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Research

Effects of grain size and niche breadth on species distribution modeling

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Scale is a vital component to consider in ecological research, and spatial resolution or grain size is one of its key facets. Species distribution models (SDMs) are prime examples of ecological research in which grain size is an important component. Despite this, SDMs rarely explicitly examine the effects of varying the grain size of the predictors for species with different niche breadths. To investigate the effect of grain size and niche breadth on SDMs, we simulated four virtual species with different grain sizes/niche breadths using three environmental predictors (elevation, aspect, and percent forest) across two real landscapes of differing heterogeneity in predictor values. We aggregated these predictors to seven different grain sizes and modeled the distribution of each of our simulated species using MaxEnt and GLM techniques at each grain size. We examined model accuracy using the AUC statistic, Pearson's correlations of predicted suitability with the true suitability, and the binary area of presence determined from suitability above the maximum true skill statistic (TSS) threshold. Habitat specialists were more accurately modeled than generalist species, and the models constructed at the grain size from which a species was derived generally performed the best. The accuracy of models in the homogenous landscape deteriorated with increasing grain size to a greater degree than models in the heterogenous landscape. Variable effects on the model varied with grain size, with elevation increasing in importance as grain size increased while aspect lost importance. The area of predicted presence was drastically affected by grain size, with larger grain sizes over predicting this value by up to a factor of 14. Our results have implications for species distribution modeling and conservation planning, and we suggest more studies include analysis of grain size as part of their protocol.

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Introduction

Spatial scale has long been recognized as a vital component of ecological research, with complex effects that vary by species and system (Wiens 1989). Specifically, the grain of the sample and the extent of the study area are the components of spatial scale that must be defined in the research and management of an ecological phenomenon (Levin 1992). Spatial scale is important to consider in species distribution models (SDMs), an increasingly widely used suite of methods for both ecological research and conservation management. SDMs have been applied to a large range of taxa to estimate occurrence across landscapes and seascapes (see review in Guisan and Thuiller 2005, Leipold et al. 2017). They can aid in understanding of species–habitat relationships and delineating species distributions. They also have direct application to prioritizing areas for protection and can model future effects of land-use and climate change on species habitat and distributions (Porfirio et al. 2014). SDMs use environmental predictors combined with species presence and absence or background points to make these estimations (Elith and Leathwick 2009). Although building SDMs only requires predictor values at species presence and absence/background locations, making predictions about species occurrence across a landscape requires spatially explicit environmental predictors. The continuing improvement of remote sensing technology, such as light detection and ranging (LiDAR, Hudak et al. 2009) methods, has resulted in higher resolution environmental variables available to be included as predictors in SDMs.

Despite this increase in the variety of available data resolutions, research on the effect of grain size on SDMs is scant and usually limited to comparing three or fewer grain sizes (Guisan et al. 2007a, b, Revermann et al. 2012, Bean et al. 2014). There is also some uncertainty within the existing body of literature on the effects of increasing grain size of environmental predictors on SDMs. Guisan et al. (2007a, b) found that a 10-fold increase in grain size degraded the accuracy (as measured by AUC) of SDMs of some species, but did not result in large changes and in fact improved AUC in other species. Additional studies have found small effects of increasing grain size on SDMs of birds (Seoane et al. 2004), generally concluding that coarser grains capture the necessary habitat variation. A study of bird habitat occupancy in Germany found that grain size was important in model performance, however, with several species modeled with the highest AUC at a fine resolution of 1 m (Gottschalk et al. 2011). A recent investigation of marine predator habitat at six grain sizes ranging from 3 to 111 km found that finer resolution variables improved models unless data were missing due to cloud cover (Scales et al. 2017).

Effects of grain size on SDMs at a large spatial scale have also been investigated on plant species, with applications to climate change projections. Seo et al. (2009) analyzed the effect of increases in grain size (seven grains from 1 km to 64 km) on SDMs of several tree species in California, and found that AUC declined while the predicted area of occurrence increased. A similar relationship was identified by Trivedi et al. (2008) in a comparison of similar SDMs on plants under climate change. They concluded that coarse models in rugged terrain likely overestimate the ability of species to persist under climate change. Another recent study likewise found that total predicted area of presence was greater at coarser grain sizes (4 km vs 800 m data), but important potential climate refugia were detected at a 90-m grain that were lost at the 4-km grain size (Franklin et al. 2013).

This wide range in findings indicates a significant lack of consensus regarding the importance of grain size to SDMs. There is also a lack of research into the effects of grain size on models of species that utilize a narrow range of habitat conditions (specialists) vs species that utilize a wider range of habitat (generalists), and the effects of grain size on models of species in landscapes of varying heterogeneity. These questions are difficult to answer because the true habitat responses of any given species, and consequently the true suitability of an area to that species, cannot be known. Because of this, the simulation of virtual species across a landscape, using predefined responses to habitat variables, is increasingly being used to answer questions related to ecology and the modeling of species distributions. Examples of previous research using this technique include simulation of species to compare different SDM modeling techniques (Elith and Graham 2009), effects of prevalence and sampling bias on SDMs (Jimenez-Valverde et al. 2009), and effects of different methods for selecting pseudo-absences on SDMs (Barbet-Massin et al. 2012). To investigate the effects of grain size and niche breadth on SDMs, we adapted this simulation approach to model habitat suitability for a set of four virtual species across two landscapes of contrasting heterogeneity. We hypothesized that the best models would be built at the grain size at which the species was simulated (defined in methods, hereafter referred to as 'correct' grain size). We predicted that small changes in grain size (1 aggregation, or doubling of grain size, i.e. 25 to 50 m) would not have significant effects on model performance, but larger changes (2 aggregations or greater, i.e. 25 to 100 m or more) would significantly deteriorate model accuracy. We also hypothesized that changes in grain size would more greatly affect models of the narrow-niched (specialist) species as compared to the wide-niched (generalist) species.

Methods

We selected two landscapes of approximately 40 000 km^2 upon which to simulate our species. One encompasses the southeastern range of the Scandinavian Mountains in Norway and Sweden, while the other lies in southern Finland. We chose these areas because of the availability of environmental predictors with small grain size and large differences in variance of the included predictor variables between the two (one 'homogenous' landscape and one 'heterogeneous'

landscape). These predictor variables were elevation, aspect, and percent forest. In the heterogeneous landscape a random draw of 1 000 000 cells resulted in predictor values with standard deviations of 368.48, 109, and 33.96 for elevation, aspect, and percent forest, respectively, while the homogenous landscape had corresponding values of 34.03, 113.54, and 27.35. Additionally, all pair-wise combinations of these three variables had Pearson's correlation coefficient values of less than 0.3, suggesting that multi-collinearity was not an issue. (Dormann et al. 2013). The terrain model and a tree cover density raster, which we labeled percent forest for the simulation of our species, were obtained from the European Environment Agency's Copernicus Land Monitoring Service (DEM resolution = 25 m, tree cover density = 20 m, EU 2016). Elevation and aspect were derived from the EUDEM dataset, a digital elevation model produced by hybridizing data from the SRTM and GDEM missions through a weighted averaging approach. The tree cover density raster was resampled to 25-m resolution. We then aggregated the environmental variables to larger grain sizes by calculating the mean values within moving windows with sizes of 50, 100, 200, 400, 800, and 1600 m.

We created two virtual species whose environmental suitability and ultimately presence on the landscape depended on these three variables (Fig. 1). Suitability responses were kept to normal distributions over the range of each variable. These were then combined in a simple multiplicative formula to come to a final suitability response for the species: percent forest × elevation × aspect. We then rescaled suitability values for each pixel between 0 and 1 for a final reference probabilistic suitability map on which to later test models against. We created one species with a narrower range of suitability across each of the variables (hereafter referred to as specialist), and one species with a wider range (standard deviation of response distribution doubled) of suitability across each of these variables (hereafter referred to as generalist, Fig. 1). We built two species with each of these suitability responses, one from the environmental variables at a fine scale (grain size of 25 m) and the other from the environmental variables at a coarser scale (200 m). This was performed to investigate the effect of using grain sizes that are both smaller and larger than the 'correct' grain size at which a species responds. In the homogenous landscape, the suitable elevation values had to be decreased due to the large differences in elevation between the two landscapes, but otherwise the suitability responses were kept the same.

After calculating environmental suitability values for each species, we used a logistic curve of probability pivoting around a suitability threshold of 0.5 to generate presence and absence values throughout the study area. In this process, a cell with a suitability value of 0.7 is more likely to become a presence cell than a cell with a suitability value of 0.4, but the latter cell does have a chance to become a presence cell according to the probability derived from the logistic curve. We then randomly selected 2000 points across each landscape for both the generalist and specialist species to use as presence/absence data input for the SDMs, the results of which are summarized in Table 1.

We modeled species' distributions using two different methods across all grain sizes. These were maximum entropy (MaxEnt) (Phillips et al. 2006) and generalized linear modelling (GLM). Although MaxEnt has been argued to be equivalent to a Poisson point-process model and thus can be viewed as a type of regression (Renner and Warton 2013), these two techniques have been used extensively and produce distinct results (Elith and Graham 2009, Merow et al. 2013), warranting their inclusion and evaluation. We divided the presence data into training (80%) and validation (20%) sets using a k-fold partitioning design, with k = 5, and used the same method on the absence points for the GLMs.

MaxEnt – MaxEnt is a machine learning method that has gained wide popularity in species distribution modeling. It uses presence-only data and environmental predictor variables to come up with a distribution of probability that minimizes the relative entropy in the predicted suitability values at the presence vs background points (Elith et al. 2011). We used the k-fold partitioned sets of presence points described above as input into the models of the species they corresponded to. We randomly selected an additional 10 000 random background points to serve as pseudo-absences. All other model parameters were left at their default values. In the MaxEnt models we calculated variable permutation importance at each grain size. This was determined by changing the values of each variable among the training presence and background points, and measuring the loss in AUC. We did this for each variable separately, and the final values were normalized to percentages.

GLM – we used the k-fold partitioned presence and absence points from the generated presence absence map as input for our GLMs, which we built for each virtual species at each grain size. We included cubic, quadratic, and linear terms for each environmental variable in multiplicative and additive relationships and used the 'step' function to remove variables until the optimum model was reached based on AIC. The GLMs were fit with a 'binomial' family and the 'logit' link function.

We calculated the area under receiving operating characteristic curve (AUC), which measures the ability to discriminate between observed presence and absence, for each model. We then randomly chose 10 000 points across the study area to extract model suitability predictions, and ran Pearson's correlation tests between model predictions and the 'true' suitability across the same points. To analyze the effects of grain size on predicted area of presence, we made presence/absence range maps based on threshold at which the value of the true skill statistic (TSS) was maximized (Liu et al. 2013). The TSS measures model sensitivity and specificity and unlike kappa is independent of prevalence (Allouche et al. 2006). We calculated the area of presence predicted by each model based on this threshold and compared it to the true simulated presence area. Our reported results across all analyses are the average of all five training/evaluation runs for each model.

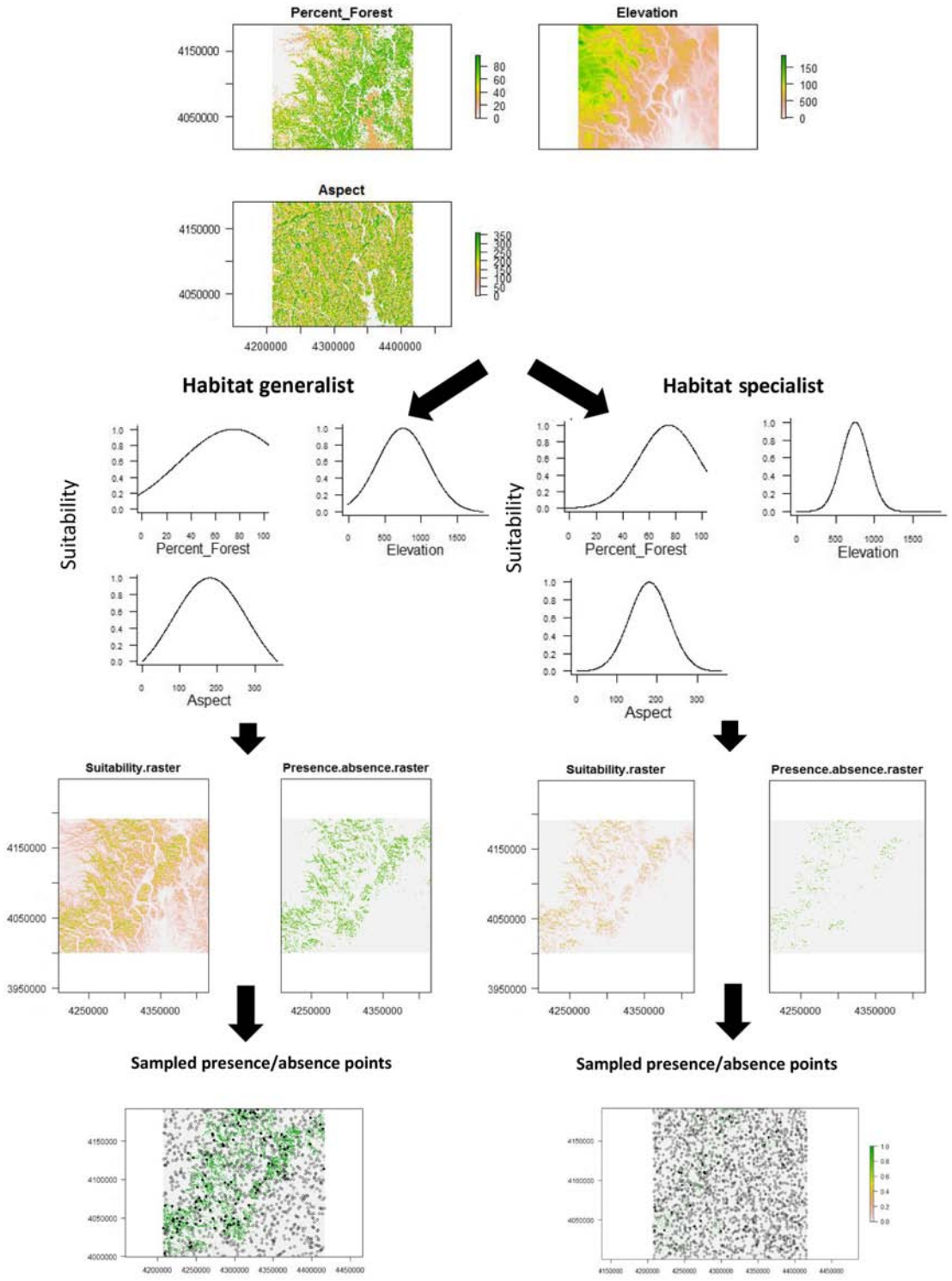

Figure 1. Flowchart of steps to simulate virtual species presence on a landscape.

In order to test for significant differences in model accuracy (measured by AUC) of both the MaxEnt models and GLMs separately at different grain sizes, we used a Van der Waerden normal scores test on the AUC outputs of each training/testing run. There were thus 5 AUC scores for each of 7 different models across 4 model/species combinations. The Van der Waerden test is an effective alternative to Tukey's or analysis of variance (ANOVA) when data is not normally distributed (Conover 1999). If significance was found in this test we then performed pairwise comparisons using Van der

Table 1. The results of a random sampling of n = 2000 points across the 8 landscape/species combinations modeled.

Landscape/species	Presence points	Absence points	Prevalence
Heterogeneous/fine-scale generalist	172	1828	0.09
Heterogeneous/coarse-scale generalist	220	1780	0.11
Heterogeneous/fine-scale specialist	31	1964	0.02
Heterogeneous/coarse-scale specialist	17	1983	0.01
Homogeneous/fine-scale generalist	503	1497	0.25
Homogeneous/coarse-scale generalist	646	1354	0.32
Homogeneous/fine-scale specialist	176	1824	0.09
Homogeneous/coarse-scale specialist	234	1766	0.12

Waerden normal score tests to look at individual comparisons of the different grain sizes in the virtual species being analyzed.

All analyses were conducted using the R software platform (R Core team). We used the package 'virtualspecies' (Leroy et al. 2015) to create the virtual species, the 'dismo' package (Hijmans et al. 2011) for MaxEnt and model comparison analyses, the 'glm' function to build the GLMs, and the 'PMCMR' package to conduct the Van der Waerden tests.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8mp74> (Connor et al. 2017).

Results

The performance of our models varied with grain size, with generally decreasing AUC values as grain size was varied further from the correct grain size for the given species (Table 2, Fig. 2). These decreases in AUC were often significant within 1 aggregation (i.e. 25 vs 50 m), and almost always significant at 2 aggregations or more (i.e. 25 vs 100 m, Table 1). The major exception to this was the MaxEnt models of the coarse-scale habitat specialist, in which AUC values were significantly higher at 50 m and 100 m, compared to the correct grain size of 200 m. AUC values were also higher in the heterogeneous landscape compared to the homogeneous landscape, higher in the habitat specialist compared to the habitat generalist, and generally higher in the MaxEnt models compared to the GLMs (Fig. 2). Increasing grain size deteriorated model accuracy in the homogeneous landscape to a greater degree than in the heterogeneous landscape (Fig. 2).

The Pearson's correlation coefficients between predicted suitability and true suitability in all the derived species were highest in the models built at the correct grain sizes, and decreased drastically as grain size increased and/or decreased from these optimum models (Table 2, Fig. 3). In the fine-scale habitat specialist Pearson's r decreased from a high of 0.95 in the MaxEnt model built at the 'correct' grain size of 25 m to a low of 0.47 in the MaxEnt model built at the 1600-m grain (Fig. 3). These decreases with changes in grain size were much less pronounced in the GLMs, but predictions from the GLMs of all four species had lower correlations with the true suitability values than the MaxEnt models (Table 2). Similar to the AUC values, model predictions of the habitat specialist generally had higher correlations with the true suitability than model predictions of the habitat generalist. Models of the generalist improved relative to the specialist as the distance from the optimum 200-m grain increased, however, and often surpassed them in Pearson's correlation coefficient at just one aggregation from the correct grain size (Table 2).

The permutation importance of aspect, elevation, and percent forest to the MaxEnt models varied with grain size – in the fine-grain versions of both the generalist and specialist in the heterogeneous landscape the variable percent importance was fairly even in the model at the correct (25-m) grain size. As grain size increased, the discrepancy between variables' importance also increased, with elevation gaining importance and aspect losing importance (Fig. 4A, B). Although the variables were further spread apart in their permutation importance values in the coarse-grain generalist species, a similar pattern emerged with the model at the correct (200-m) grain size having a more even distribution. In the homogeneous landscape, the permutation importance of the predictor variables were substantially different, with elevation less important and aspect/percent forest more important to the models (Fig. 4C, D). However, the trend in which the importance of elevation went up at the expense of that of aspect with increasing grain size was consistent in both landscapes.

The predicted area of presence based on the TSS was greater than the true presence area across all models of each species in each landscape (Fig. 5). The closest models to the truth were those at or close to the correct grain size, with increasingly severe over-predictions in models of increasing grain size. For example, the true presence area of the fine-scale generalist in the heterogeneous landscape was 3691 km^2, and the 25-m MaxEnt model this species predicted 4591 km^2 (1.24 times more area) while the 1600-m Maxent model predicted 14 907 km^2 (4.03 times more area, Fig. 5A, Fig. 6). The over prediction was even more pronounced in the specialist species, for which the true area of presence in the fine-scale species was 527 km^2. The closest model to the truth was the MaxEnt model at 50 m, which predicted 1116 km^2 (2.94 times more area), while the 1600-m MaxEnt model predicted 7260 km^2 (13.77 times more area). These over predictions were even larger in most of the GLMs, though

Table 2. Area under the receiver operating characteristic curve (AUC) and Pearson's correlation coefficients between predicted and true suitabilities of models at increasing grain size of the simulated species. Different letters in the AUC columns indicate values that are significantly different from others in that species/model group (b is significantly different from a and c, but not another b).

	MaxEnt				GLM			
	Fine-scale species		Coarse-scale species		Fine scale-species		Coarse-scale species	
Grain size (m)	AUC	Pearson's r	AUC	Pearson's r	AUC	Pearson's r	AUC	Pearson's r
(a) Heterogeneous landscape, habitat generalist.								
25	0.95_{a}	0.90	0.90_{a}	0.77	0.93_{a}	0.67	0.90_{a}	0.71
50	$0.94_{a,b}$	0.83	0.90_{a}	0.79	0.92_{a}	0.63	0.90_{a}	0.73
100	0.93_{b}	0.78	0.91_{a}	0.84	$0.91_{a,b}$	0.61	0.91_{a}	0.77
200	$0.91_{b,c}$	0.72	0.93_{b}	0.90	$0.90_{b,c}$	0.59	0.93_{b}	0.81
400	0.89_{c}	0.66	0.90_{a}	0.82	$0.89_{b,c}$	0.57	$0.91_{b,c}$	0.78
800	0.86_{d}	0.62	0.87_{c}	0.76	0.87_{c}	0.56	$0.90_{a,c}$	0.74
1600	0.82_{e}	0.58	0.84_{d}	0.70	0.85_{c}	0.56	0.89_{a}	0.70
(b) Heterogeneous landscape, habitat specialist.								
25	0.99_{a}	0.97	$0.96_{a,c}$	0.66	0.95_{a}	0.55	0.91_{a}	0.52
50	$0.98_{a,b}$	0.87	0.99_{b}	0.71	$0.95_{a,b}$	0.53	0.91_{a}	0.53
100	$0.96_{b,c}$	0.78	0.99_{a}	0.77	$0.94_{b,c}$	0.51	0.94_{a}	0.58
200	0.96_{c}	0.68	0.96_{a}	0.93	$0.92_{b,c}$	0.47	0.96_{a}	0.62
400	0.95_{c}	0.58	$0.96_{a,c}$	0.75	$0.92_{c,d}$	0.45	0.94_{a}	0.59
800	0.91_{d}	0.52	$0.95_{c,d}$	0.64	$0.91_{c,d}$	0.43	0.93_{a}	0.55
1600	0.90_{e}	0.45	0.91_{d}	0.54	0.91_{d}	0.42	0.93_{a}	0.52
(c) Homogeneous landscape, habitat generalist.								
25	0.86_{a}	0.94	$0.74_{a,b}$	0.75	0.81_{a}	0.65	0.79_{a}	0.65
50	0.83_{b}	0.85	0.76_{a}	0.77	0.81_{a}	0.63	0.79_{a}	0.67
100	0.80_{c}	0.76	0.75_{a}	0.83	$0.79_{a,b}$	0.59	0.79_{a}	0.71
200	0.76_{d}	0.64	0.81_{c}	0.94	$0.77_{b,c}$	0.54	0.84_{b}	0.76
400	0.69_{e}	0.53	0.73_{b}	0.78	$0.73_{c,d}$	0.49	0.79_{a}	0.70
800	0.64_{f}	0.45	0.68_{d}	0.65	$0.70_{d,r}$	0.44	0.75_{a}	0.62
1600	0.61_{g}	0.38	0.64_{e}	0.53	0.66_{e}	0.37	0.71_{c}	0.53
(d) Homogeneous landscape, habitat specialist.								
25	0.94_{a}	0.92	0.84_{a}	0.63	0.81_{a}	0.46	0.84_{a}	0.47
50	0.92_{b}	0.84	0.85_{a}	0.65	0.79_{a}	0.45	0.85_{a}	0.50
100	$0.89_{b,c}$	0.73	0.86_{a}	0.71	0.76_{b}	0.44	0.86_{a}	0.55
200	0.84_{c}	0.59	0.93_{b}	0.92	$0.72_{b,c}$	0.39	0.90_{b}	0.63
400	0.76_{d}	0.45	0.84_{a}	0.67	$0.70_{c,d}$	0.36	0.85_{a}	0.55
800	0.68_{e}	0.33	0.77_{c}	0.52	$0.67_{d,e}$	0.31	0.80_{c}	0.47
1600	0.65_{e}	0.27	0.73_{d}	0.42	0.65_{e}	0.27	0.75_{c}	0.40

they improved relative to the MaxEnt models at very large grain sizes (Fig. 5).

Discussion

Our simulation of virtual species and subsequent testing of models of those species revealed complex effects of niche breadth and grain size on SDMs. Without considering grain size, our results show species are more accurately modeled across heterogeneous landscapes compared to homogeneous landscapes. This is likely due to the larger differences in the predictor variables that drive suitability in heterogeneous landscapes, meaning that it is easier for the models to delineate areas of high vs low suitability (and thus presence and absence on a landscape). Along similar lines, specialist species are more accurately modeled than more generalist species. This may be due to the fact that modeling algorithms should more easily differentiate between areas of higher suitability and areas of lower suitability when suitability is more restricted. Higher accuracy in models of the specialist species was seen even though there were a seventh or less of the presence points in the specialist compared to the generalist species. Greater accuracy in modeling specialist compared to generalist species has also been found in empirical studies (Hernandez et al. 2006, McPherson and Jetz 2007, Tsoar et al. 2007, Evangelista et al. 2008), and the results of our simulation corroborate this.

Although our results have implications for the modeling of species with different niche breadths, they do not have direct applications to niche theory and modeling habitat specialization. This is because true habitat specialists will have evolved traits that make them more effective in certain environments compared to generalists, which is not captured in our virtual species. Examples of species that outperform others in a wide variety of environments are

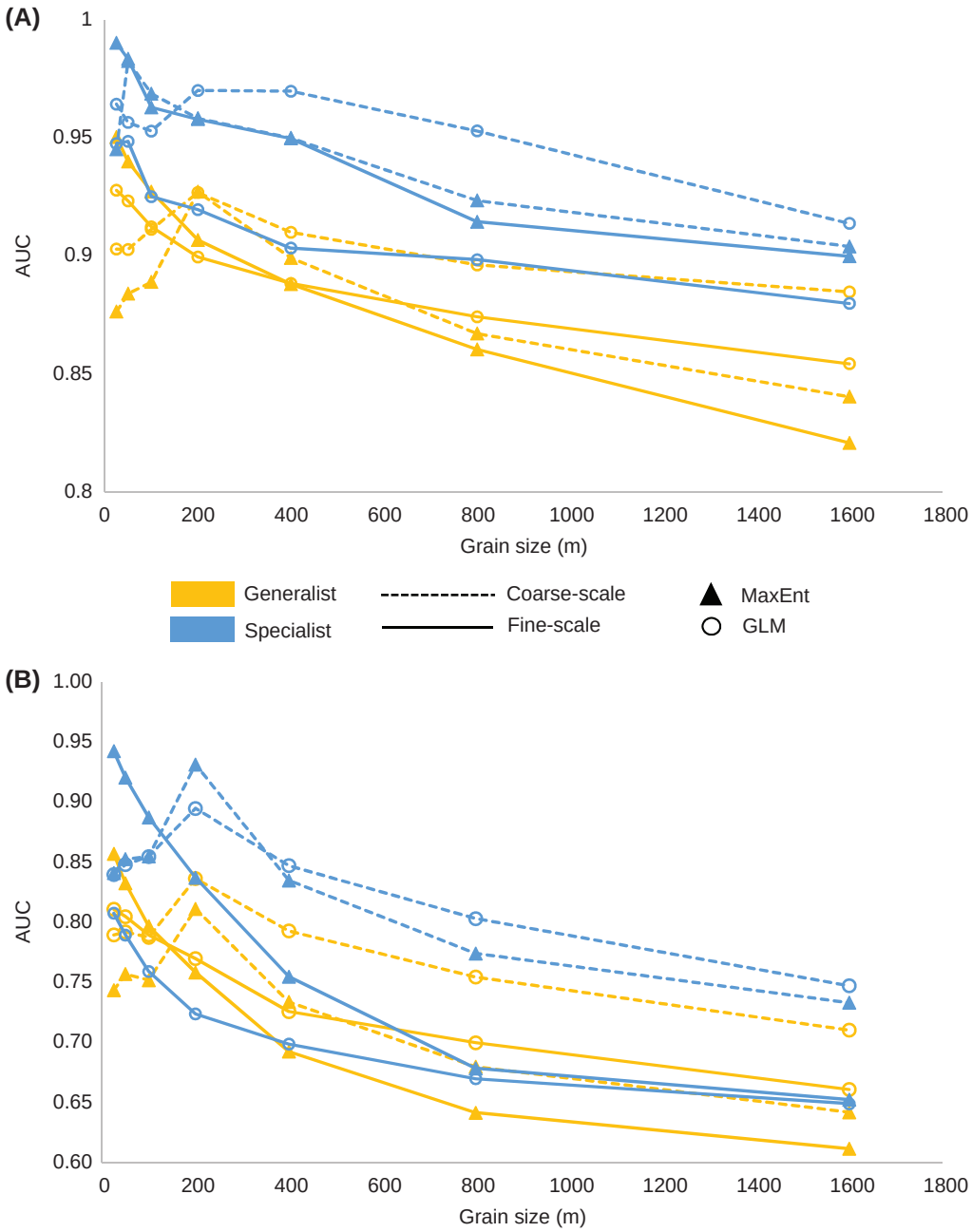

Figure 2. AUC scores of MaxEnt models and GLMs of virtual species across 7 grain sizes in (A) heterogenous landscape and (B) homogeneous landscape.

on the rise, however, particularly with the species invasion phenomenon. Invasive species often have much broader success across landscapes and habitat conditions than native species (Richards et al. 2006). Predicting the spread of invasive species is an increasingly important endeavor for ecological research and conservation, and our results indicate that this will be challenging for successful invaders with broad niches. Our study kept suitability responses for each predictor to normal distributions. We acknowledge that this is a simplification, and therefore additional research to investigate different suitability response curves is necessary. This would more accurately simulate niche specialization and show its influence on the grain-size effects of the environmental variables.

Considering grain size, our results suggest that using predictors at the scale at which a species responds (in our case the scale at which it was simulated) will generally maximize model accuracy. However, the extent of these differences in accuracy varied by landscape, model, and virtual species. The habitat specialist species built at a coarser grain (200 m) in the heterogeneous landscape, for example, was in fact better modeled at smaller grain resolutions (50 and 100 m) than

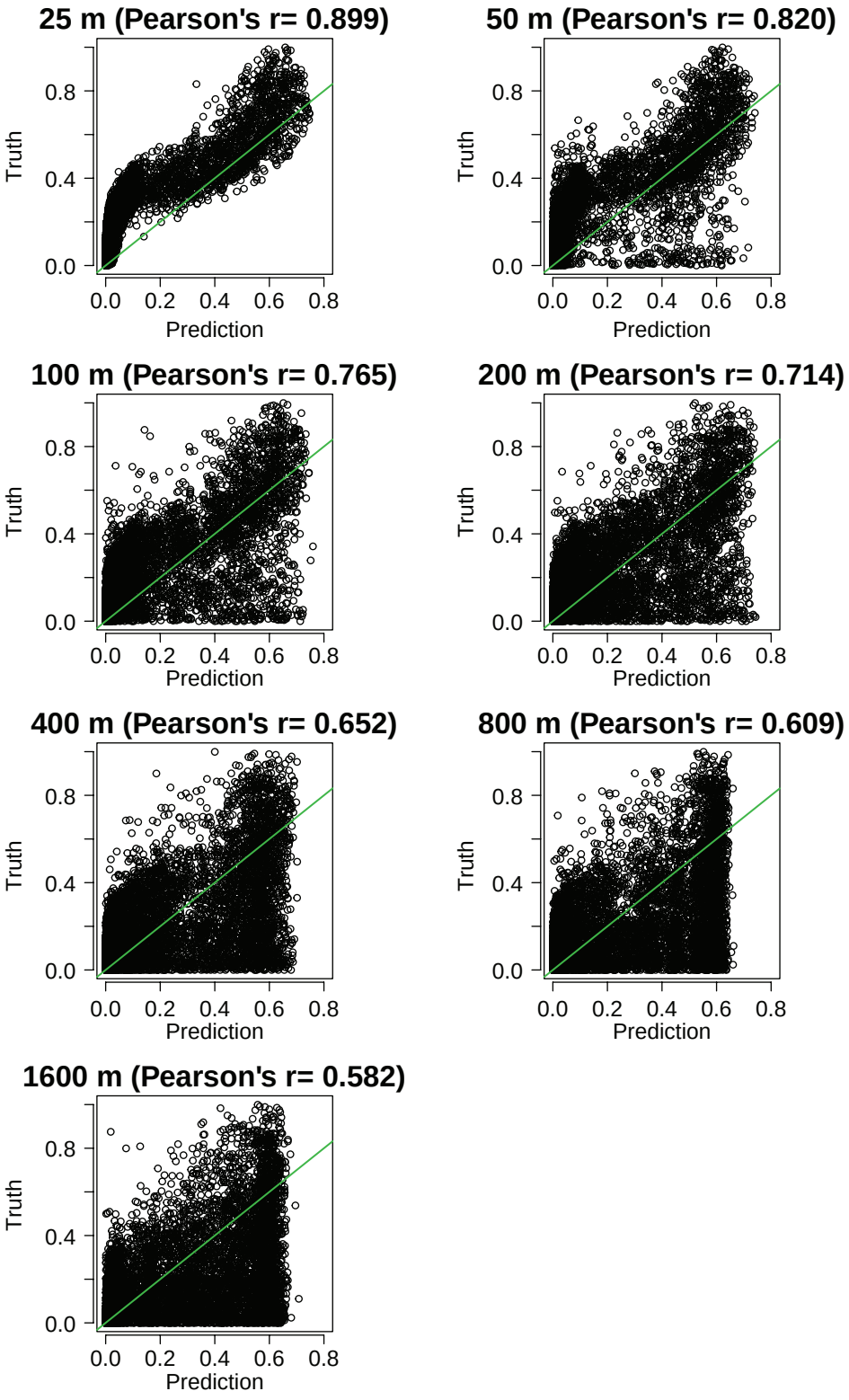

Figure 3. Scatterplots and Pearson's correlation coefficients of suitability predictions from MaxEnt models of and the true suitability values of the fine-scale habitat generalist species simulated in the heterogeneous landscape.

the one at which it was simulated. This suggests that in species with a narrower niche, selecting a fine enough grain to capture more details in the variation of the environmental variables is important. On the other hand, the deterioration in model accuracy at larger grain sizes was greater in the habitat generalist than in the habitat specialist. The deterioration

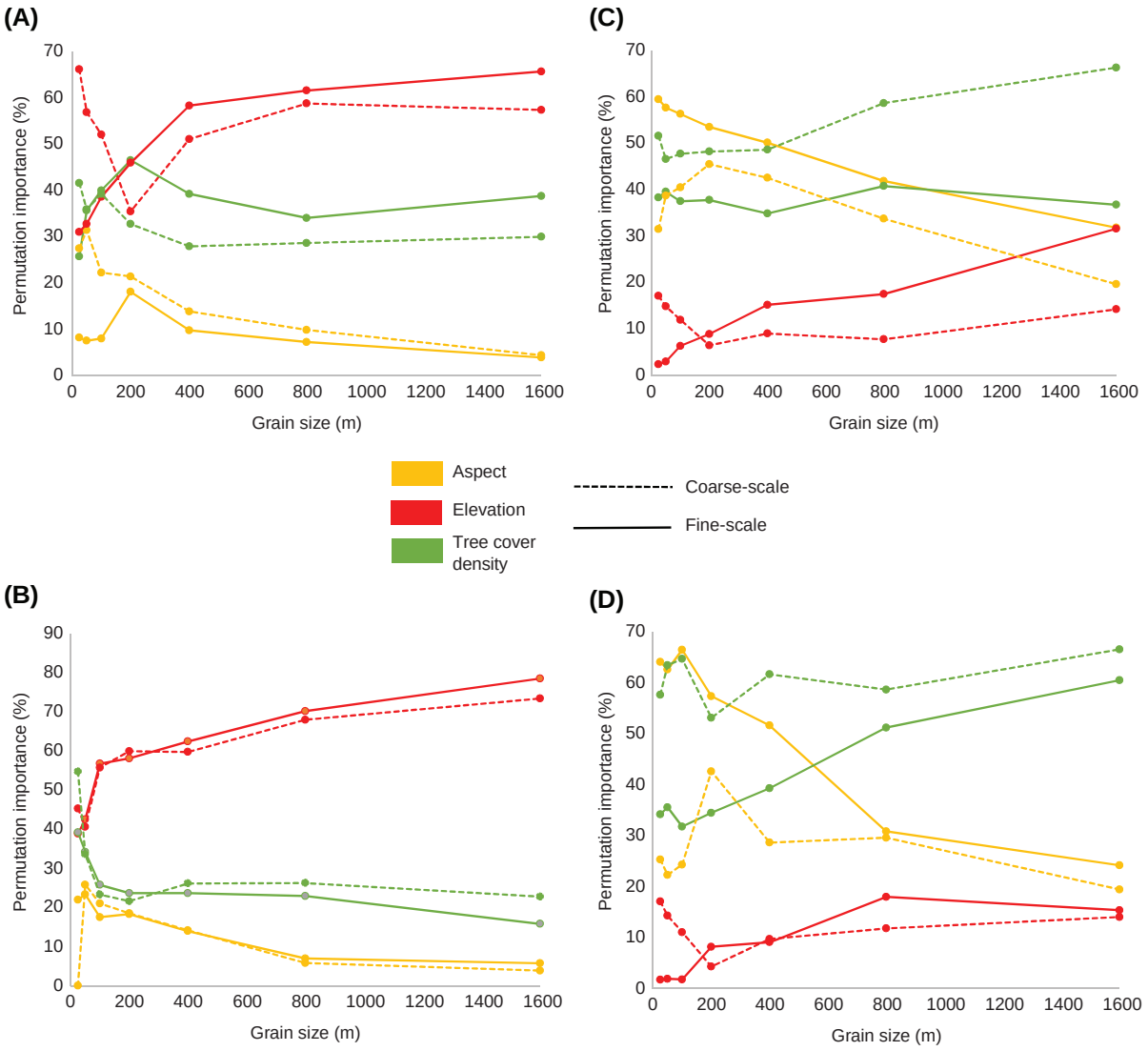

Figure 4. Permutation importance of variables to the MaxEnt models of (A) habitat generalist in heterogeneous landscape, (B) habitat specialist in heterogeneous landscape, (C) habitat generalist in homogeneous landscape, and (D) habitat specialist in homogeneous landscape.

of model accuracy with increasing grain size was also higher in the homogeneous landscape than the heterogeneous landscape. This makes sense considering there is a smaller suitability 'signal' embedded in the background landscape for both habitat generalists and species in homogeneous landscapes, and our results indicate that this signal becomes harder to capture when increasing the grain size of the environmental predictors.

It is interesting to consider how variable importance changed with increasing grain size. The overwhelming importance of elevation in the heterogeneous landscape at the expense of aspect at larger grain sizes is likely because the average elevation value across a larger area is more meaningful than the average aspect value: consider the largest grain size of 1600 m. The average elevation of the area around a mountain top will produce a decent approximation with meaning to the model, while the average aspect will be a poor representation of the range of suitable aspect values throughout that cell. In the homogeneous landscape, elevation was far less important due to the small variance in its values across the landscape, but followed a similar trend of increasing importance at the expense of aspect with increasing grain size. This has implications for any study system in which important variables lose meaning at coarser scales.

An additional advantage of modeling a species at the correct grain size was that it generally resulted in the most accurate measure of total area of presence based on the TSS. Our results suggest that if producing binary distribution or habitat maps for presentation or downstream applications, modeling at an inappropriate grain size will vastly overestimate a species' presence area. Models just 1 aggregation apart resulted in up to 3 times more predicted presence

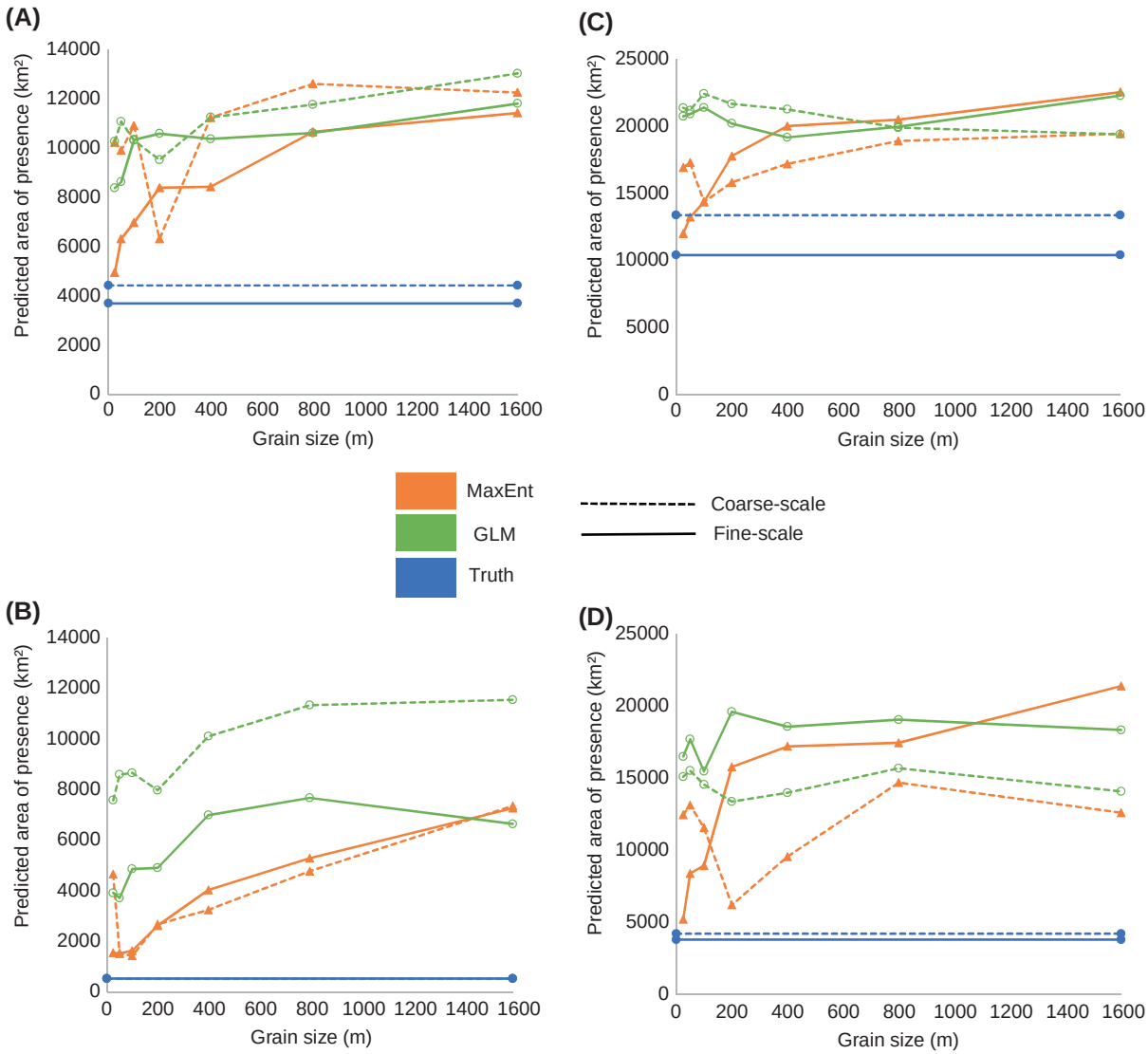

Figure 5. Total predicted area of presence above maximum TSS threshold in (A) habitat generalist in heterogeneous landscape, (B) habitat specialist in heterogeneous landscape, (C) habitat generalist in homogeneous landscape, and (D) habitat specialist in homogeneous landscape.

area while models at the largest grain size of 1600 m predicted up to 14 times more area than the true presence area. Similar relationships in landscape modeling have been described regarding increasing erosion area (Schoorl et al. 2000) and increasing predicted areas of landslide vulnerability (Claessens et al. 2005) with increasing grain size. Other ecological studies have likewise found an effect of larger predicted areas of presence from larger grain sizes (Seo et al. 2009), but ours is the first to measure the effect against the 'truth' known from a derived virtual species. This has large implications for conservation planning when vital decisions about areas to protect and manage must be made with as accurate information as possible. The fact that all models overestimated each species' presence area is also an important point to keep in mind when making conservation decisions on a landscape – species are likely less widely distributed then even models at empirically accurate scales are predicting.

Unfortunately, many of the climate data used as environmental predictors in SDMs are only available at grain sizes of 1 km or greater, which are often interpolations from even coarser data (Hijmans et al. 2005). Although generally avoided in ecological studies, there is potential in using geostatistical interpolation methods to further disaggregate predictor variables at larger grain sizes to match ecologically important variables for the species in question at smaller ones. Methods of obtaining finer resolution land cover information have been advanced in remote sensing sciences using super-resolution mapping (Atkinson et al. 2008), and textural analysis of remotely sensed imagery has recently been used to characterize sub-pixel habitat heterogeneity at global scales (Tuanmu and Jetz 2016). Further research should investigate

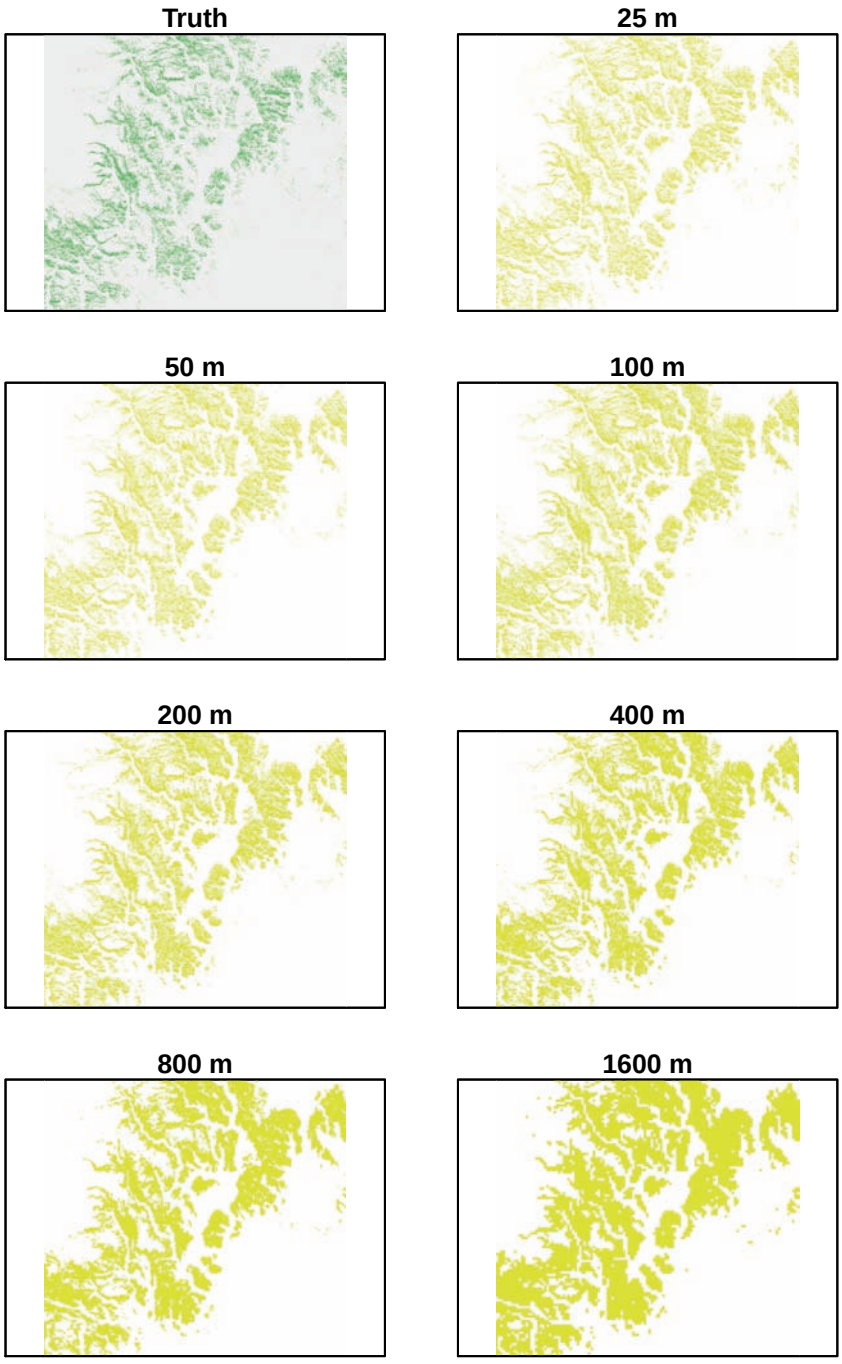

Figure 6. Presence maps of the fine-scale habitat generalist species simulated on the heterogeneous landscape produced by MaxEnt models of increasing grain size.

the best methods of disaggregation for SDM application and the effects of disaggregating predictor variables on SDMs.

A lion most likely perceives habitat at a much larger scale than a shrew, and thus it makes more sense to model its habitat at larger grain sizes than those used to model a shrew's habitat. In addition to this point, however, is the fact that any given species is likely respond to their environment at a variety of scales. It is important to consider this scale-mismatch within a species distribution model. For example, the scale at which a species responds to water availability may be finer than that at which it responds to air temperature. The variation of response-scales across species is likely one reason that there has been a wide variety of findings with regards to the effects of grain size across studies. There is precedent in modeling species distributions with multiple scales of predictors in a single model (Bellamy et al. 2013, Bradter et al. 2013), but research has also shown that including multiple empirically-selected grain sizes for predictors

does not necessarily improve model performance over single-grain sized models (Martin and Fahrig 2012). The task becomes more complicated when considering model evaluation and selection criteria, as even commonly used statistics like AUC have been criticized as inappropriate in some cases (Lobo et al. 2008). In evaluating models of real species in which the true environmental suitability of an area is unknown, additional metrics such as explained deviance, AIC, BIC (for Bayesian models), and point biserial correlation (Kraemer 2006) should be employed, depending on the modeling method and research goals.

In the face of these complications, our results suggest that model accuracy and presence area predictions can be improved by evaluating models at multiple grain sizes and selecting the most accurate one. We increased grain size using mean values from the smaller cells, as our simulated species responded simply to values of the variables within a cell. Different summary statistics (such as variance, median, minimum value, etc.) may better explain a species' response to a given environmental variable when increasing grain size, depending on the study system. We recommend that every study modeling a species' distribution or habitat suitability across a landscape explicitly perform an analysis of grain size to decide what scale to model their species, as even well-founded expert opinion can be inaccurate (Peterman et al. 2014). Considering our findings that grain sizes larger than those at which species respond distort model accuracy and predictions to a greater degree than smaller ones, if a full analysis of grain-size effects is not feasible for a given project it is likely better to use smaller grain sizes.

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References

Allouche, O. et al. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). – J. Appl. Ecol. 43: 1223–1232.

Atkinson, P. M. et al. 2008. Downscaling cokriging for super-resolution mapping of continua in remotely sensed images. – IEEE Trans. Geosci. Remote Sens. 46: 573–580.

Barbet-Massin, M. et al. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? – Methods Ecol. Evol. 3: 327–338.

Bean, W. T. et al. 2014. Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales. – J. Appl. Ecol. 51: 1116–1125.

Bellamy, C. et al. 2013. Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. – J. Appl. Ecol. 50: 892–901.

Bradter, U. et al. 2013. Identifying appropriate spatial scales of predictors in species distribution models with the random forest algorithm. – Methods Ecol. Evol. 4: 167–174.

Claessens, L. et al. 2005. DEM resolution effects on shallow landslide hazard and soil redistribution modelling. – Earth Surface Process. Landforms 30: 461–477.

Connor, T. et al. 2017. Data from: Effects of grain size and niche breadth on species distribution modeling. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.8mp74>.

Conover, W. J. 1999. Practical nonparametric statistics. – Wiley.

Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.

Elith, J. and Graham, C. H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. – Ecography 32: 66–77.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. – Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

Elith, J. et al. 2011. A statistical explanation of MaxEnt for ecologists. – Divers. Distrib. 17: 43–57.

Evangelista, P. H. et al. 2008. Modelling invasion for a habitat generalist and a specialist plant species. – Divers. Distrib. 14: 808–817.

Franklin, J. et al. 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? – Global Change Biol. 19: 473–483.

Gottschalk, T. K. et al. 2011. Influence of grain size on species-habitat models. – Ecol. Model. 222: 3403–3412.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – Ecol. Lett. 8: 993–1009.

Guisan, A. et al. 2007a. Sensitivity of predictive species distribution models to change in grain size. – Divers. Distrib. 13: 332–340.

Guisan, A. et al. 2007b. What matters for predicting the occurrences of trees: techniques, data, or species' characteristics? – Ecol. Monogr. 77: 615–630.

Hernandez, P. A. et al. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. – Ecography 29: 773–785.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – Int. J. Climatol. 25: 1965–1978.

Hijmans, R. J. et al. 2011. Package 'dismo'. – <http://cran.r-project.org/web/packages/dismo/index.html>.

Hudak, A. T. et al. 2009. LiDAR utility for natural resource managers. – Remote Sens. 1: 934–951.

Jimenez-Valverde, A. et al. 2009. The effect of prevalence and its interaction with sample size on the reliability of species distribution models. – Commun. Ecol. 10: 196–205.

Kraemer, H. C. 2006. Biserial correlation. – Encyclopedia of Statistical Sciences 1.

Leipold, M. et al. 2017. Species distribution modeling and molecular markers suggest longitudinal range shifts and cryptic northern refugia of the typical calcareous grassland species *Hippocrepis comosa* (horseshoe vetch). – Ecol. Evol. 7: 1919–1935.

Leroy, B. et al. 2015. virtualspecies, an R package to generate virtual species distributions. – Ecography 39: 599–607.

Levin, S. A. 1992. The problem of pattern and scale in ecology. – Ecology 73: 1943–1967.

Liu, C. R. et al. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. – J. Biogeogr. 40: 778–789.

Lobo, J. M. et al. 2008. AUC: a misleading measure of the performance of predictive distribution models. – Global Ecol. Biogeogr. 17: 145–151.

Martin, A. E. and Fahrig, L. 2012. Measuring and selecting scales of effect for landscape predictors in species-habitat models. – Ecol. Appl. 22: 2277–2292.
McPherson, J. M. and Jetz, W. 2007. Effects of species' ecology on the accuracy of distribution models. – Ecography 30: 135–151.
Merow, C. et al. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. – Ecography 36: 1058–1069.
Peterman, W. E. et al. 2014. Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. – Mol. Ecol. 23: 2402–2413.
Phillips, S. J. et al. 2006. Maximum entropy modeling of species geographic distributions. – Ecol. Model. 190: 231–259.
Porfirio, L. L. et al. 2014. Improving the use of species distribution models in conservation planning and management under climate change. – PLoS One 9: e113749.
Renner, I. W. and Warton, D. I. 2013. Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. – Biometrics 69: 274–281.
Revermann, R. et al. 2012. Habitat at the mountain tops: how long can rock ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in the Swiss Alps? A multi-scale approach. – J. Ornithol. 153: 891–905.
Richards, C. L. et al. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. – Ecol. Lett. 9: 981–993.
Scales, K. L. et al. 2017. Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. – Ecography 40: 210–220.
Schoorl, J. M. et al. 2000. Three-dimensional landscape process modelling: the effect of DEM resolution. – Earth Surface Process. Landforms 25: 1025–1034.
Seo, C. et al. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. – Biol. Lett. 5: 39–43.
Seoane, J. et al. 2004. Are existing vegetation maps adequate to predict bird distributions? – Ecol. Model. 175: 137–149.
Trivedi, M. R. et al. 2008. Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. – Global Change Biol. 14: 1089–1103.
Tsoar, A. et al. 2007. A comparative evaluation of presence-only methods for modelling species distribution. – Divers. Distrib. 13: 397–405.
Tuanmu, M. N. and Jetz, W. 2016. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. – Global Ecol. Biogeogr. 24: 1329–1339.
Wiens, J. A. 1989. Spatial scaling in ecology. – Funct. Ecol. 3: 385–397.