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# Rule-Based Models for Evaluating Mechanisms of Distributional Change

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**Abstract:** *Viability models assume that particular mechanisms (e.g., decreased probability of colonization in isolated habitats) drive the pattern of population invasion and extinction. Although authors often provide evidence supporting the inclusion or exclusion of a mechanism, there has been no means of rigorously comparing different factors for a given species. We present a method of evaluating alternative mechanisms of distributional change that relies on two or more surveys of species presence-absence across a large number of sites, a dataset often available (or at least attainable) for many taxa. The key idea of our approach is to use hypotheses to specify rules for dividing sites into classes. Our model estimates class-specific probabilities of invasion and extinction and then uses these rates to assign invasions and extinctions to sites in multiple stochastic simulations. The output of the model is a frequency distribution of mistakes generated by comparing predicted distributions with the actual distributions. As a first attempt to apply the approach we modeled invasions and extinctions of 14 amphibian species across 32 ponds in Michigan. We compared hypotheses that amphibian distributions changed as a result of the spatial arrangement of sites, as a result of succession, or randomly. Overall, the spatial approach provided a poor explanation of distributional changes, performing no better than the random model for all species. In contrast, the succession model, based on temporal changes in breeding sites, performed better than the null model for at least three species. These results were surprising as spatial effects are thought to be important to the dynamics of pond-breeding amphibians. Our results say little about the general importance of fragmentation and other spatial effects, but do suggest that alternative mechanisms of change can be important. Because of their ability to assess the importance of different mechanisms, rule-based models could provide useful input into the design of biodiversity management strategies.*

Modelos Basados en Reglas para la Evaluación de Mecanismos de Cambio Distribucional.

**Resumen:** *Los modelos de viabilidad asumen que mecanismos particulares (i.e., probabilidad disminuida de colonización de hábitats aislados) conducen el patrón de invasión poblacional y extinción. Aunque algunos autores frecuentemente proveen evidencias que soportan la intrusión o exclusión de un mecanismo, no han habido medios de comparación rigurosa de diferentes factores para una especie determinada. Presentamos un método de evaluación de mecanismos alternativos de cambios distribucionales que se basan en dos o mas muestreos de presencia-ausencia de especies a lo largo de un gran número de sitios, una base de datos siempre accesible (o al menos obtenible) para muchos taxas. La idea clave de nuestra aproximación es la de usar hipótesis particulares para especificar reglas y dividir los sitios en clases. Nuestro modelo estima probabilidades específicas por clase de invasión y extinción y posteriormente utiliza estas tasas para asignar invasiones y extinciones en sitios por simulaciones estocásticas múltiples. El resultado del modelo es una distribución de frecuencias de errores generados al comparar distribuciones predecidas con las distribuciones actuales. Como un primer intento para aplicar esta aproximación, modelamos invasiones y extinciones de 14 especies de anfibios en 32 estanques a lo largo de Michigan. Comparamos las hipótesis de que la distribución de los anfibios cambia como resultado del arreglo espacial de los sitios, como un resultado de sucesión o debido al azar. En general, la aproximación espacial mostró una explicación pobre de los cambios distribucionales, no mejor que el modelo al azar par todas las especies. En contraste, el modelo de sucesión,*

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basado en cambios temporales de sitios de reproducción proporcionó mejores resultados que el modelo nulo para al menos tres especies. Estos resultados fueron sorprendentes, ya que los efectos espaciales son considerados importantes en la dinámica de anfibios de reproducción en estanques. Nuestros resultados dicen poco sobre la importancia general de la fragmentación y otros efectos espaciales, pero sugieren que mecanismos alternativos de cambio pueden ser importantes. Debido a su habilidad para evaluar la importancia de diferentes mecanismos, modelos basados en reglas pueden proveer importantes ideas en el diseño de estrategias para el manejo de la biodiversidad.

## Introduction

Spatially-explicit models of population viability are being used increasingly in the management of threatened and endangered species (Dunning et al. 1995; Turner et al. 1995). Drawing from the theory of metapopulations (Levins 1969), recent incarnations of these models have presumed that isolation among patches of habitat drives patterns of occupancy by influencing rates of colonization (e.g., Liu et al. 1995). One of the most important predictions of this approach is that fragmentation of landscapes can lead to metapopulation extinction even though perfectly good sites remain vacant. In the context of widespread human induced fragmentation, the specter raised by fragmentation driven extinction is undoubtedly fueling rapid integration of spatially explicit viability models into the evaluation of management options.

The effects of fragmentation on patterns of invasion and extinction are often presumed rather than evaluated, however, and alternative mechanisms are often not considered (see Liu 1993 for an exception). The purpose of this paper is to lay out a method of using presence-absence information from repeated samples to create "rule-based" models for evaluating competing hypotheses for distributional change. We illustrate the approach using field presence-absence data recording patterns of distributional change of amphibians.

Pond-breeding amphibians are an ideal group for such a test. They have populations centered around breeding ponds that are connected by low rates of dispersal. These attributes have been used to single them out as particularly appropriate for applying metapopulation approaches (Gill 1978; Harrison 1991; Sjogren-Gulve 1994).

## Rule-based Models of Distributional Change

Rule-based models use the pattern of invasions and extinctions across a set of sites to evaluate different hypotheses for distributional change (Fig. 1; Kareiva et al., in press). Each hypothesis is used to divide the set of sites into classes according to different rules. These classes can be created arbitrarily as a null hypothesis (i.e., a random rule). Alternatively, they can be based on

a putative mechanism that forms the basis of the rules used to classify sites.

The form of the model we apply here is a simple computer simulation, although analytical approaches are also possible (Appendix). The minimum data required are the presence or absence of a species across a set of sites during two survey periods. The model is developed sepa-

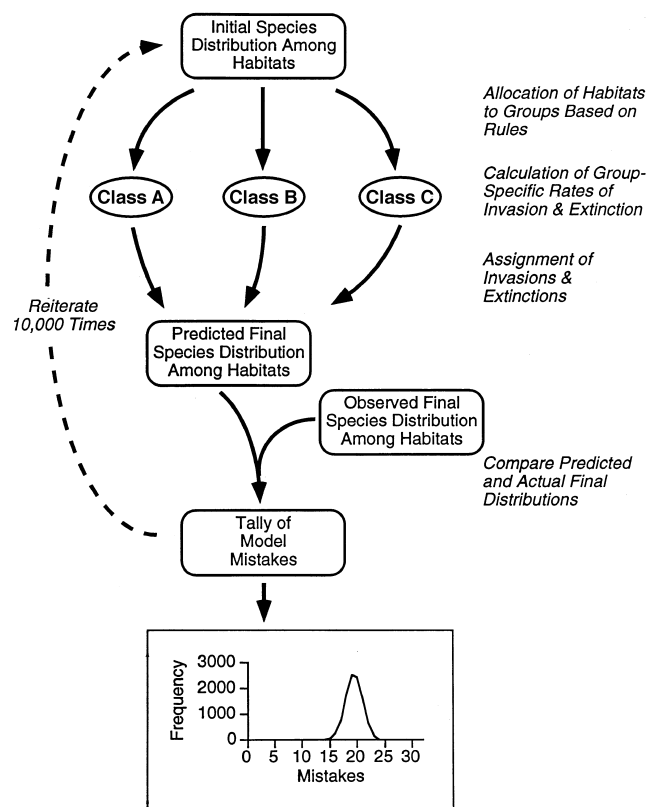


Figure 1. Primary steps in a "rule-based" model of distributional change. Rules used to divide habitats into classes are based on hypothesized mechanisms of distributional change (e.g., random, habitat isolation, succession). The model is run 10,000 times in order to generate a frequency distribution of the number of mistakes made in assigning species presence or absence to the set of habitats. Different hypotheses can be compared to estimate the relative effectiveness of different mechanisms in explaining distributional changes.

rately for each hypothesis. Once the sites have been assigned to classes, rates of invasion and extinction are calculated within each class. The simulation then cycles through each site as it existed in the first survey and, based on the class-specific probabilities, stochastically assigns invasions to empty sites and extinctions to occupied sites. Then the simulation checks the model outcome against what actually happened in each site, tallying the number of times the model mistakenly assigned distributional change where none occurred, or missed a change that did occur. This process is repeated 10,000 times in order to generate a frequency distribution of the number of mistakes made under a given hypothesis.

Because hypotheses will vary among systems, the easiest way to illustrate the rule-based approach is with an example. Amphibians were surveyed in a set of ponds at the E. S. George Reserve (540 ha; Livingston Co., Michigan) from 1967 to 1974 (Collins & Wilbur 1979), and again from 1988 to 1992 (D. K. Skelly, E. E. Werner, and S. A. Cortwright, unpublished data). Thirty-two ponds were surveyed for frogs and 25 ponds were surveyed for salamanders. Between these surveys most of the 14 resident species showed high rates of turnover among ponds (mean = 48% turnover). Across all species there were 40 invasions and 34 extinctions.

We are interested in determining why these species showed dramatic shifts among sites in a relatively short period of time. We considered two possibilities, comparing each with a null hypothesis of random change. The first hypothesis was that distributional shifts are related to the spatial arrangement of ponds. More isolated ponds may be more difficult to colonize and may be more vulnerable to extinction because of the absence of a rescue effect (reviewed by Hanski 1991). The second hypothesis was that temporal changes in ponds and surrounding terrestrial sites may alter the suitability of ponds as breeding sites for particular species. We had provisional support for both hypotheses. Examination of the spatial pattern of colonizations and extinctions showed that the probability of invasion was halved in more isolated ponds, whereas the probability of extinction doubled at greater distances (D. K. Skelly, E. E. Werner, and S. A. Cortwright, unpublished data). It is also well known that amphibians are selective about the ponds in which they choose to breed (e.g., Dale et al. 1984) and that ponds can undergo changes in important characteristics over time (e.g., pond permanence). The E. S. George Reserve has been undergoing rapid succession since agricultural activity ceased in the 1920s and the area was converted to a conservation and research reserve (Evans 1975). Forest cover has more than doubled in this time. In short, there is reason to suspect that both isolation among sites as well as successional changes could have contributed to amphibian distributional changes.

In order to determine the contributions of isolation and succession to patterns of amphibian distributional

change, we built models based on each mechanism. The isolation model divided ponds into three classes based on the distance of the pond to the nearest population (during the first survey). Classes were chosen to divide the number of records across all species into three categories: less than 80 m, 80–420 m, and greater than 420 m. These categories were chosen to reflect likely differences in colonization by amphibians whose dispersal distances are typically on the order of hundreds of meters (e.g., Gill, 1978). We performed a sensitivity analysis to determine whether our choice of distance classes influenced our interpretation of distributional changes. The succession model divided ponds into three classes based on pond characteristics. These included open canopy ponds, closed canopy temporary ponds (dry each year) and closed canopy ponds of intermediate permanence (dry some years). The three classes in the succession model were chosen to reflect successional trends apparent from comparisons between surveys. Ponds are becoming enclosed by forest canopies and are drying up sooner with a given amount of rainfall (D. K. Skelly, S. A. Cortwright, & E. E. Werner, unpublished data). Both changes could have pronounced effects on the ability of many species to successfully complete larval development (Skelly 1995; Werner, unpublished data).

We also created a null model. During each run of the null model, ponds were arbitrarily assigned into one of three classes. There was no restriction on the number of ponds in each class and the classes were rechosen before each run of the model, but on average there was an equal number of ponds in each class.

Finally, we created a set of nested models to test for additive and interactive effects between isolation and succession. These nested models each had four classes: two succession classes (open canopy ponds, closed canopy ponds) crossed with two isolation classes (<240 m,  $\geq$ 240 m). We ran both a fully-nested model, a succession-only model where ponds were distributed randomly into the two isolation classes, an isolation-only model, and a null model where ponds were distributed randomly across all four classes.

The models were used in two ways. First, we ran the isolation, succession, null, and all nested models individually for each of the 14 species. These results were used to compare the relative performance of the three hypotheses in explaining the distributional changes of individual species. Second, we pooled the results across species to evaluate each model's performance in predicting final species composition and species richness. In both cases (species-by-species or summed over all species), the critical indicator of model performance was the number of mistakes. A mistake was defined as (1) the incorrect assignment of a population to a site that, in reality, was vacant during the second survey or (2) the failure by the model to assign a population to a site where the species was present during the second survey. Dur-

ing each stochastic run this form of the model compared the predicted and observed identity and number of species occupying each pond during the second survey. The model summed the deviations from actual species composition and species richness across all 32 ponds and repeated this process during 10,000 runs.

For each species outcomes from models based on different hypotheses were compared using *t* tests. Results generated during 10,000 model iterations provided estimates of mean and standard deviation of mistakes made by a given model. Sample size for each "population" being tested was the number of ponds sampled (32 ponds for frogs and 25 ponds for salamanders).

## Model Results

### Single Factor Models

Across the 14 species, model results fell into three categories (Table 1). For six species (a) the succession model tended to perform best, for two species (b) the isolation model tended to perform best, and for six species (c) the null model equalled or exceeded the performance of either alternative model (Fig. 2). Differences in performance among models were sizable for three frog species (*Hyla versicolor*, *Pseudacris crucifer*, *P. triseriata*); for each of these species the succession model made significantly fewer mistakes than either the null

model or the isolation model (*t* tests,  $p < 0.01$  in each case). In the best instance, the succession model made ca. two-thirds fewer mistakes than either alternative. Although the isolation model tended to make fewer mistakes than either the succession or null models for two salamanders (*Ambystoma laterale*, *A. maculatum*), these differences were not significant. We performed a sensitivity analysis of our choice of distance classes to determine whether our interpretation of the data would be influenced by choosing different distance categories. Either halving or doubling thresholds for distance classes (40 or 160 m instead of 80 m; 210 or 840 m instead of 420 m) had minor effects on the qualitative ranking of the best performing models and no influence on interpretations of *t* test results. We conclude that the lack of isolation effects implied by our analysis is robust to particular choices of distance classes.

For six species neither alternative model exceeded the performance of the null model (e.g., *Rana pipiens*, Fig. 2c). Five of these species experienced very few distributional changes overall ( $\leq 3$  in each case). This result shows a limitation of the approach: resolution among alternative models requires a database over enough sites and time to show sufficient numbers of invasions or extinctions.

We also pooled results across species to compare the ability of the different models to explain patterns of species composition and species richness during the second survey (Fig. 3). In both cases the succession model tended to make fewer mistakes than isolation or null models; however the trend was significant only for species richness (*t* test,  $p < 0.05$ ). In neither case did the isolation model make significantly fewer mistakes than the null model; although it did make significantly more mistakes than the succession model in explaining patterns of species richness (*t* test,  $p < 0.05$ ).

**Table 1.** Average number of mistakes made by three different models in explaining pond occupancy during the 1988–92 survey of the E. S. George Reserve, Michigan.

Taxon	Null	Succession	Isolation
<b>Salamanders</b>			
Ambystomatidae			
<i>Ambystoma laterale</i>	7.2	5.4	5.2
<i>A. maculatum</i>	8.1	7.7	6.1
<i>A. tigrinum</i>	7.4	6.9	8.2
Plethodontidae			
<i>Hemidactylum scutatum</i>	1.7	1.8	1.9
Salamandridae			
<i>Notophthalmus viridescens</i>	8.3	6.2	8.4
<b>Frogs</b>			
Bufonidae			
<i>Bufo americanus</i>	10.1	10.1	11.5
Hylidae			
<i>Acris crepitans</i>	0.0	0.0	0.0
<i>Hyla versicolor</i>	4.1	1.5	4.6
<i>Pseudacris crucifer</i>	10.5	3.6	10.9
<i>P. triseriata</i>	10.3	6.2	10.5
Ranidae			
<i>Rana catesbeiana</i>	2.6	3.4	2.9
<i>R. clamitans</i>	2.6	3.3	3.2
<i>R. pipiens</i>	4.4	5.1	4.4
<i>R. sylvatica</i>	9.5	8.3	9.6

### Nested Models

Results from models that incorporate both isolation and succession parallel those from single factor models. The only models that provided significantly improved performance over the null model included classes based on successional characteristics. Models based on succession alone and succession and isolation together made significantly fewer mistakes than either null or isolation only models for the same three frog species (*H. versicolor*, *P. crucifer*, *P. triseriata*) and a salamander species (*Notophthalmus viridescens*) (*t* tests,  $p < 0.05$  in each case). There was no evidence that adding isolation improved the explanatory power of a model based on succession alone. In fact, for one species adding isolation actually decreased model performance (for *H. versicolor* the succession alone model made significantly fewer mistakes than the nested model).

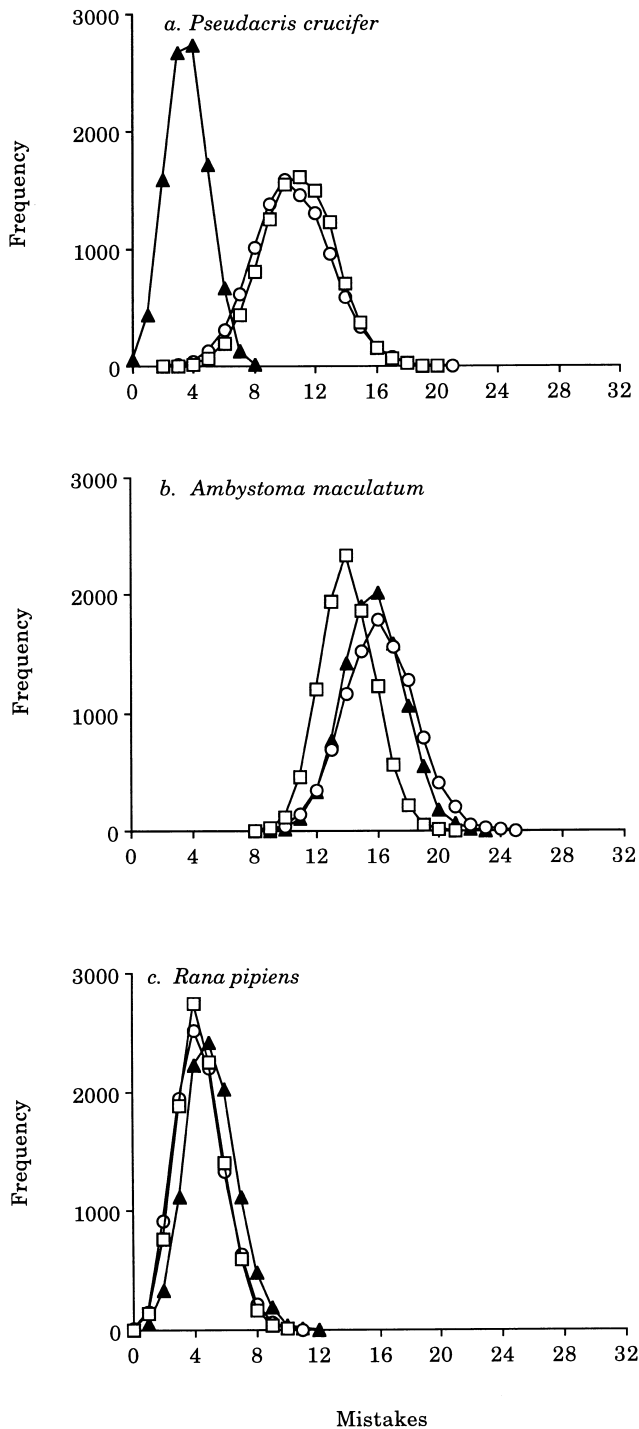


Figure 2. The number of mistakes in distributional changes made by succession (solid triangles), isolation (open squares), and null (open circles) models for three different species. The x-axis is the number of mistakes made in a single run of the model, each model was run 10,000 times for each species. Peaks closer to the origin represent models that were more effective at explaining distributional changes of that species: *Pseudacris crucifer* where the succession model performed best (a); *Ambystoma maculatum* where the distance

## Discussion

As conservation becomes more proactive, there are frequent calls for better monitoring programs (e.g., LaRoe et al. 1995). The justification has usually been that knowledge of population trends for a number of "indicator" species or groups will provide early warning of declines. Our results suggest that even relatively coarse information on presence and absence can be put to an equally important use: as survey information accumulates it becomes a source of insight for managers interested in determining *why* species distributions are changing, not just *if* they are changing.

The example we have presented is a first attempt at using presence/absence data to elucidate mechanism of change, and it strongly suggests that succession can be an important mechanism of distributional change for some pond-breeding amphibians. In particular, successional changes seemed strongly related to distributional changes for three hylid species. Each species is typically associated with open canopy habitats (Conant & Collins 1991). Canopy closure may prevent successful development of some species (E. E. Werner, unpublished data), perhaps due to increased oxygen stress, decreased pond permanence, or changes in food resources that accompany successional changes. Whatever the reason, it is apparent that small temporary ponds that were overtopped by forest canopies have become depauperate over the last three decades.

In strong contrast to our results using succession-based hypotheses, isolation of pond habitats appeared slightly more effective than a hypothesis of random change in explaining distributional changes. There was no evidence that interactions between isolation and succession obscured any influence of isolation. This result is surprising because the breeding system of these species would seem to promote the kinds of spatial effects on invasion and extinction included in many metapopulation models. The lack of importance for isolation in our models may reflect the relatively close proximity of most breeding habitats at the E. S. George Reserve (on the order of hundreds of meters at most). For most amphibian species, except perhaps notably poor dispersers such as some *Ambystoma* species (Cortwright 1987), the barriers imposed by isolation among E. S. George Reserve ponds appear to contribute little to patterns of distributional change. Undoubtedly isolation will be important for amphibians in other places where distribution of aquatic habitats is different (e.g., Sjogren-Gulve 1994).

model performed best (b); and *Rana pipiens* where no model performed better than the null model (distributional change was random) (c).

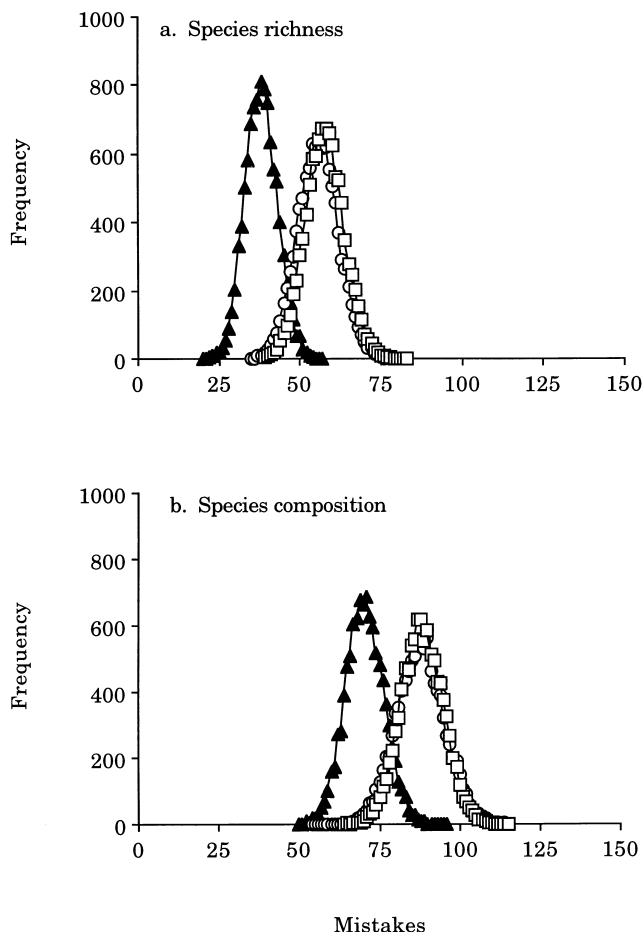


Figure 3. Number of mistakes made by succession, isolation, and null models in explaining species richness (a) and species composition (b) of 32 ponds at the E. S. George Reserve (1988–92). Symbols as in Fig. 2.

These results are a warning for those making management recommendations. There is a significant need to consider and evaluate different mechanisms of change in order to make reliable projections of viability. In particular, it is critical to delineate between the action of a factor and its implications for the actual pattern of distributional change. Establishing that probabilities of invasion and extinction change with variation in a factor is a necessary but insufficient prerequisite for establishing that a factor is driving distributional change. By directly estimating the relationship between a putative mechanism and the pattern of change, rule-based models establish the importance of a factor to the pattern itself.

Although rule-based models can provide guidance, there are some important caveats in their application. The success or failure of the approach depends squarely on which hypotheses are considered and how they are formally structured in the models. In our example we considered just two simple alternative models to a null

hypothesis and a nested model which included both alternatives. In other instances more complicated models may be desired. For example, the mechanisms underlying invasion and extinction may be different, requiring different rules for each process. Many datasets are likely to have more than two surveys. The availability of multiple samples presents opportunities to evaluate the importance of alternative mechanisms over different time scales and at different points in time.

As with other statistical techniques, the rule-based approach will be limited by the size of the dataset. When the number of classes is increased, the number of sites within classes declines. The result is that the overall explanatory power of the model increases and the ability to resolve among models decreases. At the extreme, a model with as many classes as sites will be perfectly able to explain patterns of change. In addition, the distribution of sites among classes can affect explanatory power. In general, models where the number of sites is evenly divided among classes perform best. In a preliminary simulation using the E. S. George Reserve amphibian data, this “evenness” effect was relatively minor compared to explanatory differences among hypotheses. These issues can be summarized by two general rules: 1) It is critical to control for the number of classes among hypotheses, 2) All else being equal, it is better to have fewer classes. With more complicated models it may be harder to see differences among models and also more difficult to interpret those differences. As demonstrated by our results, adding a factor can actually degrade the performance of a model in some cases.

Finally, like regression, the ability to explain a pattern with a rule-based model is not the same as showing causation. Sometimes it will be possible to make independent inferences about competing mechanisms. For example, transplant experiments at the E. S. George Reserve have shown the importance of “successional” pond qualities to the performance of amphibian larvae (Skelly 1995; E. E. Werner, unpublished data). In most management settings, however, field experiments are not likely, and it will be important to appreciate the limitations of the inference made by rule-based models.

Before constructing the rule-based models described here it was unclear why amphibian distributions at the E. S. George Reserve had been undergoing dramatic changes over the last 25 years. There were reasons to suspect both isolation of pond habitats as well as succession. This scenario is likely to be familiar to managers confronted with a number of plausible reasons for changes in animal distributions. Because the implications of different mechanisms potentially mean conflicting management recommendations, deciding which mechanisms are important is crucial.

Regional and national monitoring programs exist for a number of taxa and have been proposed for several more (LaRoe et al. 1995). These surveys document patterns of

change (and warn of declines) but they also contain subtler information. Our results suggest that rule-based models may help conservation biologists determine which of the myriad potential factors are important for different species.

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**Appendix: Analytical analogues of computer simulations**

For class *i* of one of the three models we discuss above, let  $u|u_i$  be the number of ponds in that class unoccupied in both the first and second surveys,  $u|o_i$  be the number of ponds unoccupied in the first survey but occupied by the second survey,  $o|u_i$  the number of ponds first occupied and then unoccupied, and  $o|o_i$  the number of ponds occupied in both surveys. Then the colonization rate,  $c_i$ , for that class is

$$c_i = u|o_i / (u|o_i + u|u_i),$$

and the extinction rate,  $e_i$ , is

$$e_i = o|u_i / (o|u_i + o|o_i).$$

The number of mistakes we expect the model to make in that class,  $m_i$ , is

$$m_i = c_i * u|u_i + (1 - c_i) * u|o_i + e_i * o|o_i + (1 - e_i) * o|u_i.$$

The mistakes we expect the whole model to make will simply be the sum of the mistakes made for each class:

$$\sum_{i=1}^{N_C} m_i,$$

where  $N_C$  is the total number of classes in the model.

The formula for the null model is more complicated because we are reassigning ponds to classes during each run of the simulation. Consider a single pond that goes extinct between surveys (a pond of type  $o|u$ ). In a null model with  $N_C$  classes, the probability that this pond will be in a class with  $a$  other ponds of type  $o|u$  and  $b$  other ponds of type  $o|o$  is

$$\left( \frac{(N_{o|u} - 1)!}{a!(N_{o|u} - a - 1)!} \right) \left( \frac{N_{o|o}!}{b!(N_{o|o} - b)!} \right) \left( \frac{1}{N_C} \right)^{(a+b)} \left( 1 - \frac{1}{N_C} \right)^{(N_{o|u} + N_{o|o} - a - b - 1)}$$

where  $N_{o|o}$  is the total number of ponds which are occupied in both surveys and  $N_{o|u}$  is the number of ponds which are occupied in the first survey and unoccupied in the second (from which we subtract 1 for the pond we are considering).

The chance of the model making a mistake for this pond when it is in a class with  $a$  ponds of type  $o|u$  and  $b$  ponds of type  $o|o$  is

$$1 - \frac{a+1}{a+b+1}$$

Thus the total chance of the model making a mistake for this pond is the summation of the above two formulas across all the possible combinations of ponds

$$m_{o/u} = \sum_{a=0}^{N_{o|u}-1} \sum_{b=0}^{N_{o|o}} \left( \frac{(N_{o|u} - 1)!}{a!(N_{o|u} - a - 1)!} \right) \left( \frac{N_{o|o}!}{b!(N_{o|o} - b)!} \right) \left( \frac{1}{N_C} \right)^{(a+b)} \left( 1 - \frac{1}{N_C} \right)^{(N_{o|u} + N_{o|o} - a - b - 1)} \left( 1 - \frac{a+1}{a+b+1} \right),$$

where  $m_{o|u}$  is the chance of a mistake for a pond of type  $o|u$ .

The number of mistakes made for ponds of the three other types can be calculated similarly

$$m_{o|u} = \sum_{a=0}^{N_{o|u}} \sum_{b=0}^{N_{o|o}-1} \left( \frac{N_{o|u}!}{a!(N_{o|u}-a)!} \right) \left( \frac{(N_{o|o}-1)!}{b!(N_{o|o}-b-1)!} \right) \left( \frac{1}{N_c} \right)^{(a+b)} \left( 1 - \frac{1}{N_c} \right)^{(N_{o|u}+N_{o|o}-a-b-1)} \left( 1 - \frac{b+1}{a+b+1} \right)$$

$$\left( \frac{1}{N_c} \right)^{(d+e)} \left( 1 - \frac{1}{N_c} \right)^{(N_{u|o}+N_{u|u}-d-e-1)} \left( 1 - \frac{e+1}{d+e+1} \right),$$

where  $d$  and  $e$  in the last two equations are the number of ponds of types  $u|o$  and  $u|u$  respectively.

Then the total number of expected mistakes will be just the sum of chance of a mistake for each pond

$$m_{u|o} = \sum_{d=0}^{N_{u|o}-1} \sum_{e=0}^{N_{u|u}} \left( \frac{(N_{u|o}-1)!}{d!(N_{u|o}-d-1)!} \right) \left( \frac{N_{u|u}!}{e!(N_{u|u}-e)!} \right) \left( \frac{1}{N_c} \right)^{(d+e)} \left( 1 - \frac{1}{N_c} \right)^{(N_{u|o}+N_{u|u}-d-e-1)} \left( 1 - \frac{d+1}{d+e+1} \right)$$

$$N_{o|u}m_{o|u} + N_{o|o}m_{o|o} + N_{u|o}m_{u|o} + N_{u|u}m_{u|u}.$$

