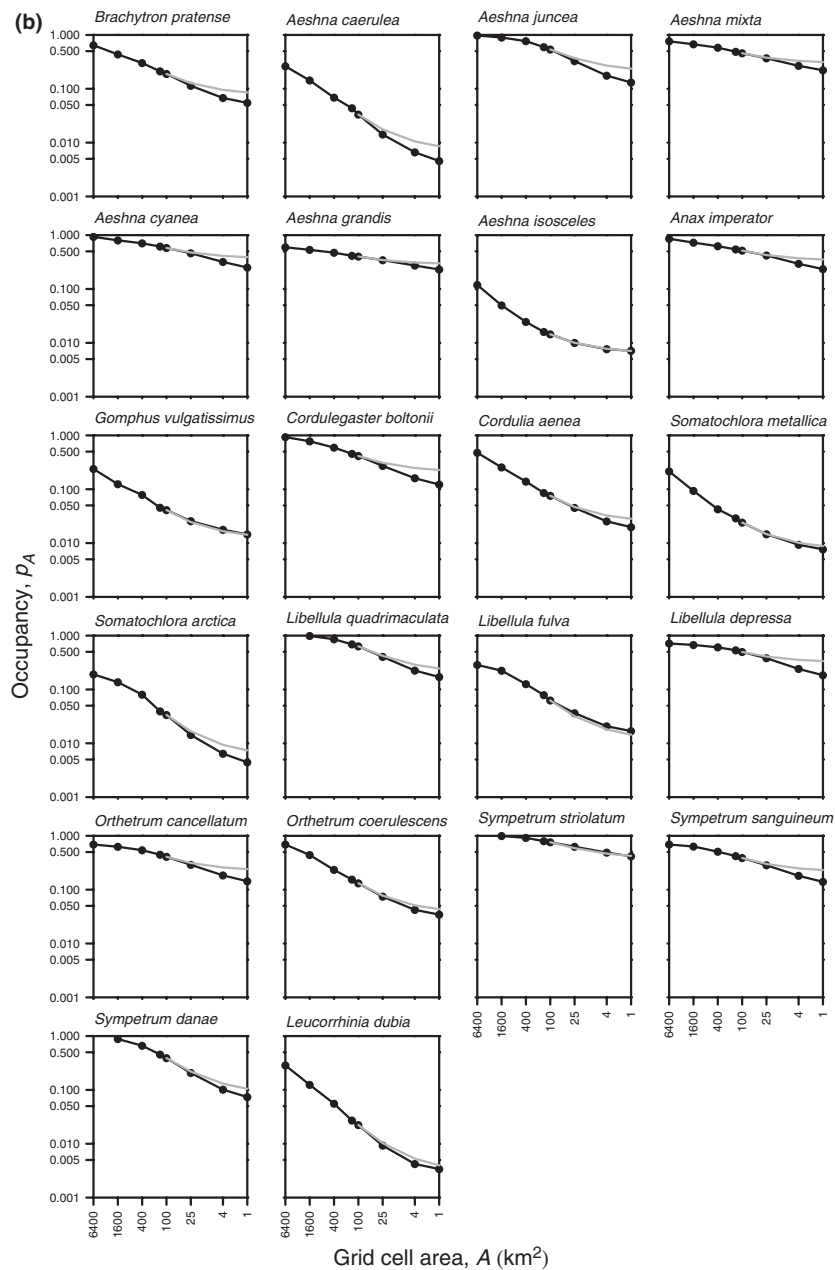


Figure 2 (Continued).

observed sigmoidal OARs for many of the 38 species, a shape that has not previously been reported. Second, extrapolating the OAR across two orders of magnitude delivers sensible estimates of fine-grain occupancy, even for highly mobile insects. Third, the Hui model outperforms nine other downscaling models. Finally, we have shown that downscaling accuracy varies systematically with species traits in Odonata. These findings have several implications, and applications for how distributional data are used across scales.

The two-parameter Hui model outperforms nine other downscaling models, three of which have an additional parameter. Moreover, it requires data at only one spatial grain. The Hui model has previously given accurate predictions of occupancy for *Drosophila* species in a mesocosm

experiment (Hui *et al.*, 2006) and predictions of the regional-scale abundance of southern African bird species (Hui *et al.*, 2009).

The success of the Hui model reflects that it is the only model tested here to predict an OAR with a slope that becomes shallower at finer grains. The OAR is typically convex at coarse grains for widespread species (approaching saturation), and it is this combination of convex at coarse grains and concave at fine grains that generates the overall sigmoidal relationship. This property indicates that individuals are most aggregated at the finest grain (i.e. 1 km^2), perhaps reflecting the characteristic grain of British wetlands and the dependence of Odonata on freshwater for reproduction. The fragmented pattern of freshwater bodies in the

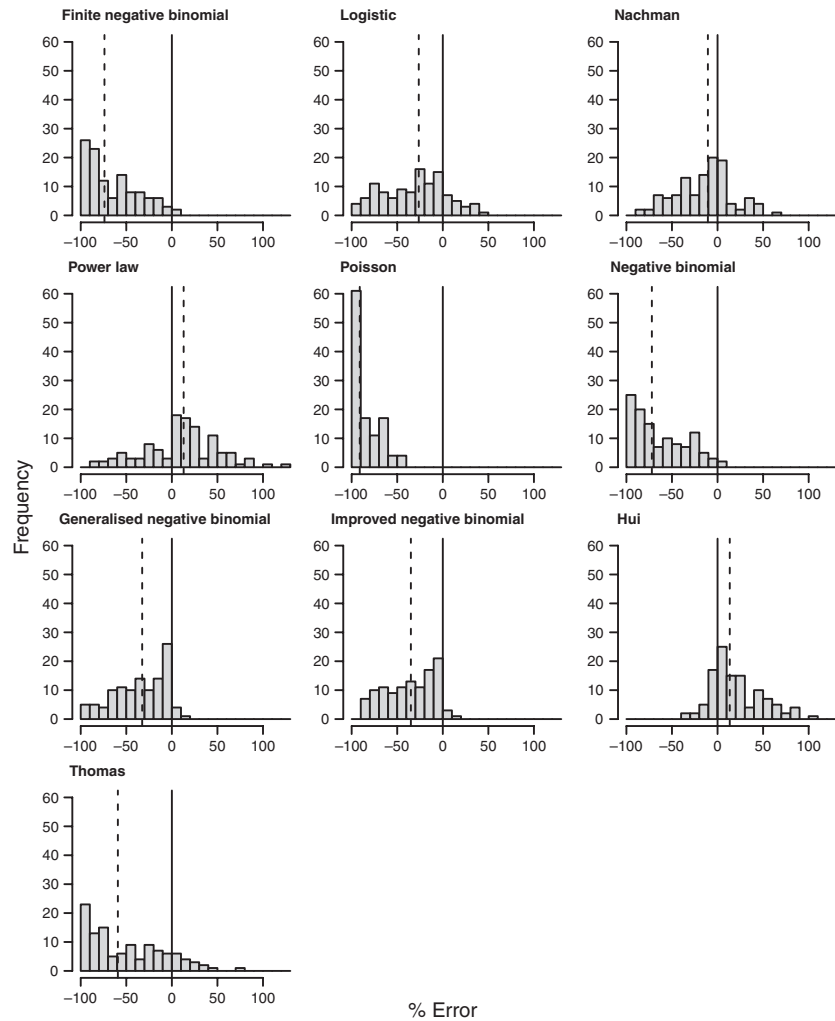


Figure. 3 Distribution of errors in downscaling predictions for 114 species: grain combinations. Percentage errors are calculated as $\frac{p_{A,i}^{\text{pred}} - p_{A,i}^{\text{ob}}}{p_{A,i}^{\text{ob}}} \cdot 100$, where $p_{A,i}^{\text{ob}}$ and $p_{A,i}^{\text{pred}}$ are the observed and predicted occupancies at grain A for species i . The percentage errors for 114 species: grain combinations are binned into intervals of 10. Vertical solid lines represent zero error in downscaling predictions. Vertical dashed lines are the median % errors. See Table 1 for a summary of comparative model performance.

landscape would also explain the steeper slope of the OAR at intermediate grains. Observed OARs for Barro Colorado Island tree species (He & Condit, 2007), Alaskan tree species (Lennon *et al.*, 2002) and British plant species (Kunin, 1998) do not consistently show the sigmoidal patterns seen here for British Odonata. However, successful predictions for Odonata do not imply that the Hui model is constrained to produce sigmoidal OARs. It will be important to investigate the generality of a sigmoidal OAR (and, therefore, the generality of the Hui model's success) among taxa without strong habitat associations.

Variation in the shape of the OAR between studies and taxa (and variation in model performance) could also reflect the window of scales through which the OAR is viewed. Dispersal, biotic interactions, disturbances and habitat availability affect the intensity of intraspecific aggregation (and therefore the slope of the OAR) at characteristic scales (Hortal *et al.*, 2010; Procheş *et al.*, 2010). It is possible that the range of scales used in this study and those in Kunin (1998), He & Condit (2007) and Lennon *et al.* (2002) are not sufficiently broad to capture the full range of variation in the slope of the OAR. Our results suggest that the shape of the

OAR may be more complex when viewed across the full range of scales. This mirrors the development of theory describing the slope of the SAR. Crawley and Harral (2001) observed multiple phases of increase and plateau in the species–area relationship (SAR) for vascular plants from 0.01 m² to 110 ha. More recently, the assumed shape of the SAR has shifted from power law to triphasic (Drakare *et al.*, 2006; Sizing *et al.*, 2011; Storch *et al.*, 2012), while the assumed shape of the OAR has developed from linear (reflecting a fractal distribution across scales: Kunin, 1998) to concave down (reflecting saturation in a finite study area: Azele *et al.*, 2012) to sigmoidal (this study). The theory of OAR and SAR is not merely developing in parallel; the two patterns are linked, conceptually (McGill, 2010b). Summing species' occupancies at each grain provides an estimate of the mean number of species for a given area (Sizing & Storch, 2007). By varying the area, we therefore obtain the SAR and may be able to infer properties of the SAR from the OAR.

The shape of the predicted OAR depends on each model's depiction of intraspecific aggregation. Spatial structure can be incorporated into OAR models in spatially implicit way

Table 2 Model selection. Three models selected from 16 candidate linear models quantifying the effects of species-level traits of British Odonata on the percentage error of downscaling predictions.

	Model rank			Importance
	1	2	3	
Distribution type	•	•	•	1
Log ₁₀ UQ dispersal ability (km)	•	•	•	1
Range change (1970–2012)		•		0.188
Habitat breadth			•	0.147
R ²	0.590	0.596	0.590	–
DF	6	7	7	–
AIC _c	358.637	361.170	361.660	–
ΔAIC _c	0	2.533	3.024	–
Akaike weight	0.666	0.188	0.147	–

The global model was Percentage Error ~ Distribution type + log₁₀ UQ dispersal ability + Habitat breadth + Range change. Dispersal ability is measured as the upper quartile (UQ) of all distances (km) to newly colonized cells between 1990 and 2012. The symbol • denotes the variables in each candidate model. Models were ranked by AIC_c scores, which applies a correction for small sample sizes to the AIC. R² is the amount of variation explained by each model and DF is the number of degrees of freedom. ΔAIC_c is the difference in AIC_c scores between models. Models with ΔAIC_c < 4 were selected for weighted model averaging. Akaike weight is the relative likelihood of each model within the subset of models selected. Importance is the relative importance of predictor variables and is the sum of Akaike weights across all models including that predictor.

(describing spatial variance only) or a spatially explicit way (e.g. pair correlation functions) (Wiens, 2000; Hui & McGeoch, 2007; Hui *et al.*, 2010; McGill, 2011). Spatially explicit information has been identified as a key property improving the predictions of several biodiversity patterns (Hui *et al.*, 2006; Morlon *et al.*, 2008; Conlisk *et al.*, 2009; Hui, 2009). Our results are consistent with this trend: the Hui model is the only one of our candidate models to incorporate information about the relative positions of occupied cells. In fact, the downscaling formula for the Thomas model, as derived in Azaele *et al.* (2012), can incorporate spatially explicit information, like the Hui model, but here was implemented without using such information. When including spatially explicit information, for example, by calculating the correlation function, the model might be expected to deliver downscaling predictions that are comparable with the Hui model. A second property of the Hui model likely to be associated with its predictive accuracy is the assumption that intraspecific aggregation is strongest at the finest spatial grains and approaches random at coarse grains, while spatially implicit models typically predict the reverse (Hui *et al.*, 2006). Empirical evidence is generally consistent with the assumptions of the Hui model (Hartley *et al.*, 2004; Wiegand *et al.*, 2007; Procheş *et al.*, 2010). The shape of the OARs we observed indicates that Odonata species are generally more

aggregated at fine grains (higher occupancy) than are assumed by the other downscaling models, all of which consistently under-predict fine-grain occupancy (with the exception of the Power Law). The poorer predictions for range limited species are also consistent with the Hui model assumption of weaker aggregation at coarse grains. Climatic range limits represent strong intraspecific aggregation at the coarsest scales, thus violating one of the assumptions of the Hui model (Hui *et al.*, 2006).

While the predictive accuracy of downscaling models is encouraging, there are a number of ways in which our results can inform downscaling improvements.

All downscaling models, as fitted here, do not incorporate environmental information from the study region. Although the Hui model uses spatially explicit information, its predictions are spatially implicit. A potentially useful approach to improving downscaling predictions would be to integrate the concepts used in species distribution modelling (SDM) with downscaling models. The incorporation of climatic or habitat correlates would surely improve the errors associated with Hui model predictions for species with a climatic range limit. Moreover, SDMs would allow us to predict where occupied cells are likely to be. There have been previous attempts to downscale SDMs with varying success (Araújo *et al.*, 2005; McPherson *et al.*, 2006; Niamir *et al.*, 2011), but only one method has attempted to incorporate the spatial structure captured by the OAR (Keil *et al.*, 2012). The reverse approach, of integrating SDMs into downscaling models, has not been attempted, but offers great potential for deriving accurate predictions that are both fine-grain and spatially explicit.

The accuracy of downscaling models is crucial to a range of applications including monitoring of range change at multiple spatial scales. The slope of the OAR contains information about recent range expansion and contraction (Wilson *et al.*, 2004; Pocock *et al.*, 2006; Hui, 2011). Moreover, time-slicing occurrence data and constructing the OAR for two or more time periods would predict changes in occupancy at multiple scales. Our results also suggest that downscaling may be a promising tool for estimating abundance over spatial extents that are too large to sample using traditional methods. If accurate downscaling can be achieved at sufficiently fine grains that each occupied cell contains just one individual, then downscaling methods can be used to predict national-scale abundance (Kunin, 1998) and to link population dynamics across scales. However, scaling discontinuities (poor correlations between occupancy at neighbouring spatial grains) have been identified at the grain of human land use and may present an obstacle to downscaling to abundance (Hartley *et al.*, 2004; Webb *et al.*, 2007). Our OARs do not extend to sufficiently fine grains to confirm whether the same scaling discontinuity can be seen within the Odonata. A useful exercise would be to investigate the degree of correlation between fine-grain occupancy predictions and mean local abundance. If this is sufficiently accurate, downscaling could provide a proxy for multisite monitoring of populations.

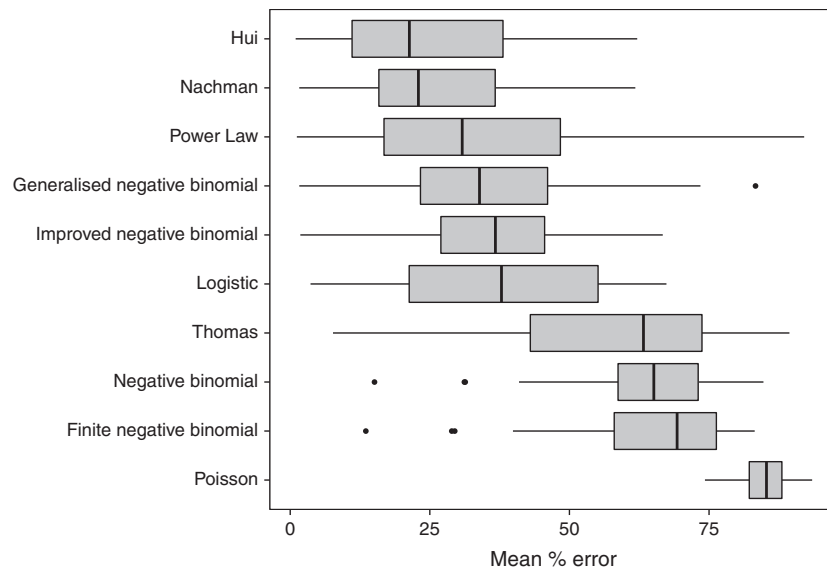


Figure 4 Predictive performance of ten downscaling models for 38 British Odonata species. Each boxplot represents the distribution of mean absolute percentage errors in predictions at 25, 4 and 1 km² for 38 species. Mean absolute percentage errors for each species are calculated as $\frac{1}{n} \sum_{A=1}^n \frac{|p_{A,i}^{\text{pred}} - p_{A,i}^{\text{ob}}|}{p_{A,i}^{\text{ob}}} \cdot 100$, where $p_{A,i}^{\text{pred}}$ and $p_{A,i}^{\text{ob}}$ are the predicted and observed occupancy at grain A for species i and n is the number of spatial grains for which there are predictions ($n = 3$). The solid line in the centre of the boxes is the median % error, and the box is the interquartile range (25th and 75th percentiles). The solid lines are the range of the data, and the black points are outliers. Models are ordered by the number of species for which they gave the best overall predictions (Table 1).

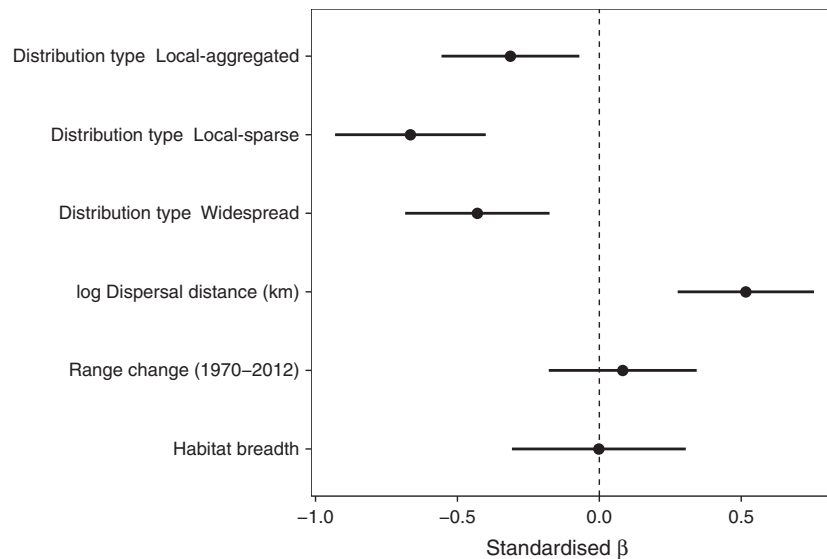


Figure 5 Relative effect sizes of species-level traits on the percentage error of Hui model downscaling predictions. Standardized β is the standardized parameter estimate derived from weighted model averaging across three linear models with $\Delta\text{AIC}_c < 4$. Each variable is rescaled to a mean of 0 and a standard deviation of one for comparison of effect sizes among traits. The reference group for distribution type is climatic range limit, which has a standardized parameter estimate of zero. The percentage error of downscaling predictions was significantly lower for the three distribution types shown than for the species with a climatic range limit. Error bars are the 95% confidence intervals of the mean of the standardized parameter estimates.

While the DRN records are among the richest available datasets for exploring the OAR over two orders of magnitude, it is worth reflecting on the imperfections in these data. In particular, we have assumed that a single record

within a 1 km² grid cell reflects evidence that other species are absent. This is probably not the case at 100 km², which is the scale at which species atlases are traditionally published (BDS will publish a new atlas in 2014). In reality,

grid cells differ markedly in sampling intensity, and our estimates of occupancy for most species are likely to be systematically under-estimated at the finest grain. It follows that we have over-estimated the performance of eight underpredicting models and under-estimated the downscaling accuracy of the Hui model, which was our best performing model overall and over-predicted at the finest scales (Fig. 2; Fig. 3).

We tested four hypotheses about interspecific variation in the predictive accuracy of downscaling models: collectively, these traits explained more than half the observed variation. In particular, dispersal ability and distribution type may be of use for identifying species for which downscaling predictions are unlikely to be successful. Species with a range limit in Britain were less well predicted than other distribution types. Climatic range limits reflect coarse-scale environmental heterogeneity. In fact, no downscaling model is currently equipped to incorporate information about environmental heterogeneity. The Hui model assumes that intraspecific aggregation becomes weaker at coarse grains, therefore range limited species violate one of the assumptions of the Hui model (Hui *et al.*, 2006). A climatic range limit also generates species OARs that approach the scale of endemism (as defined in Fig. 1), which contains little information for the purposes of downscaling. One way to address this would be to calculate the Hui parameters, P_+ and $Q_{+/+}$, while excluding cells outside of the range margin, thereby avoiding the portion of the OAR that approaches the scale of endemism. Downscaling predictions were more successful for species with limited dispersal abilities and relatively poor for the most mobile species. One reason could be that mobility reduces aggregation at the finer scales, thus violating the Hui model assumption that spatial structure is strongest at fine-spatial grains. Alternatively, dispersive species experience higher rates of population turnover (Simmons & Thomas, 2004; Pöyry *et al.*, 2009; Hill *et al.*, 2011; Hof *et al.*, 2012; Jaeschke *et al.*, 2013) and vagrancy (individuals recorded during migration between suitable habitat patches), such that records collated over many years overestimate the average number of occupied fine-grain cells in any 1 year. Like many of the predictions that emerge from macroecological theory, we assumed the data are static and do not incorporate temporal dynamics (Fisher *et al.*, 2010; White *et al.*, 2010).

Describing species' spatial structure is central to understanding and linking biodiversity patterns and informing our conservation efforts, but atlas data are typically too coarse to address these issues effectively. We have demonstrated that downscaling models can provide accurate estimates of fine-grain occupancy for highly mobile insects, observed a sigmoidal OAR for many species and found the Hui model to provide the most accurate downscaling estimates. In doing so, we have identified some properties that explain the success and failure of downscaling models and which will contribute to their development and future application to a range of theoretical and conservation issues.

ACKNOWLEDGEMENTS

We thank Stephen Freeman and Cang Hui for help with fitting downscaling models and Steve Brooks, Chris Hassall and the British Dragonfly Society for sharing their natural history expertise. We are grateful to Gary Powney and Phil Martin for useful discussions and Steve Sait, Petr Keil and two anonymous reviewers for helpful comments on the manuscript. LB is funded by a NERC studentship, and SA and WEK are supported by the EU SCALES project.

REFERENCES

- Araújo, M.B., Thuiller, W., Williams, P.H. & Reginster, I. (2005) Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography*, **14**, 17–30.
- Azaele, S., Cornell, S.J. & Kunin, W.E. (2012) Downscaling species occupancy from coarse spatial scales. *Ecological Applications*, **22**, 1004–1014.
- Barton, K. (2013) MuMIn: Multi-model inference. R package version 1.9.13. <http://CRAN.R-project.org/package=MuMIn>
- Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., Dengler, J., Fritz, S.A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Krefl, H., Schneider, A.-K., Winter, M. & Dormann, C.F. (2012) What's on the horizon for macroecology? *Ecography*, **35**, 673–683.
- Boitani, L., Maiorano, L., Baisero, D., Falcucci, A., Visconti, P. & Rondinini, C. (2011) What spatial data do we need to develop global mammal conservation strategies? *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, **366**, 2623–2632.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A practical Information-Theoretic Approach*. Springer, New York.
- Conlisk, E., Conlisk, J., Enquist, B., Thompson, J. & Harte, J. (2009) Improved abundance prediction from presence-absence data. *Global Ecology and Biogeography*, **18**, 1–10.
- Cowley, M.J.R., Thomas, C.D., Wilson, R.J., Gutiérrez, D. & Bulman, C.R. (2001) Density – distribution relationships in British butterflies. II. An assessment of mechanisms. *Journal of Animal Ecology*, **70**, 426–441.
- Crawley, M.J. & Harral, J.E. (2001) Scale dependence in plant biodiversity. *Science*, **291**, 864–868.
- Development Core Team, R. (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Drakare, S., Lennon, J.J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters*, **9**, 215–227.
- Fisher, J.A.D., Frank, K.T. & Leggett, W.C. (2010) Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography*, **19**, 1–15.
- Fitt, R. (2013) Range expansion under climate change in UK Odonata. MSc Thesis, University of York, York, UK.

- Gaston, K.J. & He, F. (2011) Species occurrence and occupancy. *Biological Diversity: Frontiers in Measurement and Assessment* (ed. by A.E. Magurran and B.J. McGill), pp. 141–151. Oxford University Press, New York.
- Green, J.L. & Plotkin, J.B. (2007) A statistical theory for sampling species abundances. *Ecology Letters*, **10**, 1037–1045.
- Green, J.L., Harte, J. & Ostling, A. (2003) Species richness, endemism, and abundance patterns: tests of two fractal models in a serpentine grassland. *Ecology Letters*, **6**, 919–928.
- Hanski, I. & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, **275**, 397–400.
- Hartley, S. & Kunin, W.E. (2003) Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology*, **17**, 1559–1570.
- Hartley, S., Kunin, W.E., Lennon, J.J. & Pocock, M.J.O. (2004) Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society of London B*, **271**, 81–88.
- He, F. & Condit, R. (2007) The distribution of species: occupancy, scale, and rarity. *Scaling Biodiversity* (ed. by D. Storch, P.A. Marquet and J.H. Brown), pp. 32–50. Cambridge University Press, New York.
- He, F. & Gaston, K.J. (2000) Estimating species abundance from occurrence. *American Naturalist*, **156**, 553–559.
- He, F. & Gaston, K.J. (2003) Occupancy, spatial variance, and the abundance of species. *American Naturalist*, **162**, 366–375.
- He, F., Gaston, K.J. & Wu, J. (2002) On species occupancy-abundance models. *Ecoscience*, **9**, 119–126.
- Hill, J.K., Griffiths, H.M. & Thomas, C.D. (2011) Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, **56**, 143–159.
- Hof, C., Brändle, M., Dehling, D.M., Munguía, M., Brandl, R., Araújo, M.B. & Rahbek, C. (2012) Habitat stability affects dispersal and the ability to track climate change. *Biology Letters*, **8**, 639–643.
- Hortal, J., Roura-Pascual, N., Sanders, N.J. & Rahbek, C. (2010) Understanding (insect) species distributions across spatial scales. *Ecography*, **33**, 51–53.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Oxford.
- Hui, C. (2009) On the scaling patterns of species spatial distribution and association. *Journal of Theoretical Biology*, **261**, 481–487.
- Hui, C. (2011) Forecasting population trend from the scaling pattern of occupancy. *Ecological Modelling*, **222**, 442–446.
- Hui, C. & McGeoch, M.A. (2007) Capturing the “droopy-tail” in the occupancy-abundance relationship. *Ecoscience*, **14**, 103–108.
- Hui, C., McGeoch, M.A. & Warren, M. (2006) A spatially explicit approach to estimating species occupancy and spatial correlation. *Journal of Animal Ecology*, **75**, 140–147.
- Hui, C., McGeoch, M.A., Reyers, B., le Roux, P.C., Greve, M. & Chown, S.L. (2009) Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecological Applications*, **19**, 2038–2048.
- Hui, C., Veldtman, R. & McGeoch, M.A. (2010) Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, **33**, 95–102.
- Jaeschke, A., Bittner, T., Reineking, B. & Beierkuhnlein, C. (2013) Can they keep up with climate change? - Integrating species specific dispersal abilities of protected Odonata in species distribution modelling. *Insect Conservation and Diversity*, **6**, 93–103.
- Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology & Evolution*, **27**, 151–159.
- Keil, P., Belmaker, J., Wilson, A.M., Unitt, P. & Jetz, W. (2012) Downscaling of species distribution models: a hierarchical approach. *Methods in Ecology and Evolution*, **4**, 82–94.
- Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., Jones, K.E., Price, T., Redding, D.W., Owens, I.P.F. & Isaac, N.J.B. (2012) What is macroecology? *Biology Letters*, **8**, 904–906.
- Kunin, W.E. (1998) Extrapolating species abundance across spatial scales. *Science*, **281**, 1513–1515.
- Kunin, W.E., Hartley, S. & Lennon, J.J. (2000) Scaling Down : on the challenge of estimating abundance from occurrence patterns. *American Naturalist*, **156**, 560–566.
- Lennon, J.J., Kunin, W.E. & Hartley, S. (2002) Fractal species distributions do not produce power-law species-area relationships. *Oikos*, **97**, 378–386.
- Lennon, J.J., Kunin, W.E., Hartley, S. & Gaston, K.J. (2007) Species distribution patterns, diversity scaling and testing for fractals in southern African birds. *Scaling Biodiversity* (ed. by D. Storch, P.A. Marquet and J.H. Brown), pp. 32–50. Cambridge University Press, Cambridge.
- Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**, 1424–1442.
- McGill, B.J. (2010a) Matters of scale. *Science*, **328**, 575–576.
- McGill, B.J. (2010b) Towards a unification of unified theories of biodiversity. *Ecology Letters*, **13**, 627–642.
- McGill, B.J. (2011) Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany*, **98**, 481–502.
- McGill, B.J. & Nekola, J.C. (2010) Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. *Oikos*, **119**, 591–603.
- McPherson, J., Jetz, W. & Rogers, D. (2006) Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions—possibilities and limitations. *Ecological Modelling*, **192**, 499–522.
- Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. & Green, J.L. (2008) A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, **11**, 904–917.
- Nachman, G. (1981) A mathematical model of the functional relationship between density and spatial distribution of a population. *Journal of Animal Ecology*, **50**, 453–460.

- Niamir, A., Skidmore, A.K., Toxopeus, A.G., Muñoz, A.R. & Real, R. (2011) Finessing atlas data for species distribution models. *Diversity and Distributions*, **17**, 1173–1185.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. & Pearce, W. (2013) The caper package: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. <http://CRAN.R-project.org/package=caper>
- Pocock, M.J.O., Hartley, S., Telfer, M.G., Preston, C.D. & Kunin, W.E. (2006) Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology*, **94**, 581–596.
- Powney, G., Brooks, S., Barwell, L., Bowles, P., Fitt, R., Pavitt, A., Spriggs, R. & Isaac, N. (2014) Morphological and geographical traits of the British Odonata. *Biodiversity Data Journal*, **2**, e1041.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saari- nen, K. (2009) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**, 732–743.
- Procheş, Ş., Warren, M., McGeoch, M.A. & Marshall, D.J. (2010) Spatial scaling and transition in pneumatophore arthropod communities. *Ecography*, **33**, 128–136.
- Robertson, M.P., Cumming, G.S. & Erasmus, B.F.N. (2010) Getting the most out of atlas data. *Diversity and Distributions*, **16**, 363–375.
- Roy, H.E., Adriaens, T., Isaac, N.J.B., Kenis, M., Onkelinx, T., Martin, G.S., Brown, P.M.J., Hautier, L., Poland, R., Roy, D.B., Comont, R., Eschen, R., Frost, R., Zindel, R., Van Vlaenderen, J., Nedvěd, O., Ravn, H.P., Grégoire, J.-C., de Biseau, J.-C. & Maes, D. (2012) Invasive alien predator causes rapid declines of native European lady- birds. *Diversity and Distributions*, **18**, 717–725.
- Simmons, A.D. & Thomas, C.D. (2004) Changes in dispersal during species' range expansions. *American Naturalist*, **164**, 378–395.
- Sizling, A.L. & Storch, D. (2007) Geometry of species distribu- tions: random clustering and scale invariance. *Scaling Biodi- versity* (ed. by D. Storch, P.A. Marquet and J.H. Brown), pp. 77–99. Cambridge University Press, Cambridge.
- Sizling, A.L., Kunin, W.E., Sizlingová, E., Reif, J. & Storch, D. (2011) Between geometry and biology: the problem of universality of the species-area relationship. *American Nat- uralist*, **178**, 602–611.
- Storch, D., Sizling, A.L., Reif, J., Polechova, J., Sizlingova, E. & Gaston, K.J. (2008) The quest for a null model for mac- roecological patterns: geometry of species distributions at multiple spatial scales. *Ecology Letters*, **11**, 771–784.
- Storch, D., Keil, P. & Jetz, W. (2012) Universal species-area and endemics-area relationships at continental scales. *Nature*, **488**, 78–83.
- Szabo, J.K., Vesk, P.A., Baxter, P.W.J. & Possingham, H.P. (2010) Regional avian species declines estimated from vol- unteer-collected long-term data using List Length Analysis. *Ecological Applications*, **20**, 2157–2169.
- Tosh, C.A., Reyers, B. & Van Jaarsveld, A.S. (2004) Estimat- ing the abundances of large herbivores in the Kruger National Park using presence-absence data. *Animal Conser- vation*, **7**, 55–61.
- Van Strien, A.J., Termaat, T., Kalkman, V., Prins, M., Knijf, G., Gourmand, A.-L., Houard, X., Nelson, B., Plate, C., Prentice, S., Regan, E., Smallshire, D., Vanappelghem, C. & Vanreusel, W. (2013) Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly *Calopteryx splendens*. *Biodiversity and Conservation*, **22**, 673–686.
- Veldtman, R., Chown, S.L. & McGeoch, M.A. (2010) Using scale-area curves to quantify the distribution, abundance and range expansion potential of an invasive species. *Diver- sity and Distributions*, **16**, 159–169.
- Webb, T.J., Noble, D. & Freckleton, R.P. (2007) Abundance- occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *Journal of Animal Ecology*, **76**, 123–134.
- White, E.P., Ernest, S.K.M., Adler, P.B., Hurlbert, A.H. & Lyons, S.K. (2010) Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society of London - Series B: Bio- logical Sciences*, **365**, 3633–3643.
- Wiegand, T., Gunatilleke Savitri, C.V., Gunatilleke Nimal, I.A.U. & Huth, A. (2007) How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Sciences USA*, **104**, 19029–19033.
- Wiens, J.A. (2000) Ecological heterogeneity: an ontogeny of concepts and approaches. *The Ecological Consequences of Heterogeneity* (ed. by M.J. Hutchings, E.A. John and A.J.A. Stewart), pp. 9–31. Blackwell Science, Oxford.
- Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.
- Wolfram Research, Inc. (2012) *Mathematica Student Edition. Version 9.0*. Wolfram Research Inc. Champaign, Illinois, USA.
- Wright, D.H. (1991) Correlations between incidence and abundance are expected by chance. *Journal of Biogeography*, **18**, 463.
- Zillio, T. & He, F. (2010) Modeling spatial aggregation of finite populations. *Ecology*, **91**, 3698–3706.

SUPPORTING INFORMATION

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

Appendix S1 Resident British Odonata species included in analysis.

Appendix S2 Supplementary Methods.

Appendix S3 Supplementary Results.

BIOSKETCH

Louise Barwell is a PhD student in the Biological Records Centre at the NERC Centre for Ecology and Hydrology and

the University of Leeds (UK). Her thesis uses national-scale atlas data and local monitoring scheme data to explore methods of describing and predicting spatial patterns of insect biodiversity, how these patterns change with spatial scale and how these methods can be applied for the monitoring and conservation of insect biodiversity.

Author contributions: N.J.B.I. and W.E.K. conceived the ideas and supervised the research. N.J.B.I. and L.B. developed

the methods. L.B. implemented the study and analysed the results. S.A. provided code for and advised on model fitting. L.B. wrote the manuscript, with contributions from other authors.

Editor: David Richardson