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

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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.

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; Veldman 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; Veldman 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 Pasoh, Malaysia (Hui et al., 2006), 824 tree species in 0.5 km² tropical rainforest plot in Pasoh, Malaysia (Hui & 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 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-

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_o. 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 downsampling. Occupancy cannot fall within the shaded grey area, which represents the region where occupancy < A/A_o and equates to a species occurring in less than one cell in the study region.

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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 (≥ 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 Azaele et al., 2012). The term Thomas model, as used here, refers to the downsampling formula in Appendix S2c, rather than the spatially explicit Thomas point process from which it was derived by Azaele et al. (2012). We parameterized these models using occupancy at five coarse-spatial grains (100, 144, 400, 1600 and 6400 km22) (Appendix S2c). Saturated grains contain no information for downsampling purposes (Fig. 1). For seven widespread species, the OAR was saturated (i.e. reached 100% occupancy) at the coarsest (Enallagma cyathigerum, Sympetrum striolatum, Pyrrhosoma nympha, Libellula quadrimaculata and Sympetrum danae) or two coarsest (Lestes sponsa, Ischnura 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, Qii, (an index of spatial aggregation). Bayes’ theorem can be used to express all conditional probabilities of occupancy in terms of P+, Qii, 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 km22 grains. Model predictions were obtained at three grains (25, 4 and 1 km22) 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 |pred − obs|/obs, where Ppred and Pobs 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 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 km22 (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 et al., 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 et al., 2012)      |
| Finite negative binomial      | 2        | 1    | 73.946 | 0.835    | 97.591  | (Zilio & He, 2010)         |
| Generalized negative binomial | 3        | 0    | 32.561 | 0.209    | 99.515  | (He et al., 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, \( \frac{|\text{pred}_i - \text{obs}_i|}{\text{pred}_i} \times 100 \), where \( \text{pred}_i \) and \( \text{obs}_i \) are the predicted and observed occupancy at grain \( A \) for species \( i \).

Statistical analyses

We fitted a phylogenetic generalized least squares model (Appendix S2f) with normally distributed errors using function \( \text{pgls} \) in \( \text{R} \) package caper (Orme et al., 2013). The dependent variable was the percentage error of downscaling predictions at the 1 km\(^2\) 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 \( \log_{10} \) transformation of dispersal ability. Models were ranked by Akaike information criterion with a small sample size correction (AIC\(_c\)) using the function \( \text{dredge} \) in \( \text{R} \) package MuMIn (Barton, 2013). 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 \( \text{R} \) 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
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 AICc, 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 ΔAICc < 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
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 km²), 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
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; Prochêz 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; Sizling 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: Azaele 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 (Sizling & 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.

**Figure. 3** Distribution of errors in downscaling predictions for 114 species: grain combinations. Percentage errors are calculated as \( \frac{p_{\text{pred}} - p_{\text{obs}}}{p_{\text{obs}}} \times 100 \), where \( p_{\text{obs}} \) and \( p_{\text{pred}} \) 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.
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 of downscaling predictions.

| Model rank | 1 | 2 | 3 | Importance |
|------------|---|---|---|------------|
| Distribution type | ● | ● | ● | 1 |
| Log₁₀ UQ dispersal ability (km) | ● | ● | ● | 1 |
| Range change (1970–2012) | ● | | 0.188 |
| Habitat breadth | | ● | 0.147 |
| R² | 0.590 | 0.596 | 0.590 | − |
| DF | 6 | 7 | 7 | − |
| AICc | 358.637 | 361.170 | 361.660 | − |
| ΔAIC | 0 | 2.533 | 3.024 | − |
| Akaic 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 AICc 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. ΔAICc is the difference in AICc scores between models. Models with ΔAICc < 4 were selected for weighted model averaging. Akaic 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 Akaic weights across all models including that predictor.

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.
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,

**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 $1/n \sum_{i=1}^{n} \frac{|p_{A}^{\text{pred}} - p_{A}^{\text{obs}}|}{p_{A}^{\text{obs}}} \times 100$, where $p_{A}^{\text{pred}}$ and $p_{A}^{\text{obs}}$ 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 $\beta$ is the standardized parameter estimate derived from weighted model averaging across three linear models with $\text{AIC}_c < 4$. 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.
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 downsampling 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 downsampling 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 downsampling 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 downsampling 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 downsampling. One way to address this would be to calculate the Hui parameters, $P_s$ and $Q_{s+/+}$, while excluding cells outside of the range margin, thereby avoiding the portion of the OAR that approaches the scale of endemism. Downsampling 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 downsampling 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 downsampling estimates. In doing so, we have identified some properties that explain the success and failure of downsampling models and which will contribute to their development and future application to a range of theoretical and conservation issues.

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**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.

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