Oecologia (2011) 167:199–207
DOI 10.1007/s00442-011-1979-z

COMMUNITY ECOLOGY - ORIGINAL PAPER

Sampling errors create bias in Markov models for community dynamics: the problem and a method for its solution

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Received: 19 January 2010 / Accepted: 14 March 2011 / Published online: 9 April 2011

Abstract Repeated, spatially explicit sampling is widely used to characterize the dynamics of sessile communities in both terrestrial and aquatic systems, yet our understanding of the consequences of errors made in such sampling is limited. In particular, when Markov transition probabilities are calculated by tracking individual points over time, misidentification of the same spatial locations will result in biased estimates of transition probabilities, successional rates, and community trajectories. Nonetheless, to date, all published studies that use such data have implicitly assumed that resampling occurs without error when making estimates of transition rates. Here, we develop and test a straightforward maximum likelihood approach, based on simple field estimates of resampling errors, to arrive at corrected estimates of transition rates between species in a rocky intertidal community. We compare community Markov models based on raw and corrected transition estimates using data from *Endocladia muricata*-dominated plots in a California intertidal assemblage, finding that uncorrected predictions of succession consistently overestimate recovery time. We tested the precision and accuracy of the approach using simulated datasets and found good performance of our estimation method over a range of realistic sample sizes and error rates.

Keywords Succession · Sampling error · Markov · Intertidal · Transition probabilities

Communicated by Sebastian Diehl.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-1979-z) contains supplementary material, which is available to authorized users.

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Introduction

The most common empirical approach to quantification of community dynamics, and to testing theories that seek to explain these dynamics, is to repeatedly census local community structure, thereby measuring the extent and pattern of shifting community structure (e.g., Collins 2000). In communities dominated by sessile or semi-sessile species, the most refined approach to such sampling is to focus on permanently marked plots and to use point-contact or similar spatially explicit methods to not only measure relative percent cover but also to understand the transition patterns between species at each repeatedly sampled point.

Such data are particularly useful because they allow the construction of Markov community transition matrices (Horn 1975; Tanner et al. 1994; Wootton 2001; Hill et al. 2004). Markov models are powerful tools for the exploration of community dynamics such as disturbance, succession and predation, in part because they are based on transition probabilities between every pair of species (or species groups) in the community, allowing predictions regarding whole-community dynamics and also species-specific effects. For example, when Markov models are used to study successional dynamics (e.g., Horn 1975;

McAuliffe 1988; Tanner et al. 1994; Wootton 2001; Hill et al. 2004), they can provide not only a predictive framework with which to simulate the community response to disturbance (Caswell 2001) but also a tool to study the effects of individual species and their interactions on the rate of succession. However, these and other uses rely on the accurate parameterization of a model from field data.

The key logistical challenge with gathering community data for this purpose is to accurately resample exact spatial locations, so as to correctly estimate transition probabilities between individuals. As far as we can ascertain, all previously published studies have implicitly assumed that spatial resampling is completely accurate. The tools for field sampling are often somewhat crude (e.g., PVC or metal quadrats strung with fishing line or string and cameras mounted on PVC frames), and the sizes of many individuals are often small, increasing the chances of inconsistency in relocating a specific point due to minor changes in the placement of quadrats or to parallax. In most published studies, it is clear that investigators have tried to minimize errors due to quadrat placement or photographic sampling by using devices such as a plumb-bob (Wootton 2001) or photoframe quadripod (Tanner et al. 1994; Hill et al. 2004), but we can find no indication of direct assessment of error.

While attempting to reduce resampling errors is obviously wise, even low error rates will lead to bias—not just noise—in the resulting model analyses. In particular, if error rates are substantial, transitions from relatively rare species to common ones will appear to be far more common than they actually are, while estimated stasis rates of rare species—the maintenance of the same species at a location over time—will be biased low. Since transition probabilities in most communities are often quite low, even a modest error rate could lead to substantial bias in many estimated transition probabilities. Here, we develop a generally usable, maximum likelihood-based approach to account for these errors in order to estimate corrected transition probabilities. To illustrate this approach, we use 4 years of annual censuses of a rocky intertidal community at three sites along the California coast.

Materials and methods

Field sampling

The data used in this study were collected as part of a study of community recovery in a high–mid-intertidal assemblage dominated by the red turf alga *Endocladia muricata* (hereafter referred to as *Endocladia*) in California. We calculated annual Markov chain probability matrices among species groups from three sampling sites over 4 years, using data from three permanent rectangular plots at each site, each containing 100 individual sample points on a 50 × 75 cm grid. We resampled the plots by overlaying a PVC quadrat strung with a grid of 100 points, noting the species present at each point (see Online Resource, Appendix A: Calculation of annual transition matrices). The methods used in these surveys are common and well established, and are typical of other studies in the care with which exact resampling of individual points was attempted.

The first step in correcting for resampling errors is to estimate actual error rates. Classically, ecologists think of false negatives and false positives as distinct error types, but our focus, resampling errors, make both functions of a single error term, the probability of not accurately resampling the same physical point. On 11 March 2008, one of us (L.L.C.-C.) sampled each of 11 rectangular plots three times in a row within the same low tide in the *Endocladia* zone at one of our sites (Point Sierra Nevada). Plots ranged in size from 8 × 12 cm to 50 × 75 cm and were sampled with quadrats strung with a grid to generate from 30–100 sample points (Online Resource, Appendix A, Table A2). This yielded a total of 920 points for each of the three samples. Sampling of each plot was interspersed with that of the other plots to reduce any memory of the specific species found at each point. The sampling grid was removed and replaced each time the plot was sampled in order to recreate the process of adjusting the alignment between the strung quadrat and plot markers. Since the three resamplings of each plot took place within a few hours during the same low tide, virtually all observed changes in the biota at single points were due to slight differences in the placement of the quadrat or parallax of the observer and not because of real changes in the individual plant or animal occupying any given point on the rock. However, given the large number of exact locations sampled, it is unlikely that memory of the species found at each location reduced the error rate below that which would occur in the normal annual resampling.

Development of a method to estimate corrected transition probabilities

To estimate actual transition rates between species, we must express our observed transition rates in terms of the true transition rates, the error rate, and other estimable parameters. For any resampling interval, the probability of observing a transition from species i to j is:

$$q_{ji} = (1 - e)p_{ji} + ef_{j,t} \quad (1)$$

where q_{ji} is the observed probability of seeing species j at the second sampling where species i was observed at the first sampling, p_{ji} is the true probability of transitioning

from i to j, $f_{j,t}$ is the frequency of species j at the second sampling period, and e is the probably of not correctly resampling the same point at both time periods. The first term on the right hand size of this equation represents points that are resampled correctly, while the second term is the probability of an error, e, times the probability that an erroneous resampled point will hit species j. For immediate resampling of the same points, as in our field sampling to establish an error rate, $p_{ii} = 1$, while p_{ji} for all $j \neq i$ equals 0.

Implicit in this use of the probability of an error are two simplifying assumptions. First, we assume that a single error rate applies to all species. In some cases, especially for communities where species are of extremely different size, this may be a poor assumption, since the spatial scale of sampling errors may result in substantial uncertainty in resampling the same individuals of one species, but nearly always allow accurate resampling of other species. If there are consistent differences in error rates between species, species-specific error rates could be used for each. However, errors may well vary with both the starting and ending species for each transition, potentially making estimation of specific error rates quite complicated. A more problematic assumption is that the species within a plot are randomly arranged. Equation 1 implicitly assumes that the chance of an erroneously sampled point landing on each species is strictly proportional to its plot-wide abundance. While spatial patterning is important at many scales in most communities, a correction approach that incorporated spatial structure would require much more detailed sampling at fine spatial scales, data which neither we nor most researchers have.

Equation 1 forms the basis for an expression that summarizes all the possible expected transition probabilities:

$$\boldsymbol{Q} = (1 - e)\,\boldsymbol{P} + e\boldsymbol{F}_t \tag{2}$$

here, $\boldsymbol{Q}$ and $\boldsymbol{P}$ are the full matrices of true, p_{ji}, transition probabilities ($\boldsymbol{P}$) and of observed, q_{ji}, transition probabilities values ($\boldsymbol{Q}$) over a sampling interval. For a community with s species, $\boldsymbol{F}_t$ is an $s \times s$ matrix with s identical columns, each of which represents the frequency distribution of species at the second sampling (comprised of the $f_{j,t}$ values). Finally, $\boldsymbol{F}_t$ can be re-expressed in terms of the vector of starting frequencies, $\boldsymbol{f}_0$, and $\boldsymbol{P}$,

$$\boldsymbol{Q} = (1 - e)\boldsymbol{P} + e\boldsymbol{P}\boldsymbol{f}_0\boldsymbol{1} \tag{3}$$

where $\boldsymbol{1}$ is a row vector of ones, equal in length to $\boldsymbol{F}_t$. Note that for multi-year studies, such as our example datasets, we can generate a separate estimate of $\boldsymbol{Q}$ for each of m transitions, $\boldsymbol{Q}_m$, based on separate $\boldsymbol{P}_m$ matrices, and starting frequencies that all refer back to the initial $\boldsymbol{f}_0$ frequency vector (e.g., $\boldsymbol{f}_2 = \boldsymbol{P}_2\boldsymbol{P}_1\boldsymbol{f}_0$). For rapidly resampled points, P is the identity matrix, $\boldsymbol{I}$, and this general equation simplifies to $\boldsymbol{Q} = (1–e)\boldsymbol{I} + e\boldsymbol{F}_t\boldsymbol{1}$.

With Eq. 3, we have predicted probabilities of each type of observed transition as a function of three sets of parameters: the true transition rates ($\boldsymbol{P}$), the error rate (e) and the initial frequency distribution ($\boldsymbol{f}_0$). Using multinomial probabilities, we can then assess the likelihood of making a set of observations based on our estimates of these parameters. In particular, for s number of states (species or species groups), the log-likelihood of observing an initial distribution of k sampling points with each species, k_i, and the matrix N, comprised of the numbers of points observed to transition from i to j, n_{ji}, for all possible species and over a single time interval is:

$$L(k, N; e, f_0, P) = \sum_{i=1}^{s} k_i \log(f_i) + \sum_{j=1}^{s}\sum_{i=1}^{s} n_{ji} \log(q_{ji}) \tag{4}$$

where the first quantity on the right-hand side is the log-likelihood of obtaining the observed distribution of starting numbers, and the second quantity is the log-likelihood of observing the numbers of points making each transition. For most real sampling schemes, a researcher will sample a set of plots more than once. For M resampling times, the total log-likelihood of the observed data will then be:

$$L(\text{data}; e, f_0, P_1, P_2, \ldots, P_M) = L(k; f_0) + \sum_{m=1}^{M} L(N_m; e, f_0, P_m) \tag{5}$$

where $L(k_0; f_0 = \sum k_i \log(f_i)$ *and* $L(N_m;\ e, f_0, P_m) = \sum_{j=1}^{s}\sum_{i=1}^{s} n_{ji} \log(q_{ji})$. To obtain maximum likelihood estimates of the parameters (e, f_0, and the P matrices), we minimize the sum of two negative log-likelihood functions as given in Eq. 5: one for annual sampling across multiple years, and the one for one or more rapidly repeated samples taken to estimate the error rate, for which the only unknown parameters are e and f_0 (see Online Resource, Appendix D for Matlab code).

Simulation tests

To test for bias and precision of likelihood estimates from Eq. 5, we simulated multiple datasets using defined starting frequencies and transition matrices and based on two sets of samples: two rapidly repeated samples for error estimation, and sampling over a single annual transition. To generate each simulated dataset, we used multinomial probabilities to choose random observed starting frequencies and transitions between states. We then estimated e, f_0, and P from these simulated data and compared the results to the true underlying values used to generate the sets of random data in the first place. We based all the simulations

on one of our actual estimated transition matrices and starting frequencies (from Point Sierra Nevada, Fall 2004 to Fall 2005). Importantly, these data reflect highly unequal initial frequencies of different species groups and highly variable transition probabilities. We repeated these simulations 100 times for combinations of 3 different sample sizes (250, 500, and 1,000 points for each type of resampling) and three different error rates (0.5, 0.25 and 0.1). We then assessed the community-wide proportion of correctly estimated points by summing, across all starting states i, the number of observed transitions from state i to j that were correctly predicted by the estimated transition probabilities (the minimum of the observed and predicted number of i to j observations).

Application to field data and simulated recovery dynamics

We applied this correction method to our field data, simultaneously estimating transition probabilities across the three transitions of our data. To assess the consequences of correcting for spatial errors in sampling on the predicted community response to a disturbance, we then simulated the process of succession by multiplying the raw and corrected matrices by a vector of 100% rock (bare space) and saving the community composition following each iteration of the model (sensu Horn 1975; Tanner et al. 1994; Wootton 2001; Hill et al. 2004). We also calculated the damping ratio ($\lambda_1/|\lambda_2|$; Caswell 2001) for the raw and corrected matrices to see whether the correction had a noticeable or consistent impact on the relative return time to a stable community distribution.

Results

Field sampling

Overall percent cover was very similar across the three samples at Point Sierra Nevada within the same tide (Fig. 1). This indicates that, while the errors associated with quadrat placement at this scale are potentially important for analyses of the fate of individual points over time, if the sampling objective is to calculate relative abundance of sessile organisms (as is often the case), then sampling using this widely practiced method is highly repeatable.

Patterns in error estimates from repeat sampling

In our rapid resampling of plots, there was a negative relationship between the probability of seeing an obvious error (a change in species identity or $1 - p_{ii}$), and the mean percent cover of each species (Online Resource, Appendix B, Fig. B1; $r^2 = 0.15$; $P < 0.0001$), due to the "hidden" errors for abundant species of seeing the same species during resampling, but not necessarily the same individuals.

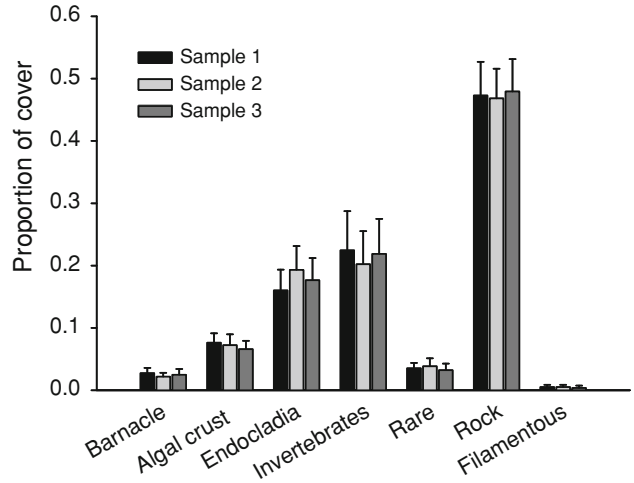


Fig. 1 Proportions of species groups in the intertidal assemblage dominated by the red turf alga *Endocladia muricata* at Point Sierra Nevada, California on 11 March 2008 over 3 consecutive samplings within the same tide (mean cover ± SE across all plots, $n = 11$). Differences in cover represent error associated with placement of the quadrat or parallax

Application of calculated error estimates to measured transition probabilities

Simultaneously using our rapidly resampling and annual sampling data resulted in an estimate of 0.353 for e, the error rate, with one-dimensional 95% likelihood confidence limits of (0.326, 0.381). The maximum likelihood estimates of corrected transition probabilities were highly correlated with the uncorrected ones at Point Sierra Nevada ($r^2 = 0.951$; $P < 0.0001$), Stairs ($r^2 = 0.960$; $P < 0.0001$) and Point Fermin ($r^2 = 0.978$; $P < 0.0001$; Table 1; Fig. 2a–c) (see Online Resource, Appendix C for all transition probabilities). Despite this high correlation, the correction also reveals substantial and systematic bias in the raw transition probabilities, with higher raw transitions typically being overestimates of true transitions and lower raw estimates being underestimates (Fig. 2a–c). In addition, the lowest transition probabilities (i.e., the transitions that occurred the least frequently) required the highest proportionate degree of correction for all three sites, such that the proportionate degree of correction was negatively correlated with raw (uncorrected) transition probabilities (Spearman's rank correlations: Point Sierra Nevada $\rho = -0.31$, $P < 0.0001$; Stairs $\rho = -0.16$, $P = 0.013$; Point Fermin $\rho = -0.34$, $P < 0.0001$; Fig. 2d–f).

Table 1 Raw and corrected transition probabilities for Point Sierra Nevada spring–spring matrices

Point Sierra Nevada	Point Sierra Nevada						
	Rock	Rare	Invertebrates	Filamentous	*Endocladia*	Algal crust	Barnacles
Raw							
Rock	0.4831	0.3438	0.2948	0.1074	0.2849	0.3059	0.3989
Rare	0.0332	0.0574	0.0123	0.1074	0.0406	0.0292	0.0806
Invertebrates	0.1033	0.079	0.3684	0.3557	0.1294	0.1416	0.0909
Filamentous	0.001	0.001	0.001	0.1074	0.001	0.0071	0.001
Endocladia	0.2264	0.2851	0.1052	0.1074	0.412	0.181	0.1808
Algal crust	0.0977	0.215	0.1917	0.1074	0.1114	0.2912	0.0893
Barnacles	0.0554	0.0187	0.0267	0.1074	0.0206	0.0439	0.1585
Corrected							
Rock	0.5629	0.3259	0.2562	0.1096	0.246	0.2812	0.4126
Rare	0.0306	0.0712	0.0108	0.1077	0.0386	0.0262	0.0966
Invertebrates	0.0713	0.0581	0.4762	0.358	0.1152	0.1353	0.083
Filamentous	0.0003	0.0006	0.0004	0.0985	0.0002	0.0064	0.001
Endocladia	0.2066	0.2788	0.0364	0.1093	0.4915	0.1362	0.1267
Algal crust	0.0709	0.2478	0.2089	0.1095	0.0995	0.374	0.07
Barnacles	0.0573	0.0176	0.0112	0.1074	0.0091	0.0406	0.2101

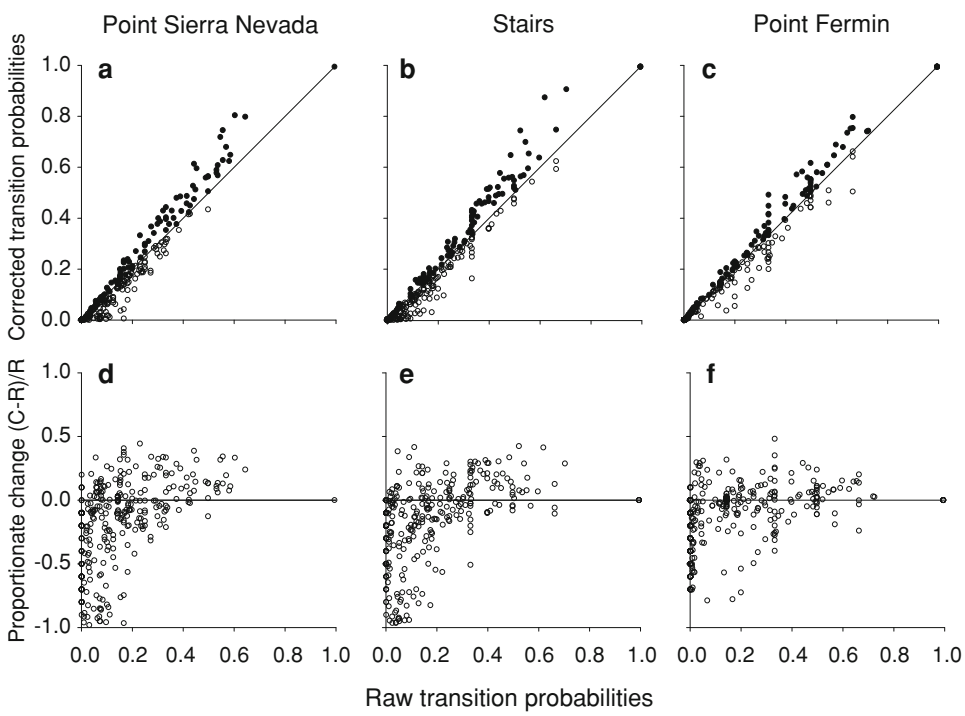


Fig. 2 **a–c** Relationship between measured (raw) and corrected transition probabilities between all pairs of species groups at Point Sierra Nevada, Stairs and Point Fermin. *Lines* indicate $y = x$. Cases where the corrected transition probability was greater than raw (*filled circles*) and less than raw (*open circles*) are shown. **d–f** Relationship between the proportionate change with correction as a function of the raw transition probabilities at each location [$(C–R)/R$, where C = corrected and R = raw estimates]

Encouragingly, while we find substantial effects from correcting for resampling errors, correcting for these errors does not result in wildly unrealistic transition probabilities. This was true across all three geographic locations. We also found that there was a slightly positive relationship between the absolute degree of correction (the absolute value of the difference between the raw and corrected transition probabilities) and the relative frequency of species j at time $t + 1$ (Online Resource, Appendix B, Fig. B2), indicating that the transition probabilities of more abundant species were altered more by the correction than less abundant ones.

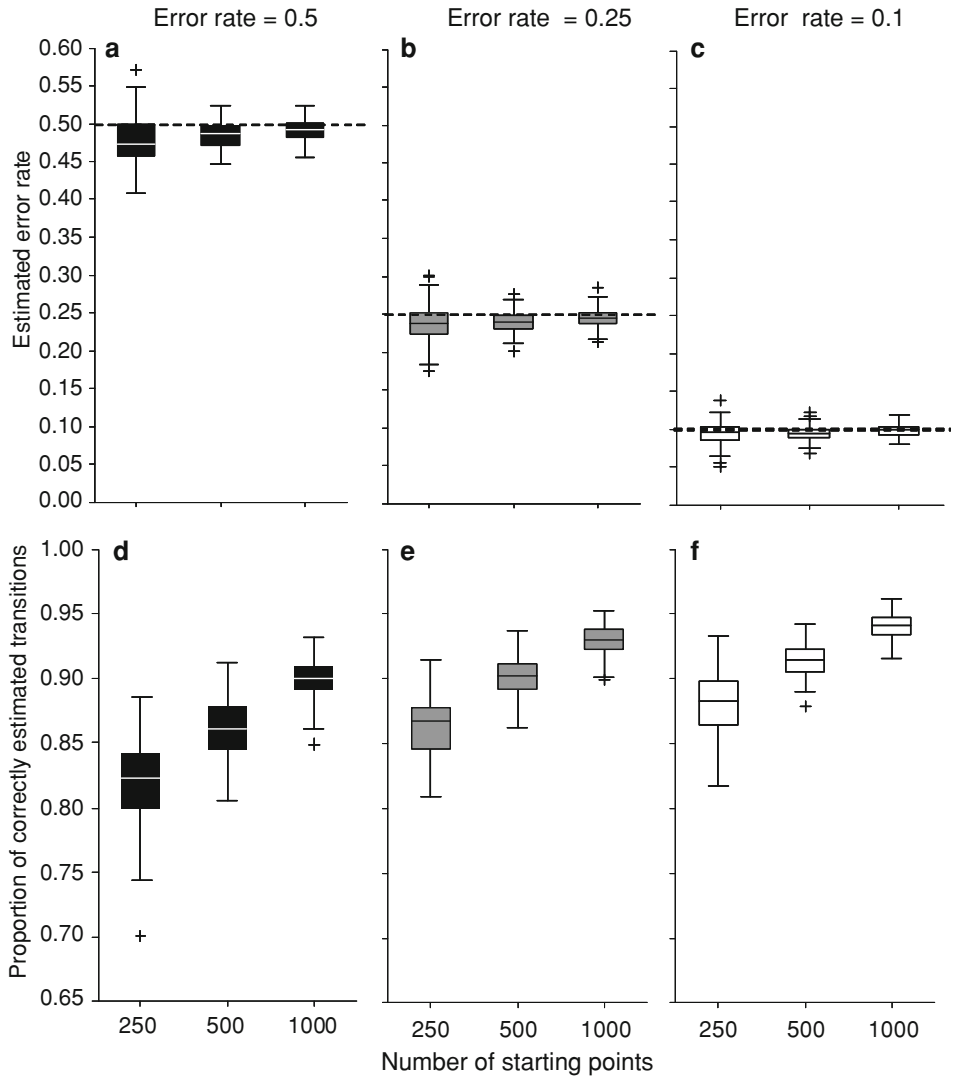


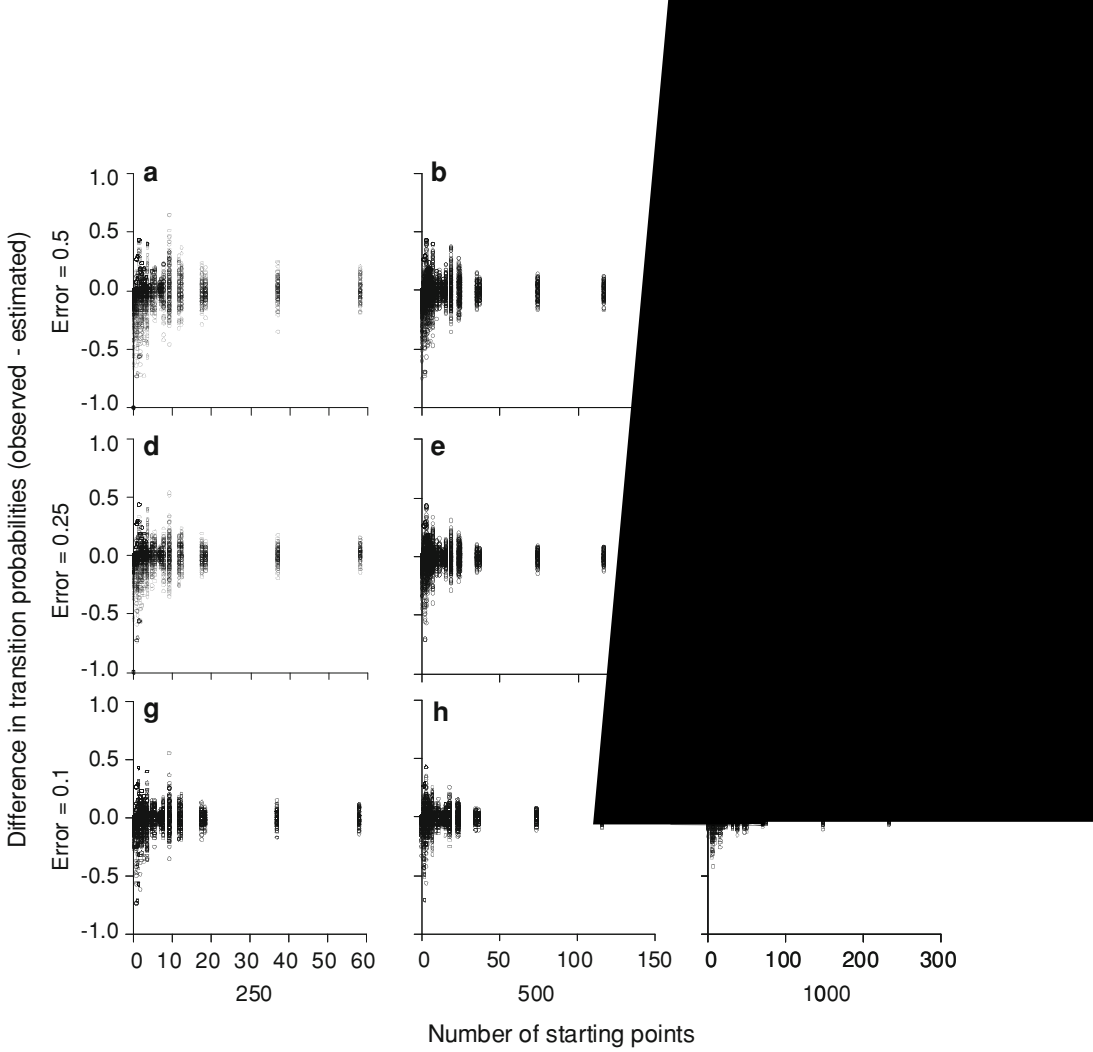
Fig. 3 **a–c** Distributions of estimated error rates and **d–f** the community-wide accuracy (fraction of correctly predicted points) of predictions made from estimated transition probabilities for simulated error rates of 0.5 (*black boxes*), 0.25 (*gray boxes*), and 0.1 (*open boxes*) using 250, 500 and 1,000 starting points

Simulation tests

Estimates of the error rates from our simulation tests were relatively accurate, though biased somewhat low, especially for the highest error rates and the lowest sample sizes (Fig. 3a–c). Intuitively, transition probabilities that started from fairly common species were more accurately estimated than were those from rare species, but even modest sample sizes (>15 starting points sampled) yield relatively good estimates of true, underlying transition probabilities (Fig. 4). There was also little indication of bias in these estimates, with the mean difference between true and simulated transitions virtually zero across all 9 error rate and sample size combinations (Fig. 4). Across all community predictions, simulations based on 500 or 1,000 sample points were far more accurate in their estimates than those based on only 250 points (Fig. 3d–f). Although, even for these higher sampling efforts, some transitions are not well estimated, the ability of estimated transition rates to correctly predict overall community dynamics is quite good, as the least common transitions are the ones with the poorest corrected estimates. Accounting for the frequency of actual transitions in a community and comparing these to the frequencies predicted by the estimated, corrected transition rates, only when error rate was 0.50 and there were only 250 sampled points did the proportion of correctly estimated transitions ever fall below 80%, and in most other scenarios, the accuracy reached 85–95% (Fig. 3d–f).

Simulated recovery dynamics

Correcting for sampling errors had substantial effects on the estimated early successional trajectories at all three sites, with the total predicted cover of biota from raw matrices consistently higher than estimates from corrected



ones (Fig. 5). The damping ratios of the raw and corrected matrices also reflected this pattern, with the damping ratios of raw matrices higher than those from corrected matrices, in all comparisons (Table 2). Thus, without correcting for resampling errors, our estimates of return time to a stable community distribution would have been substantially, and erroneously, shorter at all three locations.

Discussion

Spatially explicit sampling is fairly common in ecological studies and the data collected can be used to develop an enhanced understanding of communities by the constructing Markov transition matrices. The challenge of re-finding exact points over time is clearly not trivial, particularly if the sampled biota are physically small or if plots are

topographically complex. Despite taking measures to reduce sampling errors in the field, it is unlikely that any method of error reduction eliminates them entirely. Here, we demonstrate that correcting for sampling error is both biologically important and also mathematically and logistically feasible.

Perhaps the most striking aspect of our field results was the high error rate. While a 35% error seems high, we used typical methods to conduct these surveys and believed that great care was taken to reposition plots as accurately as possible. We do not know if these error rates are typical, since we have not been able to locate comparable studies that have sought to actually estimate their own resampling accuracy. One point to make in this regard is that the data needed to make this estimate, which is the basis of our correction method, were all gathered in a single day. Thus, it is quite feasible to collect the information needed to understand and correct for resampling error without a Herculean effort. Our simulation results further confirm that reasonable sample sizes, in the high hundreds or low thousands of points, are sufficient to yield accurate results.

The most striking consequence of correcting for sampling error was the prediction of slower recovery rates. This was demonstrated both by the lower percent cover of biota in early succession (Fig. 5) and by the lower damping ratios of the corrected matrices (Table 2). The fact that this trend was fairly consistent across all sites and seasons means that, despite the fact that successional dynamics themselves can change geographically (Conway-Cranos 2009; Dudgeon and Petraitis 2001; Foster et al. 2003) and seasonally (Foster et al. 2003), these potential differences in successional sequences do not result in a fundamental shift in the consequences of correcting for sampling errors. The systematic bias towards overestimation of recovery rates from raw transition probabilities is due to resampling errors making all transitions more similar to one another. At the extreme, if errors were far more common than accurate sampling of the same point, the probability of observing each point transitioning to each species will be identical, regardless of the starting species, and will equal the relative abundance of each species in the community.

Table 2 Damping ratios from raw and corrected fall and spring annual matrices

Site	Season	Raw	Corrected
Pt. Sierra Nevada	Fall	3.87	2.54
	Spring	3.98	2.64
Stairs	Fall	2.42	1.66
	Spring	2.19	1.54
Pt. Fermin	Fall	6.26	5.66
	Spring	3.57	3.40

In this case, the predicted successional speed will be very high, with rapid convergence on the originally observed community structure, regardless of the starting structure. High and uncorrected error rates will also paint a false portrait of specific species interactions, minimizing the measured differences between species in transition probabilities.

An important assumption that we make in this study is that the data we used to estimate measurement error (by rapid resampling) from one intertidal location (Point Sierra Nevada) are applicable across multiple regions. We think this is reasonable since both the error measurement data and the field data used to parameterize the succession model were gathered from the same intertidal biological zone at all three locations. As we discuss in "Materials and methods", other important assumptions concern the similarity of error rates across taxa and the importance of spatial patterning within plots. While these may at times complicate the use of this approach, the clear need to deal with the bias created by resampling errors makes it likely that some form of correction will improve ecological predictions over those made with uncorrected estimates.

As with treatments of other types of community sampling errors (Queenborough et al. 2010), we find that it is both feasible and important to deal with inaccuracies when turning data into model predictions. Our analysis of succession using both raw and corrected transition probabilities shows that, while errors made in spatially explicit sampling can be quite important and result in significantly different conclusions about early succession trajectories in particular, correcting for such error is mathematically feasible and can be applied post hoc to any set of transition probabilities based on the following information: (1) estimated error rates obtained through subsequent sample intervals when there is no expected biological change, and (2) estimated relative cover of each species or species groups. This approach can improve the use of datasets for the construction of community Markov analyses, thereby increasing our general understanding of communities through the enhanced use of these powerful analytical tools.

Acknowledgments We thank P. Raimondi for his input into the design of the community recovery experiment and for his comments and thoughts throughout this study. We are also grateful to the many field assistants who helped gather the data to parameterize our transition matrices including M. Bond, H. Hayford, C. Bell, L. Anderson and L. Reeve and to E. Saarman for her GIS wizardry. This manuscript benefited from insight and editing from P. Raimondi, S. Murray, I. Parker, J. Pearse, S. Diehl, and an anonymous reviewer. Our analyses and presentation were immeasurably aided by M. Spencer, who wrote the single most helpful review of any manuscript that either author has ever received. Funding was provided by the Minerals Management Service and by National Science Foundation dissertation improvement grant DEB 0808012 to LLCC and NSF DEB-0717049 and -0519004 to DFD.

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