

The relative importance of spatial and temporal variation in predicting community structure at different scales as estimated from Markov chain models

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ABSTRACT: Models that incorporate complex interactions are useful tools for estimating the relative importance of ecological processes in changing ecological communities. Multispecies Markov chain models (MMCMs) use transition probabilities to explore how complex interactions influence community structure. However, the accuracy of MMCMs over different spatial and temporal scales is not well known and likely influenced by the scales over which species interactions differ. Here we explore how MMCM predictions vary with scale in the Gulf of Maine intertidal by quantifying transition probabilities at increasing temporal (annual, biannual, seasonal) and spatial (local, meso-, regional) scales. Model predictions were accurate at local scales, even with data from coarse sampling frequencies (annual), suggesting short-term variations in ecological processes do not strongly affect stable-stage community composition over these time scales. Models were less accurate when incorporating spatial variation beyond local scales. Geographic differences in species persistence, mortality, and colonization probabilities reduced MMCM predictive capacity. Our work demonstrates that MMCMs can predict local community structure, even with data from coarse sampling intervals, and may also be useful for identifying regional differences in ecological processes that might be responsible for shifts in community structure.

KEY WORDS: Multispecies Markov chain · Rocky intertidal · Gulf of Maine · Spatial variation · Temporal variation

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INTRODUCTION

The assembly, structure, and dynamics of communities reflect the integration of many processes operating over a wide variety of spatial and temporal scales, and involve complex webs of direct and indirect species interactions that vary in nature and strength along local and regional environmental gradients (Wiens 1989, Levin 1992, Huston 1999). A major challenge in ecology is to identify the relative importance and consequences of the complex and interdependent processes that shape spatial and temporal variation in communities. Ecological models that incorporate complex interactions and are for-

mulated based on empirical data can help identify the magnitude, direction, and nature of the key processes responsible for community change (Goudard & Loreau 2008, Berlow et al. 2009). Developing empirical models that are useful in evaluating the mechanisms that mediate community change, however, requires decisions concerning the appropriate spatial and temporal scales that might be critical for system dynamics as well as for model accuracy. Quantifying the scales at which models lose their predictive capacity (i.e. are not accurate) can help to determine the scales over which ecological processes change and to identify the key processes potentially influencing community structure in complex systems (e.g.

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McIntire & Fajardo 2009, Detto & Muller-Landau 2013, Pottier et al. 2013). Here we develop a multi-species Markov chain model (MMCM) for the Gulf of Maine (GOM) intertidal community and use it to explore the temporal and spatial scales of ecological interactions (e.g. transitions among species) and to identify the scales over which changes in ecological processes cause shifts in community structure.

MMCMs (hereafter also referred to as 'Markov models') are an important class of models used extensively in ecology to estimate the relative importance of complex community interactions. MMCMs utilize a matrix of probabilities describing transitions in space occupancy of one species to another over a fixed period of time (i.e. transition probabilities). These models have been successful in estimating species composition in a variety of communities, both terrestrial (e.g. forest: Waggoner & Stephens 1970, Horn 1975, Balzter 2000; grassland: Nelis & Wootton 2010; plant: Isagi & Nakagoshi 1990, Aaviksoo 1995; insects: Usher 1979) and marine (e.g. tropical coral reef: Tanner et al. 1994; temperate subtidal: Hill et al. 2002; temperate intertidal: Wootton 2001a, 2004, 2013), suggesting applicability across a broad range of ecosystems. MMCMs incorporate a comprehensive set of potential direct and indirect species interaction pathways within a community, successfully predict community responses to novel circumstances (e.g. species removals: Wootton 2004; climate change: Wootton et al. 2008), and capture emergent patterns from local interactions (e.g. Wootton 2001b), thereby providing a powerful framework to incorporate and test the relative importance of multiple processes in controlling community structure.

However, it is unclear how well Markov models might work at larger spatial scales that incorporate regional variation in ecological processes or when smaller-scale temporal variability (e.g. seasonal) is included. Few studies have quantified MMCMs simultaneously within replicate habitat types (i.e. forest type, grassland, subtidal reef, intertidal rocky bench) or across meso- and regional-spatial scales (10s and 100s of km, respectively) in marine (but see Tsujino et al. 2010) or terrestrial systems (but see Yemshanov & Perera 2002, Tucker & Anand 2003). Time invariant transition probabilities ignore likely temporal variation in species interactions, while infrequent sampling strategies potentially miss important transitions (Spencer & Susko 2005) and do not allow for seasonality or tests of fine-scale temporal processes. In spite of these shortcomings, model predictions often capture more than 90% of variation in empirical estimates of structure (species percent

cover) in local communities (McAuliffe 1988, Tanner et al. 1994, Balzter 2000, Wootton 2001a,b, 2004, 2013, Hill et al. 2002, Nelis & Wootton 2010).

The effect of space and time on MMCMs has been explored via log-linear regression (Wootton 2001a, Hill et al. 2002) and by comparing continuous-time to discrete-time Markov models (Wootton 2001a, Spencer & Susko 2005). In both approaches, probabilities differed over space and time, but incorporating this variation into simulations of community dynamics only marginally improved model predictions (<2% explained improvement; Wootton 2001a, Spencer & Susko 2005), suggesting these levels of variation in transition probabilities were less important for community structure (e.g. stable-stage community composition). Spatial scales over which probabilities were quantified were, however, <1 km (~700 m: Wootton 2001a; ~20 m: Hill et al. 2002), and point occupancy sampling frequency was biannual at most (biannual: Wootton 2001a; annual: Hill et al. 2002; ~2 yr: Spencer & Susko 2005). The similarities of transition probabilities decay with distance (from 10s of m to 100s of km; Tsujino et al. 2010) and may differ among microhabitats (Yemshanov & Perera 2002, Tucker & Anand 2003) and experimental treatments (Nelis & Wootton 2010). Recent research has highlighted the importance of large-scale environmental gradients in modulating the species interactions responsible for transitions (Leonard 2000, Menge et al. 2004, 2011, Tylianakis et al. 2008, Henriques-Silva et al. 2013). Phenological effects can also have profound consequences on the assembly, structure, and function of ecosystems (Chuine & Beaubien 2001, Edwards & Richardson 2004, Yang & Rudolf 2010), and transition probabilities are known to differ between the spring/summer and fall/winter periods in some environments (e.g. Wootton 2001a). Thus, transition probabilities are likely to be sensitive to increases in natural levels of variation included by extending measurements over an area >1 km and/or sampling a frequency/time scale more fine than biannual. Transition probabilities may also differ over these scales to the extent that they result in very different pathways to, and predictions of, community structure. Identifying the spatial and temporal scales where MMCMs lose their predictive capacity within a system is therefore critical to determine how best to quantify and use transition probabilities, as well as to determine the spatial and temporal scales over which ecological pathways differ and potentially drive community change. How transition probabilities differ spatially and temporally should also pro-

vide key insights into the possible primary ecological forces that drive geographic variation in community structure and dynamics.

In this study, we (1) tested whether spatial and temporal variation in transition probabilities alter the accuracy of MMCMs in predicting empirical estimates of community structure and (2) used the decline in the accuracy of MMCMs to identify the probable spatial and temporal scales at which natural ecological processes change sufficiently to alter community structure regionally. We hypothesized that transition probabilities in the GOM would differ as spatial scale increased and as temporal resolution decreased, and that there would be a corresponding decay in model accuracy. Transition probabilities were quantified with data from local-, meso-, and regional-spatial scales (within site, within region, and across regions, respectively) to estimate varying magnitudes of natural spatial variation. Temporal variation was estimated by quantifying transitions at increasing sampling frequencies (annual, biannual, and seasonal). The accuracy of MMCMs in predicting community structure (species percent cover) was influenced by spatial variation on the order of 10s to 100s of km but appeared to be unaffected by temporal variation (at least over ~2.5 yr). The spatial and temporal scales over which the accuracy of model predictions declined helped to identify the putative scales over which ecological processes differed in nature, leading to changes in community structure across the GOM.

METHODS

Study system

GOM rocky intertidal environments provide an excellent model system to test the effects of spatial and temporal variation on MMCMs. Small-scale heterogeneities in topography and environmental variables interact with larger-scale gradients in physical oceanography and climate to modulate life history characteristics and interactions among species (Lubchenco & Menge 1978, Bertness et al. 2004, Kordas & Dudgeon 2011, Bryson et al. 2014). Seasonal variability in these forces can also lead to strong phenological effects (Kordas & Dudgeon 2011). Previous research in the GOM intertidal has consistently highlighted the consequences of spatial and temporal variation and has been critical for the development of models for community regulation (Menge & Sutherland 1987). In addition, MMCMs effectively

capture intertidal community dynamics and predict its structure (e.g. Wootton 2001a, 2004, 2013). Thus the GOM intertidal is an ideal habitat to estimate the robustness of MMCM predictions to spatial and temporal variation and to use them to estimate the spatial and temporal scales where community structuring processes change.

MMCMs

Markov models are parameterized with a matrix of probabilities describing transitions from occupancy of a space by one species (column) to another species (row) over a fixed period of time. In matrix M , each element m_{ji} represents the probability (Pr) that a space changes from state i at time t to state j at time $t + 1$ (Eq. 1). The space's state at time $t + 1$ is explicitly dependent on its state at time t :

$$m_{ji} = \Pr(x_{t+1} = j \mid x_t = i) \quad (1)$$

The consequences of these transitions on community composition can be simulated by multiplying matrix M by column vector P , where P_t is the proportion of units in each state i at time t :

$$P_{t+1} = M \times P_t \quad (2)$$

Long-term Markov model predictions of community composition are generated through iterated multiplication of Eq. (2), or by calculating the proportional stable-stage distribution from the eigenvector of the dominant eigenvalue of the transition matrix (Caswell 2001).

Study area

Transition probabilities were quantified for rocky intertidal communities occupying the mid-intertidal zone (1 m tide-height above mean low water) at shores experiencing intermediate wave exposures (12.67 ± 1.05 N, mean \pm SE; Morello 2015). Six replicate 25×25 cm permanent plots were sampled at each of 3 replicate sites nested within 3 regions across the GOM (Fig. 1). Spacing among regions (140.50 ± 27.58 km, mean \pm SE), sites (7.48 ± 4.49 km), and plots (random along a 200 m transect) was consistent. To minimize confounding sources of variation (e.g. light availability, susceptibility to desiccation and physical disturbance), all plots were positioned as close to 1 m tide-height above mean low water as possible and confined to horizontal emergent rocky benches. If a plot fell in an unsuitable location (i.e. in a tide pool, or

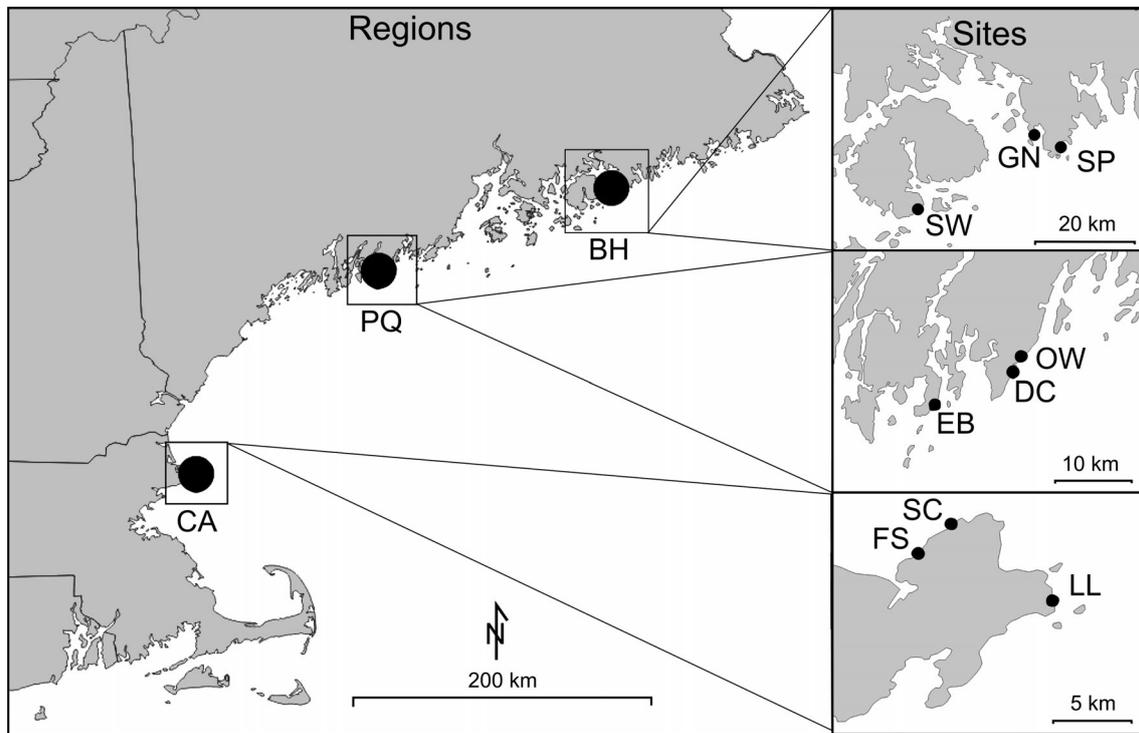


Fig. 1. Gulf of Maine showing locations of regions (BH: Bar Harbor; PQ: Pemaquid; CA: Cape Ann) and sites (SP: Schoolic Peninsula; GN: Grindstone Neck; SW: Seawall; OW: Owl's Way; DC: Dan's Cottage; EB: East Boothbay; FS: UMass Field Station; SC: Seaside Cemetery; LL: Loblolly Point) used to evaluate temporal- and spatial-scale variations in multispecies Markov chain model (MMCM) predictions of intertidal community structure

on cobbles or a vertical surface) it was relocated to the next nearest suitable point along the transect. The tidal height of each plot was measured using an Emery shore profiling method and local National Oceanographic and Atmospheric Administration tide tables (Emery 1961). Wave exposure was quantified at each site using 3 dynamometers (as described in Palumbi 1984) randomly placed along the same 200 m mid-intertidal transect. Dynamometers were checked twice between the dates of July 27, 2011 and September 3, 2011. Wave force units were converted to Newtons. Wave energy estimates that occurred during Hurricane Irene (August 28, 2011) were discarded because forces at all sites exceeded the range of the dynamometers, and at least one dynamometer was lost or incapacitated at each site by the end of sampling. To ensure plots were similar, differences in tidal heights and exposure (wave-force) among sites were tested using a full factorial ANOVA with site nested within region, and region as fixed factors. The exposure ANOVA also included dynamometer nested within site as a random factor, and data were log transformed to fit assumptions of normality. The statistical package JMP version 9.1.2 (SAS Institute 2010) was used to calculate ANOVAs.

Sampling plots

Within each permanent plot at each site, 25 evenly spaced points (4.16 cm apart) were monitored through time for occupancy of sessile intertidal species occupying the primary substratum. Spacing between points was sufficient so that 2 adjacent points did not capture the same individual organisms. To ensure that the same points were monitored at each sample period, an aluminum quadrupod with a 25 × 25 cm base was constructed with 25 evenly spaced fittings for a waterproof laser-pointer, which allowed points in a plot to be relocated. The quadrupod was repositioned during each sampling period by inserting pins at the 4 corners of the quadrupod into holes in z-spar (A-788 Splash Zone Epoxy™) anchors marking the position of the plot's 4 corners.

To ensure that the relocation and sampling of points was accurate, 17 plots (425 points) were resampled on the same day to estimate sampling error. Resampling was accomplished by unpinning and removing the quadrupod following a sampling event and immediately repositioning it and resampling points. Error was estimated as the proportion of points with resampled estimates different from initial estimates.

Data collection and quantification of transition probabilities

Points were monitored at either monthly or bi-monthly intervals between July 2011 and November 2013. Initially, monthly intervals were used at all sites (July 2011 to April 2012; 9 of 9 monthly intervals sampled). Sampling frequency was reduced to bi-monthly intervals for sites in Pemaquid and Bar Harbor regions between April 2012 and November 2013 (10 of 19 monthly intervals sampled) for logistical reasons, but the reduced frequency was deemed acceptable since the average point-occupancy turnover time (time until a species-state turned over, calculated as the reciprocal of the probability of transitioning from one state to a different state; Hill et al. 2004) until April 2012 was > 2 mo in all regions (Bar Harbor: 5.66 ± 2.35 mo, mean \pm SE; Pemaquid: 2.76 ± 0.34 mo; Cape Ann: 2.66 ± 0.52 mo). Those individual species-states with turnover times < 2 mo at the time were locally rare in abundance and typically still exceeded turnover times of 1 mo. Monthly sampling for sites in Cape Ann continued through the duration of the study (July 2011 to November 2013), though measurements were not taken in the months of January, September, and December 2012, and February 2013 due to adverse weather. The number of days between monthly (33.44 ± 12.03 d, mean \pm SE) and bimonthly (61.22 ± 9.93 d) samples was similar among sampling periods, subject to constraints of weather and tidal cycles.

For each plot at each site, the frequency of each transition between species (e.g. from barnacle to

mussel) was quantified separately for each season (spring: March–June; summer: June–September; fall: September–December; winter: December–March) across all years. Species data were collapsed into 14 species-states based on sample size and ecological equivalency (similar ecology) of less abundant species (e.g. ‘ephemeral algae’; Table 1). Since the Cape Ann dataset was larger than the Bar Harbor and Pemaquid datasets (a consequence of reducing Bar Harbor and Pemaquid sampling intervals in April 2012), 2 sets of data were derived for Cape Ann plots. The first was derived from all intervals sampled ($n = 25$ intervals), while the second was derived from intervals in common with Pemaquid and Bar Harbor data ($n = 19$ intervals). The first set of data was used to test questions about temporal variation, while the latter set was used to test questions pertaining to spatial variation. The latter set of data were also used to test model assumptions that each site’s MMCM was different, and that each MMCM was at least a first-order Markov chain. For each transition probability table, likelihood ratios were compared to the chi-square distributions with $n(n - 1)(s - 1)$, and $(n - 1)$ degrees of freedom, respectively, as outlined by Tanner et al. (1994), where n is the number of unique species-states measured at a site, and s the number of sites.

Empirical estimates of community composition were generated independently from transition probabilities at each site by sampling 6 additional 25×25 cm quadrats randomly spaced along a 200-m mid-intertidal transect at the same tide-height and

Table 1. Description of species-states with abbreviations and synonyms used to evaluate temporal and spatial scale variations in MMCM predictions of intertidal community structure in the Gulf of Maine

Species-state	Abbr.	Description
Bare rock	BS	Bare rock
<i>Ascophyllum nodosum</i>	AS	Knotted wrack
Bryozoan	BR	Bryozoa (e.g. <i>Membranipora membranacea</i> , <i>Electra</i> spp.)
Encrusting algae	EA	Encrusting fleshy red and green algae (e.g. <i>Hildenbrandia</i> spp.)
Encrusting coralline	EC	Crustose coralline algae (i.e. <i>Clathromorphum</i> spp., <i>Corallina officianalis</i> , <i>Lithothamnion graciale</i>)
Ephemeral algae	EP	Seasonal and short-lived algae (e.g. <i>Ulva lactuca</i> , <i>Porphyra</i> spp.)
<i>Fucus</i> spp.	FV	Algae in the genus <i>Fucus</i> (e.g. <i>F. vesiculosus</i> , <i>F. spiralis</i> , <i>F. distichus</i>)
Hydroid	HY	Hydrozoa (e.g. <i>Obelia geniculata</i> , <i>Campanularia</i> spp.)
<i>Mytilus edulis</i>	ME	Blue mussel (aka ‘mussels’)
<i>Petrocelis</i> spp.	PT	A crustose life history stage of <i>Mastocarpus stellatus</i>
<i>Ralfsia</i> spp.	RF	The ephemeral crustose algae <i>Ralfsia</i> sp.
Rare animal	AN	Anemones, ascidians, sponges, polychetes, etc.
Red algae	RA	Fleshy turf-like algae (<i>Mastocarpus stellatus</i> and <i>Chondrus crispus</i>)
<i>Semibalanus balanoides</i>	SB	Acorn barnacles (aka ‘barnacles’)

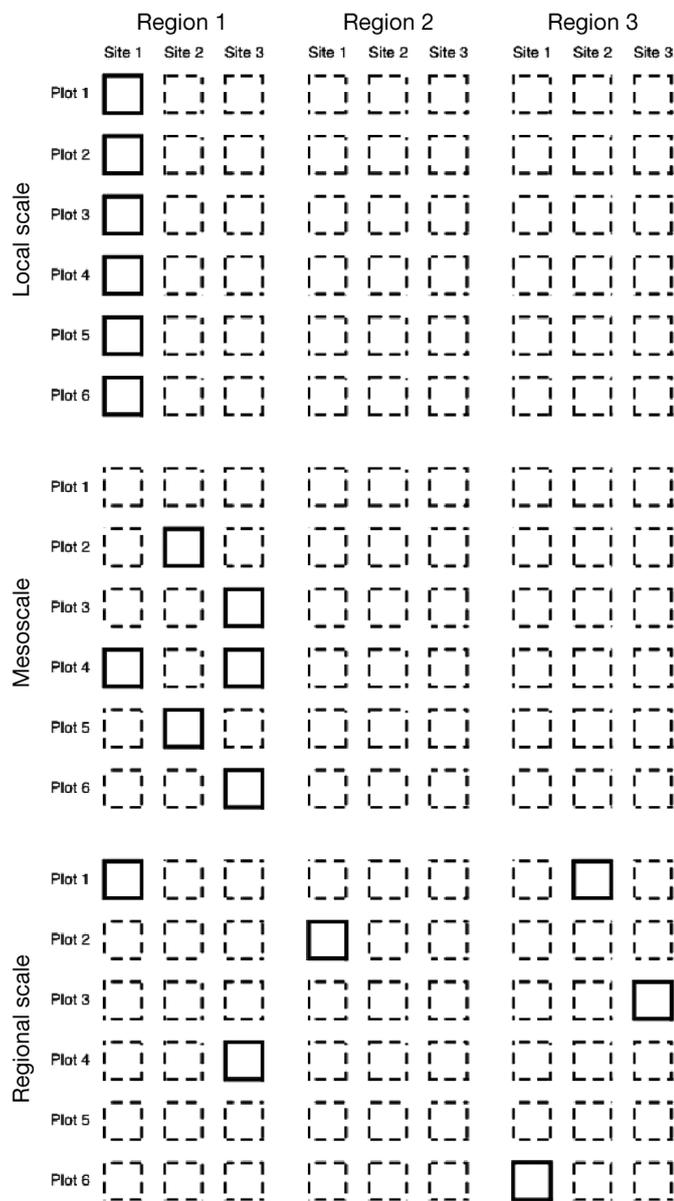


Fig. 2. A visualization of how plots from 9 sites in 3 regions of the Gulf of Maine (see Fig. 1) are pooled to generate each transition probability table when simulating spatial variation in intertidal communities in the Gulf of Maine at local, meso- and regional scales

wave exposure. Percent sessile species cover was estimated using a visual-grid method, which tends to more accurately assess community composition than does a random-dot technique (Dethier et al. 1993). These data were collected once per season each year for the duration of the study ($n = 10$ sampling sessions), though the month of sampling for each season varied among years.

Simulating spatial variation

Markov model predictions of community composition

We simulated increasing amounts of natural spatial variation in transition probabilities by pooling data on 3 spatial scales: (1) within site, (2) within region, and (3) across regions (hereafter referred to as local, meso-, and regional scales, respectively; Fig. 2). We define ‘pooling’ as combining raw data (i.e. the number of occurrences for each transition between species-states) from multiple groups (e.g. seasons, years, sites, regions) and then calculating a transition probability matrix from that frequency data. This differs from ‘averaging’, which we define as calculating a transition probability matrix for each group and then finding the mean probability among groups of transitioning between each species-state (i.e. the mean of each matrix element). Pooling allowed us to account for sample size differences among groups when calculating transition probabilities, whereas averaging would not.

Local-scale simulations pooled data from the 6 plots within each site and across all years and seasons (Fig. 2). Even though this method of pooling included both spatial and temporal variation, temporal variation was held constant (always pooling across all seasons and years) when simulating spatial variation, allowing us to test the specific effect of space. Matrices of transition probabilities were then derived from these pooled data by normalizing each column to sum to 1 (as described in Wootton 2001a). This process produced 9 unique matrices, 1 for each site. Simulations of mesoscale variability randomly selected 6 plots from within a region and pooled the data (Fig. 2). These data were also pooled across all years and seasons and a transition probability matrix derived. This process was repeated 300 times for each region producing a total of 900 unique matrices (300 per region \times 3 regions). Simulations of regional-scale variability randomly selected 6 plots from across all regions and pooled the data to create a transition probability matrix (Fig. 2). This process was repeated 900 times producing 900 unique matrices.

Predicted stable-stage community composition was derived for each individual matrix (9 local scale, 900 mesoscale, and 900 regional scale) by normalizing the eigenvector of the dominant eigenvalue to 100%, and using it as a measure of species relative abundance (Caswell 2001). In cases where simulations resulted in too few observations from a given species-state in the matrix (i.e. a species’ column sum

≤ 2), probabilities from that state were considered to be '0'. This did not dramatically alter predictions of community composition, but did guard against transition probabilities based on extremely low sample sizes that could destabilize the behavior of the Markov chain (i.e. resulting in 100% cover of a rare species). Community composition estimates derived via these methods of eigenanalysis and appropriate sample sizes typically do not differ from estimates using many (~100) iterations of the Markov chain (Wootton 2001a).

Empirical estimates of community composition

Empirical estimates of community composition (species percent cover) were similarly generated with the species percent cover data from the quadrats of independent transects, using the local, meso-, and regional scale combining methods described previously (Fig. 2). In contrast to pooling data among groups to combine transition probability data, empirical composition data was combined by averaging among groups since raw data were already percentages. Local-scale methods averaged data from all quadrats at each site across seasons and years (6 quadrats \times 10 sampling events \times 1 site = 60 quadrats), producing 1 estimate per site and a total of 9 estimates for all sites. These estimates were used as the stable-stage community composition of their respective sites and were assumed to be comparable to model stable-stage predictions, despite models utilizing data of greater temporal resolution. Our rationale was that independent transect data incorporated multiple seasons and years, and that stable-stage composition is well represented by the average community structure at each site, even though it may vary to some degree over shorter periods of time.

For mesoscale empirical estimates, the same method was used but quadrats were selected at random from within each region. Site identity was randomly selected (constrained by region), and then a quadrat selected at random from each sampling event (10 sampling events). This process was repeated 6 times and generated a sample of 60 quadrats. Data were then averaged across seasons and years and normalized to 100% cover to generate 1 estimate of community composition. This method was repeated 300 times for each region producing a total of 900 empirical estimates of community composition (300 per region \times 3 regions). Regional-scale estimates used the same method as those for the mesoscale, but without constraining site selection by

region. This process produced a total of 900 empirical estimates of community composition.

Analysis of spatial variation

The effect of spatial variation on MMCM performance was tested by estimating the magnitude of the difference between model and empirical community composition estimates for each pooling level (e.g. local-scale predictions vs. local-scale observations). Rather than using p-values from significance tests, differences were assessed using raw test statistics as suggested by White et al. (2014) when interpreting simulation model results. Prior to testing for differences in community composition, differences in dispersion were tested with a permutational multivariate dispersion analysis (PERMDISP; Anderson 2006) using Bray-Curtis dissimilarities of $\log(x + 1)$ transformed species percent cover data with group (predicted vs. empirical) as a fixed factor. PERMDISP is a resemblance-based permutation test focused on whether the average within-group distance to group centroid differs among groups. PERMDISP pseudo- F estimates can be used to measure variability of community composition among groups, but the method also tests for homogeneity of dispersion, an assumption of many multivariate analyses (e.g. ANOSIM, Mantel test). PERMDISP was run separately for each pooling level (local, meso-, and regional scales), and for each region within local and mesoscale pooling levels. Differences between MMCM and empirical estimates of community composition (species percent cover) were then tested using a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) and Bray-Curtis dissimilarities of $\log(x + 1)$ transformed species percent cover data. PERMANOVA compares multivariate means among groups and is robust to differences in dispersion, as opposed to other tests of community similarity (i.e. ANOSIM and Mantel test; Anderson & Walsh 2013). PERMANOVA is sensitive to dispersion when dealing with unbalanced designs (Anderson & Walsh 2013), which was not the case in these analyses. Again, pseudo- F test statistics were used to assess the magnitude difference among groups, rather than p-values, as recommended by White et al. (2014). As with PERMDISP analyses, PERMANOVAs were run separately for each pooling level and for each region within local and mesoscale pooling levels. Both PERMDISPs and PERMANOVAs were run using the vegan package version 2.0-7 (Oksanen et al. 2013) in R version 3.0.0 (R Development Team 2013). SIMPER (Clarke

1993) analysis using Bray-Curtis dissimilarity of $\log(x + 1)$ transformed species percent cover was used to assess the relative contribution of species-states to differences between model predictions and observations as spatial variation increased. SIMPER analyses were run using the vegan package version 2.0-7 (Oksanen et al. 2013) in R version 3.0.0 (R Development Team 2013).

To understand which transition probabilities differed most across space and which may have led to the disparity between predicted and empirical species percent cover, the mean variance was calculated for each transition probability for pooled data. This variability was calculated as the among-plot ($n = 6$ plots) variance for each transition probability when pooling data for each individual transition matrix during simulations. Mean variance is the average variance for each probability across all the matrices within a pooling group (local scale = 9 matrices; mesoscale = 900 matrices; regional scale = 900 matrices). Increasing variance values indicated greater differences in transition probabilities among pooled matrices during simulations. Variances of 0 were removed when they were the result of multiple zero probabilities. Mean variances ranged between 2.442×10^{-9} and 0.500, increasing with spatial scale from 0.0293 to 0.0379 (local scale: 0.0293 ± 0.0032 , mean \pm SE; mesoscale: 0.0350 ± 0.0003 ; regional scale: 0.0379 ± 0.0003). Heat maps were used to investigate changes in the distribution of this variance among model elements as greater spatial scales were pooled. Model elements with greater variance represented greater differences in the transition probabilities across that particular spatial scale.

Simulating temporal variation

Testing the effects of sampling frequency

Cape Ann data (the dataset with the greatest temporal resolution) were resampled at different temporal frequencies to test the effects of sampling interval on estimated community composition. Altering the sampling frequency simulated the incorporation of different scales of temporal variation in transition probabilities. Six sampling intervals pooled transitions over different periods of time (annual, biannual, and seasonal) and utilized data from either the maximum sampling frequency (using all sampled intervals; referred to as 'average') or the minimum sampling frequency (using data from the beginning and end of the time period): annual, average-annual,

biannual, average-biannual, seasonal, and average-seasonal (Fig. 3).

Annual transition probabilities were calculated from the probability of summer–summer transitions using sampling point-occupancy in the summer (July) of all years (Fig. 3). Data were pooled by site and across years producing 3 unique matrices, 1 for each Cape Ann site. Average-annual matrices sampled all transitions across all months, seasons, and years and pooled them by site (Fig. 3). This approach generated 3 transition probability matrices, 1 for each site.

For biannual and seasonal probabilities, point-occupancy was sampled at the beginning and end of each period. Biannual periods were spring/summer (sp/su; March–September), and fall/winter (fa/wn; September–March) (Fig. 3C; $n = 2$ matrices per site). Seasonal periods were spring (sp; March–June), summer (su; June–September), fall (fa; September–December), and winter (wn; December–March) (Fig. 3E; $n = 4$ matrices per site). Data were pooled by site and across all years (to retain high sample sizes), generating 1 table for each period at each site (biannual: $n = 6$ matrices; seasonal: $n = 12$ matrices; Fig. 3). 'Average' matrices sampled all point occupancy data and pooled data within sampling period, within site, and across years to create 1 matrix for each period at each site (biannual: $n = 6$ matrices; seasonal: $n = 12$ matrices; Fig. 3).

Estimates of predicted community composition were generated for each sampling frequency using eigenvalue and eigenvector analysis of the probability matrix (e.g. Caswell 2001) similarly to previously described local-scale methods when simulating spatial variation with transition probability data. These methods pooled data into 1 time-invariant probability table, producing 1 community composition estimate per site per sampling interval (6 per site; annual, average-annual, biannual, average-biannual, seasonal, average-seasonal). For biannual, average-biannual, seasonal, and average-seasonal matrices, composition was also calculated from probability matrices derived from the product of seasonal matrices (e.g. Wootton 2001a). Matrices were multiplied in sequence using all possible seasonal sequences ending with each of the 4 different seasons (biannual and average-biannual: sp/su-fa/wn and fa/wn-sp/su; seasonal and average-seasonal: sp-su-fa-wn, su-fa-wn-sp, fa-wn-sp-su and wn-sp-su-fa). This process incorporated seasonality into the MMCM and produced 2 and 4 additional community composition estimates, respectively, per site per sampling interval. In total, 18 estimates of community composition were gener-

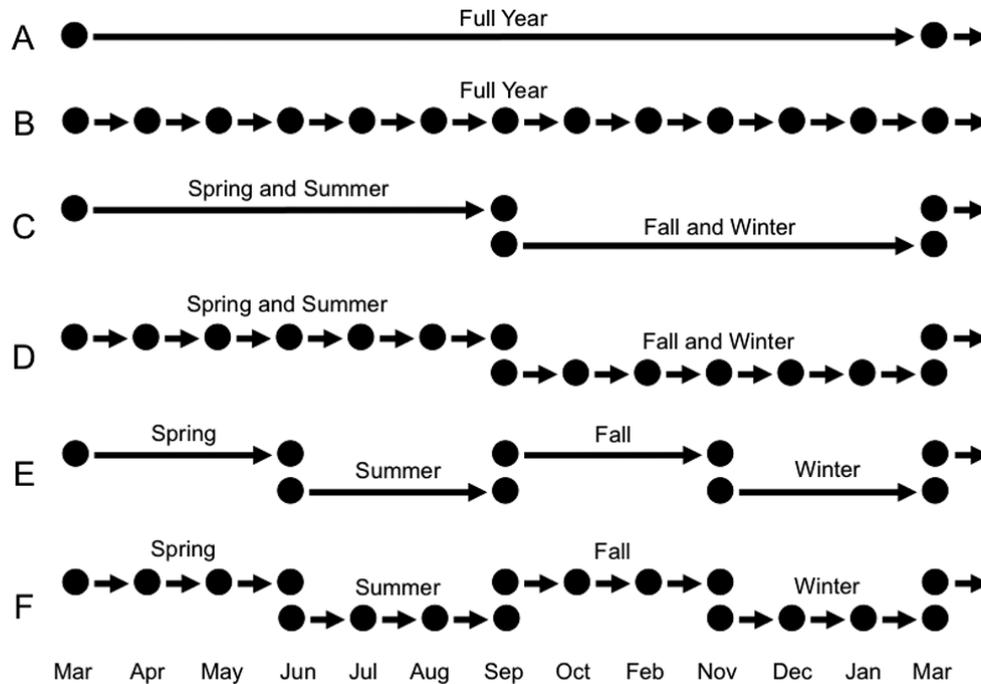


Fig. 3. A visualization of how sampling intervals (monthly) over a year are used to generate transition probability tables when simulating temporal variation (A: annual; B: average-annual; C: biannual; D: average-biannual; E: seasonal; F: average-seasonal). A unique table was generated for each season (full year, spring and summer, fall and winter, spring, summer, fall, winter) for each model scale

ated per site, each using a different sampling frequency or seasonal sequence in the MMCM).

Empirical estimates of community composition

Estimates of empirical community composition averaged all quadrats from the independent transects by site and across years and seasons and then renormalized the estimates to sum to 100% cover (similar to previously described local-scale methods when simulating spatial variation with empirical estimates of community composition). As before, this estimate was assumed to represent the average community composition of the system, and assumed to be comparable to model predictions of stable-stage. This produced 1 empirical community composition estimate per site.

Analysis of temporal variation

Temporal variation was analyzed in 3 ways: differences between predicted and empirical community composition (e.g. annual matrix MMCM estimates vs. empirical estimates), differences between the transition probabilities generated by each sampling fre-

quency (e.g. annual probabilities vs. average-annual probabilities), and differences in transition probabilities among seasons (e.g. seasonal spring probabilities vs. seasonal summer probabilities). Differences between transition probabilities among sampling frequencies ($n = 21$ comparisons) and seasons ($n = 42$ comparisons) were tested using a chi-square test with p-values calculated by Monte Carlo simulation (999 permutations). Differences between predicted and empirical community composition were estimated with PERMDISP and PERMANOVA separately for each sampling frequency and seasonal sequence. As before, pseudo- F test-statistics were used to assess the magnitude difference among groups, rather than p-values, as recommended by White et al. (2014). This method generated 18 total comparisons for each site (1 for each sampling frequency and seasonal sequence, and run with or without seasonality). Differences between predicted and empirical community composition were also tested by estimating R^2 values for relationships between MMCM predicted and empirical $\log(x + 1)$ transformed species percent cover. To further investigate the impact of decreasing sampling frequency on individual matrix elements, annual transition probabilities for each site were subtracted from their respective average-annual probabilities and patterns assessed using a heat map.

RESULTS

Site characteristics and overall model assumptions and performance

Sites and Regions did not differ in tidal height of plots (ANOVA: Site[Region], $F_{6,45} = 0.5677$, $p = 0.7537$; Region, $F_{2,45} = 0.0873$, $p = 0.9165$) or wave exposure (ANOVA: Site[Region], $F_{6,8.014} = 0.8149$, $p = 0.5871$; Region, $F_{2,8.247} = 0.0865$, $p = 0.9180$). Point-occupancy sampling error was 7% (30/425 resampled points) and did not vary among regions (logistic regression, $\chi^2 = 2.673$, $df = 2$, $p = 0.2627$). Sample sizes were not adequate to test differences in error among sites or species-states. Though it is possible that sampling error was disproportionately greater for smaller and rarer species, qualitative assessment of the dataset suggested this was not the case. Although methods exist to correct for the effects of sampling

errors (e.g. Conway-Cranos & Doak 2011), we chose to leave transitions unaltered since error was generally low. The 9 sites met model assumptions of having significantly different transition probability tables ($\chi^2 = 2637.1608$, $df = 1456$, $p < 0.0001$), justifying them being treated separately. All transition probability tables were at least first-order Markovian processes, as opposed to zero-order, also satisfying model assumptions (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m583p015_supp.pdf). Predicted species percent cover from MMCMs based on data pooled on a local scale was highly correlated with independent empirical community composition estimates for all sites, explaining on average (\pm SE) $95.7 \pm 1.3\%$ of the variation (Fig. 4) and suggesting communities resided at a stable-stage (e.g. Horn 1975). The greatest errors in predicting species percent cover involved under-predicting encrusting algal cover and over-predicting cover of the next most abundant

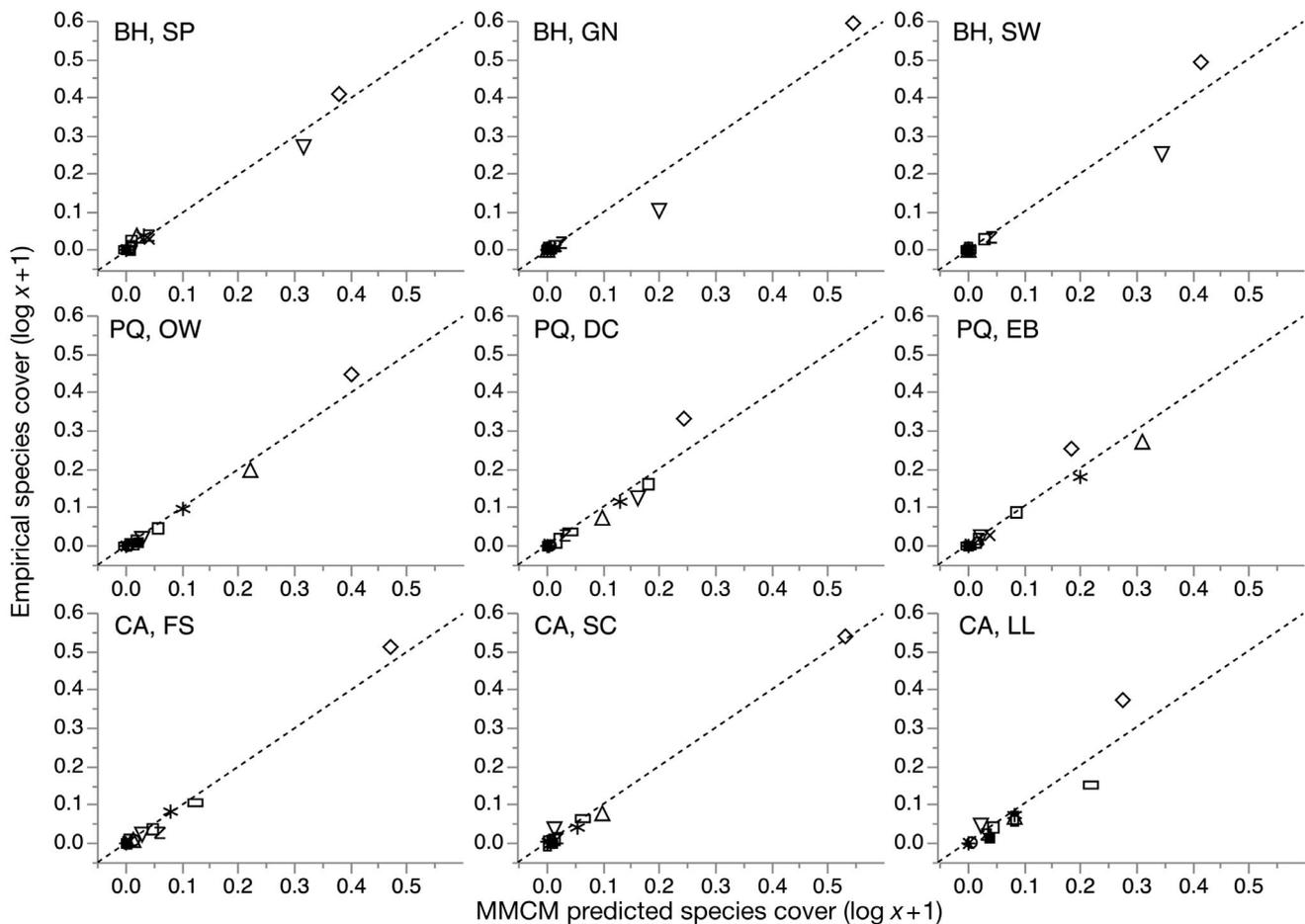


Fig. 4. Relationships between MMCM predicted and empirical $\log(x + 1)$ transformed species percent cover in intertidal communities in the Gulf of Maine, using site-specific models. Species abbreviations (see Table 1): (●) AN, (+) AS, (×) BR, (□) BS, (◇) EA, (△) EC, (▽) Ep, (Z) FV, (○) HY, (◻) ME, (◻) PT, (×) RA, (■) RF, (▽) SB. Site-specific R^2 values: SP = 0.983, GN = 0.963, SW = 0.945, OW = 0.990, DC = 0.921, EB = 0.941, FS = 0.992, SC = 0.995, LL = 0.883 (see Fig.1 legend for site name abbreviations). Dashed line represents 1:1 linear fit

species-state at a site, typically blue mussel *Mytilus edulis*, encrusting coralline, or barnacle *Semibalanus balanoides* (Fig. 4). Rare species were also generally over-predicted by the model, except for *Ascophyllum nodosum* which was, on average, under-predicted (Fig. 4).

Effects of spatial variation on model performance

As the spatial extent over which plots were pooled increased, PERMDISP and PERMANOVA pseudo-*F* values also increased, indicating predictions became less similar to observations in multivariate dispersion and center, respectively (Fig. 5). This pattern did not seem to be driven by increases in sample size with simulation scale since mean square values for the effect (the numerator) rather than the residuals (the denominator) most clearly increased with scale in the

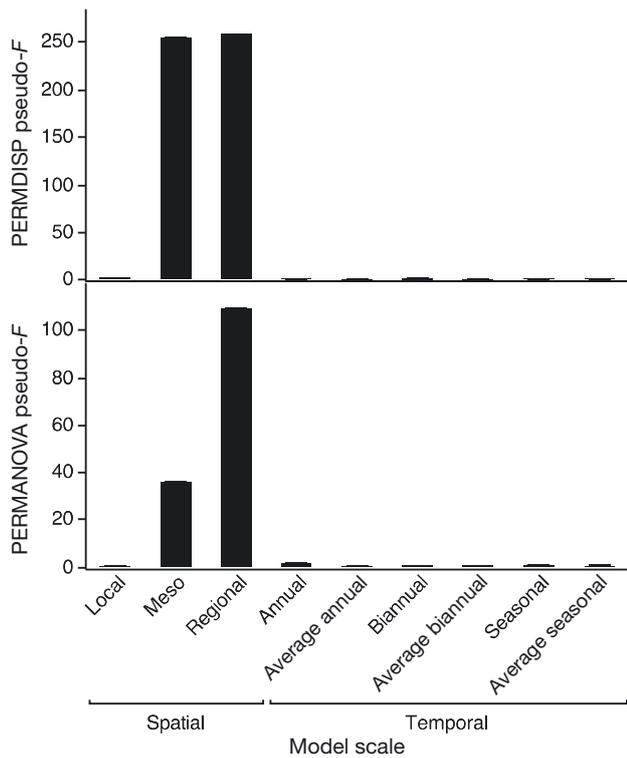


Fig. 5. Permutational multivariate dispersion analysis (PERMDISP) and permutational multivariate analysis of variance (PERMANOVA) results (pseudo-*F* test statistic) for differences between MMCM predicted and empirical log(*x* + 1) transformed species cover (%) in intertidal communities in the Gulf of Maine, incorporating increasing amounts of natural spatial (local, meso-, and regional scale) and temporal (annual, average-annual, biannual, average-biannual, seasonal, average-seasonal) variation. Values for temporal models reflect means (±SE) of multiple models within a scale, each with a different ending season (see Table 7). See Tables S2 & S3 in the Supplement for details of the analysis

calculation of pseudo-*F* (Tables S2 & S3). According to SIMPER analysis, abundant species-states (e.g. *M. edulis*, encrusting coralline, red algae, *S. balanoides*, encrusting algae) contributed the most (75% cumulative contribution) to differences between empirical and MMCM predicted percent cover at all simulated scales (Tables 2–4).

As the spatial scale over which transitions were pooled increased from local to regional, the probability of a species-state persisting (self–self transition), or transitioning to bare rock, encrusting algae, and

Table 2. Results from SIMPER analysis using Bray-Curtis dissimilarity to compare MMCM predicted and empirical log(*x* + 1) transformed percent species cover from local-scale spatial simulations of intertidal community structure in the GOM. Species-states are listed in order of percent contribution to differences. See Table 1 for abbreviations

Species-state	% contribution	Cumulative contribution
EA	0.2268	0.2268
SB	0.2016	0.4284
EC	0.1671	0.5955
RA	0.1049	0.7004
ME	0.1040	0.8045
BS	0.0782	0.8827
PT	0.0319	0.9146
FV	0.0242	0.9388
BR	0.0218	0.9605
RF	0.0150	0.9755
EP	0.0116	0.9871
HY	0.0087	0.9958
AN	0.0028	0.9986
AS	0.0014	1.0000

Table 3. Results from SIMPER analysis using Bray-Curtis dissimilarity to compare MMCM predicted and empirical log(*x* + 1) transformed percent species cover from mesoscale spatial simulations of intertidal community structure in the GOM. Species-states are listed in order of percent contribution to differences. See Table 1 for abbreviations

Species-state	% contribution	Cumulative contribution
SB	0.2100	0.2100
EA	0.1950	0.4049
EC	0.1732	0.5781
RA	0.1140	0.6921
ME	0.1123	0.8044
BS	0.0821	0.8866
PT	0.0285	0.9151
FV	0.0245	0.9397
BR	0.0228	0.9625
RF	0.0132	0.9756
EP	0.0102	0.9859
HY	0.0097	0.9956
AN	0.0028	0.9984
AS	0.0016	1.0000

Table 4. Results of SIMPER analysis using Bray-Curtis dissimilarity to compare MMCM predicted and empirical $\log(x + 1)$ transformed percent species cover from regional-scale spatial simulations of intertidal community structure in the GOM. Species-states are listed in order of percent contribution to differences. See Table 1 for abbreviations

Species-state	% contribution	Cumulative contribution
EA	0.2146	0.2146
SB	0.1684	0.3829
EC	0.1564	0.5394
RA	0.1063	0.6457
ME	0.0982	0.7439
BS	0.0919	0.8358
PT	0.0411	0.8769
FV	0.0360	0.9128
BR	0.0351	0.9479
RF	0.0200	0.9678
HY	0.0143	0.9822
EP	0.0119	0.9941
AN	0.0036	0.9977
AS	0.0023	1.0000

encrusting coralline became more different among plots (Fig. 6). The latter reflects changes in species mortality, since transitions to and from substrates otherwise available for recruitment and overgrowth by sessile species (bare rock, encrusting algae, and encrusting coralline, as suggested by Elahi & Sebens 2012) can be considered estimates of mortality and

colonization, respectively (e.g. Tanner et al. 1994). Qualitatively, differences in transitions from more rare species increased when pooling at the meso-scale (Fig. 6), while differences in transitions among more common species (*S. balanoides*, red algae, *M. edulis*), and from bare rock, encrusting algae, and encrusting coralline to common species (i.e. colonization), increased when pooling at the regional scale (Fig. 6).

Effects of sampling frequency (temporal variation) on model performance

For all sites within Cape Ann, transition probabilities differed among seasons and sampling frequencies (Tables 5 & 6). Despite these differences, decreasing sampling frequency had a marginal effect on the Markov model's ability to predict community composition (Tables 7 & 8). Pseudo- F values from PERMDISPs and PERMANOVAs were consistently low relative to spatial simulation analyses, closely resembling pseudo- F estimates from the local-scale pooling level, and well below those from the meso- and regional-scale simulations (Fig. 5). Based on correlations between empirical and MMCM predicted $\log(x + 1)$ transformed species percent cover, average-seasonal (ending the model in the summer), seasonal (without seasonality), and average-annual

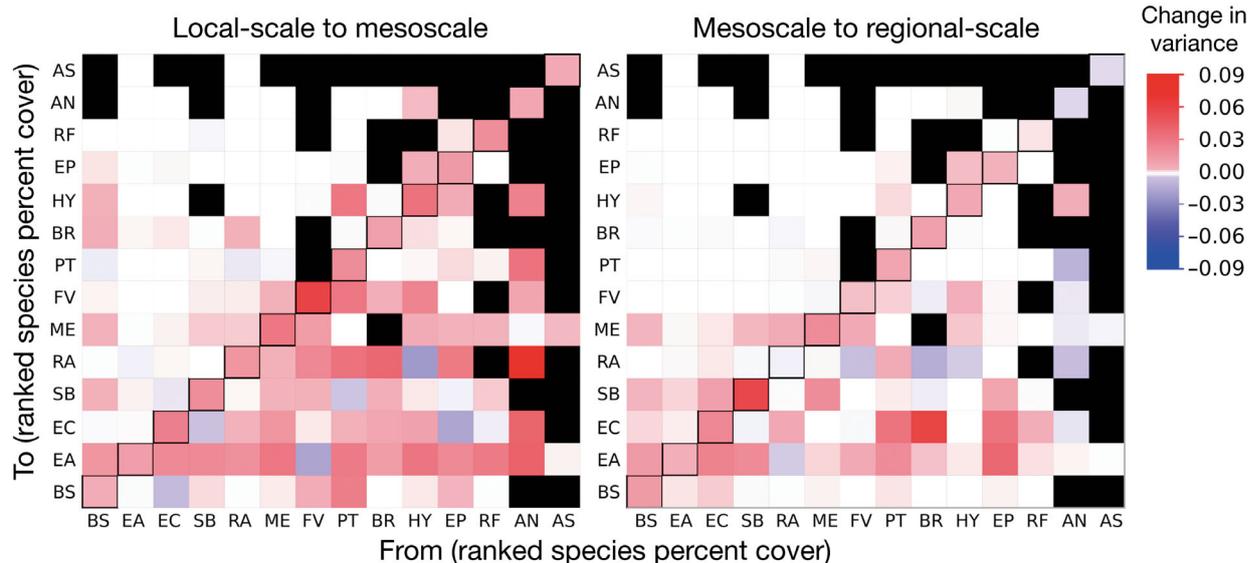


Fig. 6. Map showing changes in the mean variance for each transition probability when pooling data at increasing scales (local to meso, meso to regional). Greater amounts of red and blue represent a higher variance when pooling at the larger and smaller spatial scale, respectively. Black cells represent transitions with probabilities of zero leading to no variance on either scale. Species-states are in descending order of average abundance across all sites, except that 'available' states (bare rock, encrusting algae, encrusting coralline) are first. See Table 1 for species abbreviations

Table 5. Results from pairwise comparisons of transition probability tables for sites in Cape Ann region, Gulf of Maine for each combination of temporal model, season, and site using a chi-square test of similarity and a permutational analysis for p-values. FS: UMass Field Station; SC: Seaside Cemetery; LL: Loblolly Point. Data are displayed as χ^2 and $p < 0.001$ for all model combinations

Scale	Season	LL	SC	FS
Biannual	Spring and summer vs. fall and winter	3826.0	2437.7	2878.5
Average-biannual	Spring and summer vs. fall and winter	9813.9	3514.6	5453.0
Seasonal	Spring vs. summer	3009.1	2567.5	2143.0
	Spring vs. fall	3271.4	2888.1	3002.0
	Spring vs. winter	2940.2	2774.1	2076.5
	Summer vs. fall	4507.5	2987.6	2653.6
	Summer vs. winter	2934.7	2079.4	1931.9
	Fall vs. winter	3608.8	2301.2	2384.1
Average-seasonal	Spring vs. summer	6827.7	4196.4	5369.7
	Spring vs. fall	5661.5	2830.4	4490.7
	Spring vs. winter	4470.1	3105.7	3623.3
	Summer vs. fall	7377.8	3583.8	5211.2
	Summer vs. winter	4954.3	3066.6	3394.5
	Fall vs. winter	3875.5	2644.4	3204.4

sampling best predicted empirical estimates of community structure (Table 7). Annual sampling, and biannual and average-biannual models (ending in the spring and summer), were least capable of predicting community structure, but still managed to explain >82% of the variation in empirical estimates (Table 7). There were larger overall differences among sampling frequency estimates for Loblolly Point than for Seaside Cemetery and UMass Field-Station (Table 8), which cannot easily be explained.

Less frequent sampling (annual) consistently resulted in a lower probability of persistence for all species-states (Fig. 7). Additionally, lower sampling frequency resulted in overall lower probabilities of transitioning to and from rare species-states, and higher probabilities of transitioning to and from common species-states (Fig. 7). This change was most pronounced in probabilities of transitioning to abundant species (Fig. 7). Such a pattern highlights persistence and transitions to common species as matrix elements most heavily impacted by reduced sampling frequency and suggests a disparate impact of sampling frequency on rare and common species-states. The difference in effect on common versus rare species partly resulted from decreased sample sizes (number of total transitions from an individual species-state; S. L. Morello pers. obs.) when calcu-

lating probabilities, but also likely reflects competitively dominant species-states frequently reclaiming space in the intertidal communities.

DISCUSSION

Spatial variation in the ecological processes captured by transition probabilities (i.e. species interactions, environmental forces) at meso- and regional scales in the GOM intertidal had a greater impact on estimates of community structure, and the ability of MMCMs to predict community structure, than equivalent seasonal or annual variation. Although we expected large-scale spatial variation would be important for predicting community structure, the minimal

Table 6. Results from pairwise comparisons of transition probability tables for sites LL, SC and FS (see Table 5 legend for abbreviations) generated with minimum sampling frequency (using data from the beginning and end of the time period: annual, biannual, seasonal) and maximum sampling frequency (using all sampled intervals; referred to as 'average') for each temporal model and season using a chi-square test of similarity and a permutational analysis for p-values. Data are displayed as χ^2 , and $p < 0.001$ for all model combinations

Temporal models compared	Season	LL	SC	FS
Annual vs. average-annual	Annual	6169.3	4742.2	4887.2
Biannual vs. average-biannual	Spring and summer	5860.0	3478.7	3834.6
	Fall and winter	7053.5	2986.6	4591.3
Seasonal vs. average-seasonal	Spring	4443.1	3588.5	3899.9
	Summer	6797.1	4659.2	3696.9
	Fall	5941.3	3387.1	4683.7
	Winter	4565.0	3460.2	3526.8

Table 7. Correlations between MMCM predicted and empirical $\log(x + 1)$ transformed percent species cover for each temporal model and seasonal sequence. Note: The 'Ending season' column shows the last season in the corresponding MMCM sequence. 'Full year' indicates that seasonality was not incorporated into the model

Temporal scale	Ending season	R ² (mean ± SE)
Annual	Full year	0.863 ± 0.048
Average-annual	Full year	0.973 ± 0.021
Biannual	Full year	0.92 ± 0.05
Biannual	Spring and summer	0.829 ± 0.145
Biannual	Fall and winter	0.904 ± 0.072
Average-biannual	Spring and summer	0.903 ± 0.086
Average-biannual	Fall and winter	0.939 ± 0.052
Seasonal	Full year	0.961 ± 0.025
Seasonal	Spring	0.911 ± 0.031
Seasonal	Summer	0.957 ± 0.017
Seasonal	Fall	0.914 ± 0.063
Seasonal	Winter	0.929 ± 0.061
Average-seasonal	Spring	0.94 ± 0.045
Average-seasonal	Summer	0.979 ± 0.01
Average-seasonal	Fall	0.949 ± 0.039
Average-seasonal	Winter	0.942 ± 0.049

Table 8. Correlations between MMCM predicted and empirical $\log(x + 1)$ transformed percent species cover for all temporal models from sites LL, SC and FS. See Table 5 legend for abbreviations

Site	R ² (mean ± SE)
LL	0.837 ± 0.026
SC	0.973 ± 0.011
FS	0.967 ± 0.012

impact of seasonal and annual variation was surprising. Our results augment research from a range of ecosystems (Cornell & Harrison 2013, Fenberg et al. 2015, Ricklefs & He 2016) that suggest larger-scale and, probably, longer-term processes are the more critical drivers of pronounced shifts in the assembly, structure, and dynamics of communities. Our approach utilized Markov models that allowed us to incorporate a comprehensive set of species from the regional pool and transitions that integrated over the complex species interactions critical for accurate prediction of the consequences of ecological dynamics. MMCMs are effective at predicting community structure in a range of ecosystems and can be used to generate specific hypotheses regarding the potential drivers of community change across larger scales.

Spatial variation

The Markov models' success at predicting intertidal community composition (percent species cover) at all sites (Fig. 4) is consistent with previous studies in marine (e.g. Tanner et al. 1994, Wootton 2001a, 2004, 2013) and terrestrial (e.g. McAuliffe 1988, Balzter 2000, Nelis & Wootton 2010) systems that use MMCMs to estimate and simulate community structure on local scales. As natural spatial variation in transition probabilities beyond the local scale was incorporated into the model, model performance degraded and differences in accuracy (center, PERMANOVA) and precision (dispersion, PERMDISP) from observations became progressively more pronounced

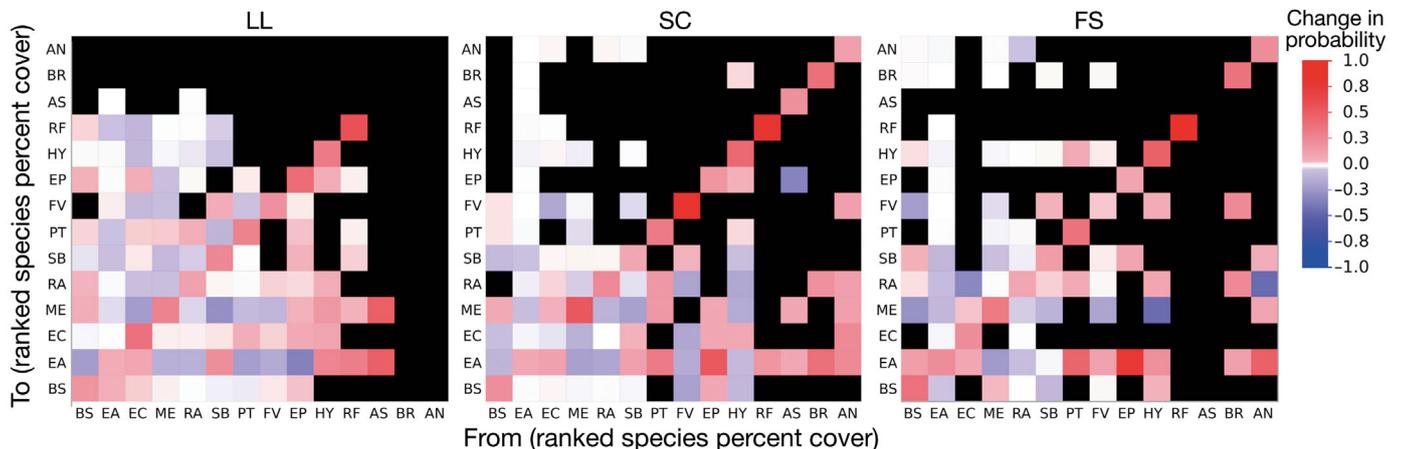


Fig. 7. Map showing magnitude difference (average-annual – annual) in each transition probability for Cape Ann site data sampled at average-annual and annual frequencies. Greater amounts of red and blue represent a higher probability in the average-annual or annual table, respectively. Black cells represent transitions with probabilities of zero for both sampling frequencies. Species-states are in descending order of average abundance across all Cape Ann sites, except that 'available' states (bare rock, encrusting algae, encrusting coralline) are first. See Table 1 for species abbreviations

(Fig. 5). Although it is unsurprising that a high magnitude of spatial variation would reduce model accuracy and precision, the results highlight the site specificity of MMCM transition probabilities and the potential for larger-scale processes to alter them. Further, the results support previous research concluding that the local-scale processes (i.e. competition, consumer pressure, disturbance) captured by our site-specific MMCMs are important to maintaining local GOM intertidal community structure (Lubchenco & Menge 1978, Menge & Sutherland 1987, Petraitis & Dudgeon 1999, Bertness et al. 2004), but suggests that processes acting on meso- and regional scales alter those at local scales, bringing about regional shifts in community structure across the GOM (e.g. Bryson et al. 2014).

Local communities differed among our regions (Morello 2015). The transitions among more common species (*Semibalanus balanoides*, red algae, encrusting coralline, *Mytilus edulis*) and those related to mortality, persistence, and colonization, varied most regionally (Fig. 6) and had the greatest impact on producing dramatically different (multivariate center and dispersion) community structures in simulations (Fig. 5). The regional shifts in transition probabilities indicate that local ecological processes changed in their nature, intensity, and/or rate. It is possible that these variations came about due to different starting conditions or environmental contexts. Regional variation in community structure was largely maintained over the course of the study (S. L. Morello pers. obs.), and so empirical differences in community structure among sites (Fig. 4; Morello 2015) reflect different starting conditions. Although we lack a means to distinguish the direct role of regional- and/or local-scale processes for driving the patterns observed, such changes are often driven by regional differences in abiotic and biotic conditions (Wiens 1989, Levin 1992). Consequently, we posit that variation in transition probabilities we observed at the regional level, and was important to MMCM community composition outcomes, is likely influenced by an interaction between local and regional ecological drivers.

Ecological processes acting on multiple scales (local: 100s of m; meso-: 10s of km; regional: 100s of km) work in concert to modulate the interactions among species, resulting in complex patterns in community structure (Wiens 1989, Levin 1992). Research in terrestrial systems demonstrates large-scale patterns in topography, climate, and air/watershed dynamics interact with local species interactions, water/soil chemistry, and temperature to structure plant, aquatic, and bacterial communities (lakes and

streams: Soranno et al. 1999, Jackson et al. 2001; insects: Menke et al. 2014; vegetation: Chase 2014, Michalet et al. 2015; deserts: Ernest et al. 2008; bacteria: Ranjard et al. 2013, Tripathi et al. 2014). Likewise, research in intertidal systems has highlighted the interaction between larger-scale physical oceanographic processes (e.g. currents, upwelling regimes) with local-scale physical (e.g. temperature, wave stress, ice scour) and biological (e.g. competition, consumer pressure) processes in causing regional shifts in community assembly and structure (Sanford et al. 2003, Navarrete et al. 2005, Blanchette et al. 2008, Menge et al. 2011, 2015).

In the GOM, transitions related to species mortality and persistence became increasingly different at larger scales (Fig. 6). Since wave exposure (the major source of physical disturbance in the system; Lubchenco & Menge 1978) did not differ among our sites, albeit over a short measurement period, meso- and regional-scale differences in persistence and mortality more likely reflect differences in the frequency of disturbance (e.g. ice scour; Wethey 1985), consumer abundance (Bryson et al. 2014), consumer efficacy (Sanford 1999, Kordas & Dudgeon 2011), and/or physiological stress (Helmuth et al. 2006, Somero 2012). Consumer pressure varies within and among regions in the GOM (Kordas & Dudgeon 2011, Bryson et al. 2014), resulting in differences in community structure for the same interactions between sessile invertebrates and fucoid algae. The fact that transitions related to colonization also differed at regional scales supports a hypothesis of shifts in species recruitment and/or growth potentially interacting with the regional variation in mortality to bring about shifts in GOM intertidal communities, as proposed by Bryson et al. (2014). Regional patterns of intertidal community structure in the GOM might be related to major physical oceanographic boundaries in the predominant coastal current (Eastern Maine Coastal Current vs. Western Maine Coastal Current; Pettigrew et al. 2005, Bryson et al. 2014) and north-south gradients in sea-surface and air temperature (Friedland & Hare 2007, Kordas et al. 2011), which differ across similar scales. Among our regions, sea-surface and air temperatures increase from Bar Harbor to Pemaquid to Cape Ann (Friedland & Hare 2007, Kordas et al. 2011), and coastal currents likely predominantly transport larvae and resources in one direction (northeast to southwest; Pettigrew et al. 2005), but may vary regionally in their frequency and degree of across-shelf exchange (Tilburg et al. 2012). Our Pemaquid and Cape Ann regions also fall within a different coastal current (Western Maine Coastal

Current) than our Bar Harbor region (Eastern Maine Coastal Current; Pettigrew et al. 2005). Any or all of these processes could influence mortality and colonization transitions alone or in concert, are the most evident ecological processes changing over regional scales in the GOM, and are probably critical to explaining the importance of large-scale spatial variation in our results.

The New England rocky intertidal is a highly variable environment however, even at small spatial scales (Lubchenco & Menge 1978, Menge & Sutherland 1987, Petraitis & Dudgeon 1999, Bertness et al. 2004), with complex micro-scale spatial variation that can be important for structuring communities (Sanford 1999, Helmuth et al. 2006). The MMCM captured the ecologically important elements of that variation in as few as ~2.5 yr with 6 randomly spaced plots, indicating it is an effective tool for understanding and forecasting community structure at local scales, even in relatively heterogeneous ecosystems. The change in transition probabilities beyond local scales indicates that MMCMs might also be useful in generating specific hypotheses regarding the ecological pathways and forces that drive changes in community structure over larger scales, which could then be tested experimentally, similarly to previous comparative studies (e.g. between treatments: Nelis & Wootton 2010; among ecosystems: Wootton 2001c, Hill et al. 2004; with environmental change: Wootton et al. 2008). Such an approach provides a novel and potentially powerful application for MMCM datasets in any ecosystem. Preliminary analysis of transition probabilities across the GOM suggest that interactions between consumer pressure and species colonization (i.e. recruitment and growth) may drive community change; specifically regional differences in mortality of the primary space occupiers, and recruitment and growth of blue mussels *M. edulis* and barnacles *S. balanoides* (Morello 2015).

Temporal variation

Reducing the sampling frequency altered the magnitude of transitions (Table 6), decreasing persistence and interactions with rare species, and increasing interactions among abundant species (Fig. 7). These changes were caused by missing transitions and led to the addition of pathways that would otherwise not have occurred. The disproportionate increase in transition probabilities of abundant species is consistent with their competitive dominance in the

community and their ability to reclaim lost space over short periods of time (Lubchenco & Menge 1978). It may also reflect strong interactions by a common 'core' group of species dominating community dynamics, while rare 'satellite' species are less important to stable stage community structure (core-satellite hypothesis; Hanski 1982). While such variation in probabilities did not significantly impact model performance, it could influence conclusions regarding complexity of species interactions, the pathways of community assembly, and community dynamics involving rare species. This problem is common with time-homogenous Markov chains utilizing infrequent sampling intervals, but can be resolved using continuous-time models (Spencer & Susko 2005) if high frequency sampling data are not available.

Nevertheless, increasing the amount of fine-scale temporal variation (more frequent sampling intervals) had only slight effects on the predictions of the MMCM. Even at one of its least predictive and most coarse temporal scales (annual sampling), the model performed well, predicting >86% of variance on average in empirical community structure at all sites (Table 7). The minor role small-scale temporal variability plays in model performance at most sites implies that the impact of interactions occurring on such short time scales (e.g. seasonality, timing of recruitment, ephemeral species, an abnormally high recruitment event) on the long-term community structure is reasonably well estimated by annual transition probabilities. This result is unexpected since some consider the GOM intertidal as more heavily influenced by seasonality than other intertidal systems (Menge & Sutherland 1987). Recent research has also highlighted the potential importance of the seasonal timing of larval recruitment on community dynamics in the GOM (Kordas & Dudgeon 2011). We did not test the effect of temporal variation beyond an annual scale, but other intertidal Markov chain studies that incorporated up to 4 yr of temporal variation with continuous time models predicted similar community structure relative to time homogenous models and captured >98% of the variance in empirical community structure (Wootton 2001a), suggesting this level of annual variation had little impact on predictions of stable-stage community structure. Though not directly tested here, our results leave open the possibility that processes acting across longer time scales (e.g. climate, dispersal pathways, exposure, regional species pool and abundance, etc.) play a more important role in the stable-stage composition of GOM intertidal communities. Long-term changes in the abundance and distribu-

tion of subtidal herbivores and predators may be important, especially as they relate to species introductions and the consequences of fishing pressure (Harris & Tyrrell 2001, Frank et al. 2005, Steneck et al. 2013). It is also thought that decadal-scale climatic cycles (e.g. North Atlantic Oscillation) are important in modulating bottom-up forces in the GOM and bringing about shifts in marine communities (Townsend et al. 2010, Greene et al. 2013, Pershing et al. 2014). To date, the impacts of long-term changes in oceanographic processes have not been quantitatively tested for GOM intertidal communities, although there is evidence that long-term changes in temperature may be critical to these communities (Kordas & Dudgeon 2011, Sorte et al. 2017), and that plankton communities (Conversi et al. 2001, Pershing et al. 2005, 2014) and the abundance of competitively dominant intertidal species (Petraitis & Dudgeon 2015) have fluctuated over similar time scales. Quantifying of transition probabilities over longer time frames might be able to capture important ecological cycles in the GOM, as in other systems (e.g. Wootton et al. 2008).

The species interactions occurring over short periods of time are still important to community dynamics. There is ample evidence that species interactions are important to the structure of communities in the GOM intertidal (Lubchenco & Menge 1978, Menge & Sutherland 1987, Petraitis & Dudgeon 1999, Bertness et al. 2004, Kordas & Dudgeon 2011, Bryson et al. 2014) and elsewhere (Dayton 1971, Grime 1973, Tilman 1982). Instead, our results suggest that the outcome of community dynamics is relatively stable over the short-term in the GOM intertidal, and that significant shifts in community composition more likely result from longer-term climatic and physical oceanographic processes than from monthly and seasonal variation in temperature, food resources, consumer pressure and/or disturbance rates. Some research has proposed that singular large disturbances can be important in shifting intertidal communities towards an alternative stable state in the GOM (Petraitis & Dudgeon 1999), but others have shown community structure to be highly deterministic and controlled by biotic and abiotic factors (Lubchenco & Menge 1978, Menge & Sutherland 1987, Bertness et al. 2004). One such disturbance was observed during this study (Hurricane Irene on August 28, 2011), clearing large sections (several meters long) of the intertidal at all sites (S. L. Morello pers. obs.), but did not result in a shift in community dominance following 5 yr of recovery (S.L. Morello pers. obs.). Since large-scale spatial variation in ecological processes

(i.e. transition probabilities) appeared to be more important than short-term temporal variation for shifts in community structure during this study, it is possible that discrepancies between experiments in the GOM (Petraitis & Dudgeon 1999 vs. Bertness et al. 2004) are at least partly driven by regional differences in ecological processes, as concluded by Bryson et al. (2014).

CONCLUSIONS

Temporal variation in community dynamics, especially over monthly and seasonal scales, did not affect our ability to predict local community structure. MMCMs effectively captured community structure on local scales in a range of ecosystems, despite infrequent sampling strategies, suggesting that short-term fluctuations in community dynamics had little influence on local-scale community structure. Long-term (>10 yr) changes are known to be critical to explaining dramatic shifts in community structure in many ecosystems (Stenseth et al. 2002, Harley et al. 2006, Parmesan 2006, Menge et al. 2011). Unfortunately, the median length of ecological studies in coastal systems is approximately 1 yr (Witman et al. 2015, Jenkins & Uyà 2016), which would miss the effects of longer-term dynamics and distort our perception of the processes that play an important role in the assembly and structure of communities. The ecological processes associated with longer-term temporal shifts in communities are often the same processes attributed to shifts over large spatial scales (e.g. climate, dispersal pathways, oceanography, landscapes, etc.). Thus, the important drivers of community change may be long-term large-scale spatiotemporal processes, which require equally long-term and large-scale ecological research to better understand and contextualize the full range of processes that shape natural ecosystems (Petraitis & Dudgeon 2015).

Generating models of complex community dynamics across multiple scales of space and time is one potential step in determining which sources of ecological variation are most important to communities, and how that variation translates into community change at various scales. The Markov models used here estimated community structure quite well at the local scales on which they are traditionally used, but were less effective at meso- and regional scales. The differences in transition probabilities among localities that caused model predictions to degrade, however, can be used to generate hypotheses regarding

the critical processes that influence regional differences in the assembly, structure and dynamics of communities. This application for MMCMs is currently underutilized, but is a logical next step for application to our data, and similar data, that can serve as a simple, useful, and powerful method for identifying the ecological processes that shape communities in a range of ecosystems.

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