

# Neutral models for testing landscape hypotheses

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**Abstract** Neutral landscape models were originally developed to test the hypothesis that human-induced fragmentation produces patterns distinctly different from those associated with random processes. Other uses for neutral models have become apparent, including the development and testing of landscape metrics to characterize landscape pattern. Although metric development proved to be significant, the focus on metrics obscured the need for iterative hypothesis testing fundamental to the advancement of the discipline. We present here an example of an alternative neutral model and hypothesis designed to relate the process of landscape change to observed landscape patterns. The methods and program, QRULE, are described and options for statistical testing outlined. The results show that human fragmentation of landscapes results in a non-random association of land-cover types that can be describe by simple statistical methods. Options for additional landscape studies are discussed and access to QRULE

described in the hope that these methods will be employed to advance our understanding of the processes that affect the structure and function in human dominated landscapes.

**Keywords** Neutral landscape models · Pattern and process · Landscape hypothesis testing · Land cover analysis

## Introduction

Natural areas are being converted into landscapes intensively used by humans at unprecedented scales (e.g., NRC 2001; Foley et al. 2005). These changes are producing significant losses in species diversity (Hanski 2005; Lindborg and Eriksson 2004), invasions of exotic organisms (McCay 2001; Vitousek et al. 1997), declines in water quantity and availability (Goetz et al. 2004; Meyer and Turner 1992), the alteration of biogeochemical cycles and reductions in ecosystem productivity (Osher et al. 2003; Williams et al. 2004). The global consequences of landscape alteration are uncertain, but evidence is increasing that landscape change may also alter the earth's climate (Copeland et al. 1996; Pyke 2004; Stohlgren et al. 1998) while promoting the spread of new diseases (Langlois et al. 2001).

Our ability to record, measure and describe the consequence of landscape change has improved

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dramatically over the past two decades. However, our understanding of the fundamental processes affecting land-use and land-cover change remains inadequate for “... society to respond effectively to environmental changes and to manage human impacts on environmental systems” (NRC 2003). Consequently, the need to understand and predict the dependency of landscape pattern on the processes that have produced these patterns has been identified as one of six “grand challenges” for the National Science Foundation’s effort to establish a national ecological observatory network (NEON, NRC 2003).

Identifying the specific processes shaping existing landscapes has been surprisingly challenging. Extensive data from remote imagery, advanced computational methods for analysis and simulation, and a plethora of pattern metrics have failed to rigorously link pattern with process. There are many practical reasons why progress has been so slow. The local co-variation in the physical template and land use change (e.g., soils, topography, climate, human population density) has created a broad spectrum of possible results; the human legacy of landscape alteration combined with natural disturbance regimes has been difficult to document and studies have been limited in scope; and the idiosyncratic nature of data classification schemes may produce unaccounted analysis errors, confounding even simple comparisons (Costanza and Maxwell 1994; Riley et al. 1997; Wickham et al. 1997). Although a number of detailed studies have been published (e.g., Dale et al. 1994; Motzkin et al. 1999; Orwig and Abrams 1994) each has required intensive, retrospective analysis with little hope for generalization of results and comparison with similar landscapes. Clearly, advancing the science of landscape ecology requires the adaptation of the principles of strong inference—the critical testing of alternative hypotheses—first outlined by Platt (1964). We suspect that most readers of this journal will be surprised to learn that a paradigm for iterative testing of alternative hypotheses, adapted to the special requirements of landscape studies, was first suggested nearly two decades ago.

Krummel et al. (1987) used land cover maps from the USGS Natchez Quadrangle (the

southern Mississippi drainage) to test the hypothesis that the physical template (i.e., topographic and hydrologic heterogeneity) produced distinct patterns of forest cover in undisturbed areas that differed from patterns within agricultural regions. The fractal index was introduced as the appropriate metric to define the scales over which these two processes have affected landscape pattern. Results confirmed that the “... current pattern of forest reflects the overlaying of many relatively small scale human disturbances on the large-scale factors that control the major successional patterns of natural vegetation” (Krummel et al. 1987). This small but important success precipitated an effort to extend the use of iterative hypothesis testing by employing neutral models based on percolation theory (Gardner et al. 1987). These neutral models were then used to “... establish a base against which data and hypotheses [could] be rigorously tested” (Gardner et al. 1987). Results from a series of neutral modeling studies have elucidated a broad variety of principles, including: the amount of habitat,  $p$ , is the single best predictor of landscape pattern (Gardner et al. 1987; Gardner and O’Neill 1990), mandating that comparisons among landscapes must occur at fixed values of  $p$  (Turner et al. 2001); the critical threshold in land cover,  $p_c$ , defined by percolation theory (Stauffer and Aharony 1992) defines a boundary above which few differences exist between random and real landscapes (Gardner and O’Neill 1990; Pearson and Gardner 1997); conversely, large differences occur below  $p_c$  making this “region” the most fruitful domain for exploring process-pattern dependencies (Gardner and O’Neill 1990); landscapes with a mixture of altered and natural habitat types have lower dispersal rates, abundance levels and population persistence (Andow et al. 1990; Fagan et al. 1999; Gustafson and Gardner 1996), with corridor usage enhanced or inhibited by adjacent matrix effects (Anderson and Danielson 1997; Bennett et al. 1994; Gardner et al. in press; Gustafson and Gardner 1996); simple organizing features of individual landscapes (i.e., hierarchical patterns or contagion) introduce threshold effects that are scale-dependent (Lavorel et al. 1994; O’Neill et al. 1992); and, as a final example, disturbances,

as illustrated by a variety of fire models, both generate and respond to critical thresholds in landscape connectivity (Maddox 1992; Romme et al. 1998; Turner et al. 1994).

Neutral landscape models have been used widely in landscape ecology over the past decade (With and King 1997; Tischendorf et al. 2003), with recent examples primarily focused on the responses of (model) populations to landscape pattern—in effect using neutral-modeling to generate random but structured templates for population processes. Thus, these applications have diverged substantially from the original goal of using neutral models to make inferences about the agents that have and are presently generating landscape pattern.

The purpose of this paper is to renew the interest among landscape ecologists in the use of strong inference to advance our understanding of process-pattern dependencies at landscape scales. We first illustrate how alternative hypotheses can be developed and tested, extending our understanding beyond that produced by simple random maps. We then show how quantitative comparison of diverse landscapes can be effected. Finally, new suggestions for advanced statistical analysis that takes advantage of the rich information provided by Monte Carlo simulations are explored.

## Background

Simple random maps can produce a surprisingly rich array of spatial patterns as  $p$ , the fraction of the area occupied by a particular land cover type, passes a critical threshold (i.e., percolation threshold) in connectivity (Stauffer and Aharony 1992). When Monte Carlo methods are used to iteratively generate and analyze random maps (holding map dimensions, resolution, number of land-cover types, and  $p$  constant) then confidence intervals for a variety of metrics and statistics can be estimated. If the pattern of the observed map lies within this 95% confidence region, then the observed pattern is said to be statistically indistinguishable from a random pattern at  $\alpha=0.05$  (Gardner and O'Neill 1990; Pearson and Gardner 1997). Because we know that real landscapes are

not randomly assembled, but rather organized by physical, biotic and human effects (Delcourt et al. 1983; Forman and Godron 1986; Urban et al. 1987), simple random maps are the most effective “neutral model” for landscape analysis.

The computer program, RULE, was developed to generate random maps, estimate a variety of landscape metrics and calculate their associated confidence intervals (Gardner 1999). A spectrum of questions have been addressed using RULE, including the variation in edge as a result of landscape fragmentation (Gardner et al. 1987), the existence of scale-dependent pattern in actual landscapes (Plotnick et al. 1993; Plotnick et al. 1996), and the effect of pattern on patch colonization (Gustafson and Gardner 1996). In all cases, a specific question was formulated, per the example of Krummel et al. (1987), and the appropriate metric employed. Blind searches for pattern using multiple metrics should be avoided—in part, because of the classic Type II error of statistics (Zar 1996): if we look at enough metrics, *something* is likely to emerge as “significant”. Multi-variate statistical approaches can reduce the information provided by multiple metrics to a few more meaningful dimensions (Fauth et al. 2000) but the value of this approach still depends on the formation of a specific, testable, a priori question.

Although much of the literature regarding landscape pattern analysis has focused on the use of metrics, the usefulness of traditional statistical testing procedures should also be considered. For instance, fragmentation effects can be evaluated via changes in the cumulative frequency distribution (cfd) of patch sizes for that cover type. Because pattern metrics are a single-numbered measure (i.e., a mean or variance, etc.) derived from a cfd, they often fail to capture subtle responses clearly revealed by an examination of the cfd. Significant change, or departures from random, of an observed cfd is easily assessed by familiar methods such as the Kolmogorov–Smirnov (KS) test (Zar 1996). If an expected cfd can be parametrically defined (Johnson and Kotz 1970a, b) then Monte Carlo methods will not be needed. Because the cfd of patch sizes varies with map dimension, resolution and methods used to classify land-cover types (Turner et al. 2001), it is

usually impossible to define an expected probability distribution in advance. In these cases one must rely on models and Monte Carlo methods to generate the “expected” cfd to compare to an observed landscape via the appropriate statistical test (Fortin 2003).

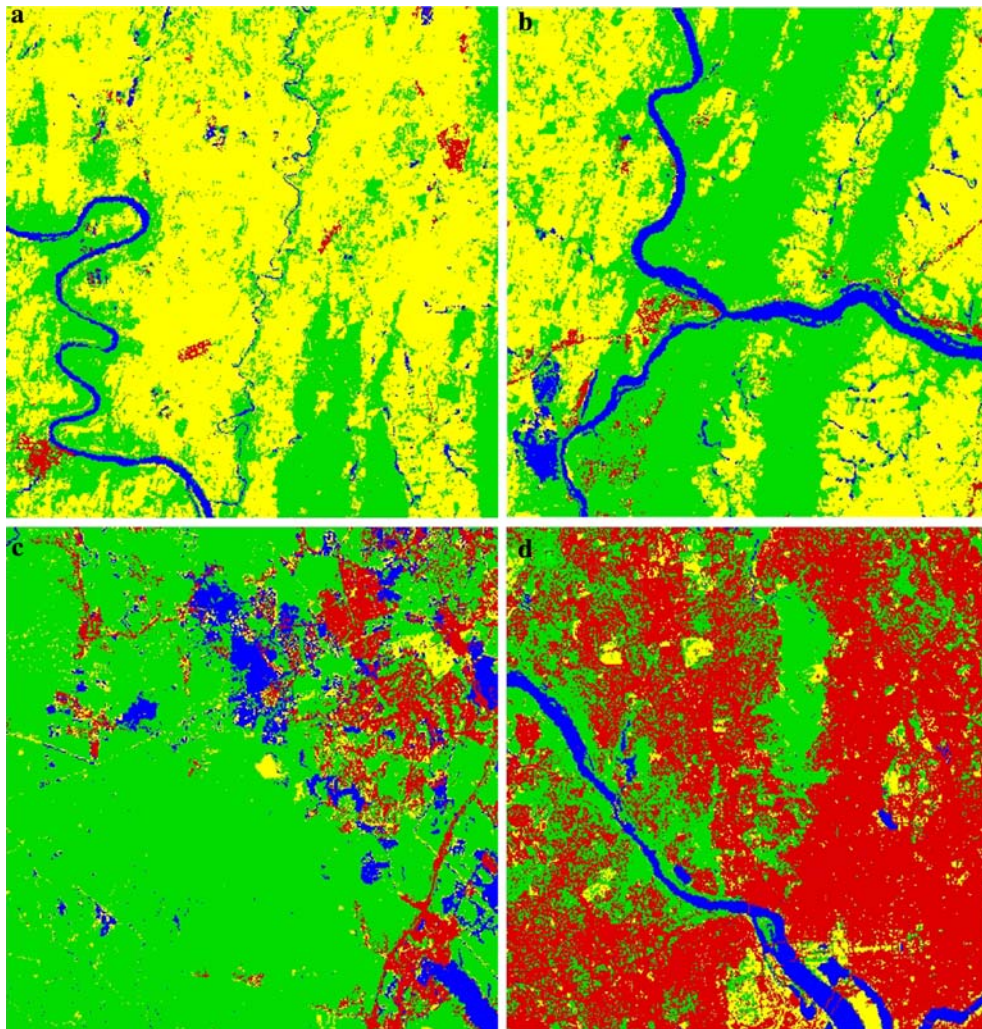
## Methods

Human activities have resulted in dynamic and continuous change in forests of the eastern United States over the past three centuries (Foster et al. 1998). Changes in forest pattern continue, with ~5% rearrangement of the spatial distribution during the past 15 years (Riitters and Coulston 2005). Rates of forest loss have been greatest near urban areas (Wickham et al. 2000), with increases in forest growth into adjacent abandoned crop and grasslands (Riitters and Coulston 2005). Conservation efforts also affect forest pattern formation, with preservation often focusing on larger remnant areas that tend to persist along streams or ridge tops (Taverna et al. 2005). Two hypotheses were investigated to explore the consequences of these activities: (1) The distribution of forest patches within human dominated landscapes, and their adjacency to other cover types, does not deviate from random. This is the neutral model hypothesis *sensu* Gardner et al. (1987) and was tested here first by comparing the cfd of patch sizes against simple random maps, and secondly by a  $\chi^2$ -test of the association matrix of cover types (i.e., the frequency matrix of site adjacencies, details below). The rejection of the first null hypothesis (i.e., observed landscapes are non-random) allows a second hypothesis to be tested: (2) Patterns of forest cover are significantly affected (statistically explained) by the constraints of topography (especially rivers) and urban development. The second hypothesis was tested by a specially developed neutral model, which formed patterns based on land cover constraints. The cfd of patch sizes for this new neutral model was then compared to the simple random maps and the observed landscapes. In addition, three landscape metrics were calculated to confirm the sufficiency of landscape constraints to statistically explain the differences in number, size and

correlation length of forest patches among map types.

Four maps were extracted from the National Land Cover Data (NLCD) set (see Vogelmann et al. 2001). These maps, based on Landsat Thematic Mapper (TM) imagery, have been classified into 21 land cover types at a spatial resolution of 0.09 ha (30 m) (Riitters et al. 2002). The four extracted landscapes were 512 × 512 pixels (786 ha) in size, located near the Antietam battleground in Maryland; Harpers Ferry on the Potomac River; Prince William Forest Park in Virginia and Rock Creek Park in Washington DC (Fig. 1). For the purposes of this analysis, the NLCD data were reclassified into four land cover types: aquatic habitat (water, wetlands); agriculture (an aggregation of seven classes including pasture, row crops, orchards and fallow lands); urban developed (residential, commercial and urban); and forest (deciduous, evergreen, mixed forests). The relative proportions of habitat found within each landscape are given in Table 1.

The RULE program was rewritten for this exercise, providing statistical summaries based on area rather than pixel counts, improving the formats of ancillary data sets that included the cfd, and adding the potential for developing and analyzing alternative neutral models. (See Appendix A for details on obtaining the documentation and source code for this revision, referred to as QRULE). QRULE retains the essential features of RULE (i.e., generation and analysis of simple and multi-fractal random maps), and was used to generate 12 simple random maps with the same proportion of forest as the four extracted maps (Table 1). Although any number of Monte Carlo iterations may be specified in QRULE, experience has shown that 12 iterations are adequate to reliably characterize the mean values for the metrics being considered (Table 2). Forest patches were analyzed using the “rook’s” rule (i.e., four cardinal neighbors), and the cfd was plotted for both the observed and random maps. Three metrics were selected for additional pattern analysis: *Nc*, the number of patches of a particular land-cover type; *Sav*, the area-weighted average patch size (ha); and *Clg*, the correlation length (*m*), which measures how compact the habitat patches are (see Gardner 1999 for additional



**Fig. 1** Four landscapes from the mid-Atlantic region (dimensions are 30.8 km and resolution 30 m): **(a)** Antietam, Md.; **(b)** Harpers Ferry at the confluence of the Susquehanna and Potomac; **(c)** Prince William, Va; and

**(d)** Rock Creek, Washington, DC. Four colors indicate rivers (blue), agriculture and grassland (yellow), forests (green) and urban (red). See text for further data description

information). Although most landscape metrics are correlated with one another (Riitters et al. 1995), these metrics were selected because they provide relatively independent assessments of pattern and provide important information about

the number, characteristic size, and pattern of habitat patches (Gardner et al. in press).

The per-pixel association of land cover types was an  $n \times n$  matrix (where  $n$  is the number of land cover types) of the frequency of adjacent

**Table 1** The proportion of land cover on four maps extracted from the NLCD land cover data (see text for details)

Map	Not classified	Forest	Agriculture	Aquatic	Urban developed
Antietam	0.02	0.29	0.67	0.01	0.01
Harpers Ferry	0.05	0.52	0.40	0.01	0.02
Prince William	0.08	0.74	0.06	0.01	0.11
Rock Creek	0.04	0.28	0.07	<0.01	0.61

**Table 2** Landscape pattern metrics<sup>a</sup> for forests within the four landscapes<sup>b</sup> of the Mid-Atlantic region. Results for two neutral models<sup>c</sup>, the *random* and *MCA* simulations, are also presented

Map	<i>P</i>	<i>Nc</i>	<i>Sav</i>	<i>Clg</i>
<i>Antietam</i>	0.2944	4419.0	616.80	2106.01
Random	0.2913	33859.9 (127.46)	0.42 (0.003)	70.84 (0.889)
MCA	0.2903	2945.2 (41.98)	828.29 (265.19)	4027.23 (477.92)
<i>Harpers Ferry</i>	0.5165	2829.0	3566.87	3472.41
Random	0.5210	14992.7 (120.21)	9.17 (0.50)	374.25 (19.83)
MCA	0.5211	2089.0 (68.9)	2762.78 (473.04)	4037.77 (94.92)
<i>Rock Creek</i>	0.280	5420.0	495.71	2538.97
Random	0.2801	34020.0 (128.7)	0.39 (0.003)	67.67 (0.73)
MCA	0.2802	7315.2 (56.0)	123.55 (28.08)	1439.29 (346.31)
<i>Prince Williams</i>	0.7426	1801.0	12621.40	5691.66
Random	0.7422	1078.5 (37.0)	17238.10 (26.04)	6293.13 (0.001)
MCA	0.7428	3081.1 (65.5)	11709.40 (317.35)	5560.05 (59.48)

<sup>a</sup>The four pattern metrics are: *p*, the proportion of the landscape that is forested; *Nc*, the number of forest patches; *Sav*, the characteristic patch size (ha); and *Clg*, the correlation length of patch sizes (*m*). The numbers in parentheses for the Random and MCA analysis represent the standard deviations of the 12 Monte Carlo iterations. See text for further description of these metrics

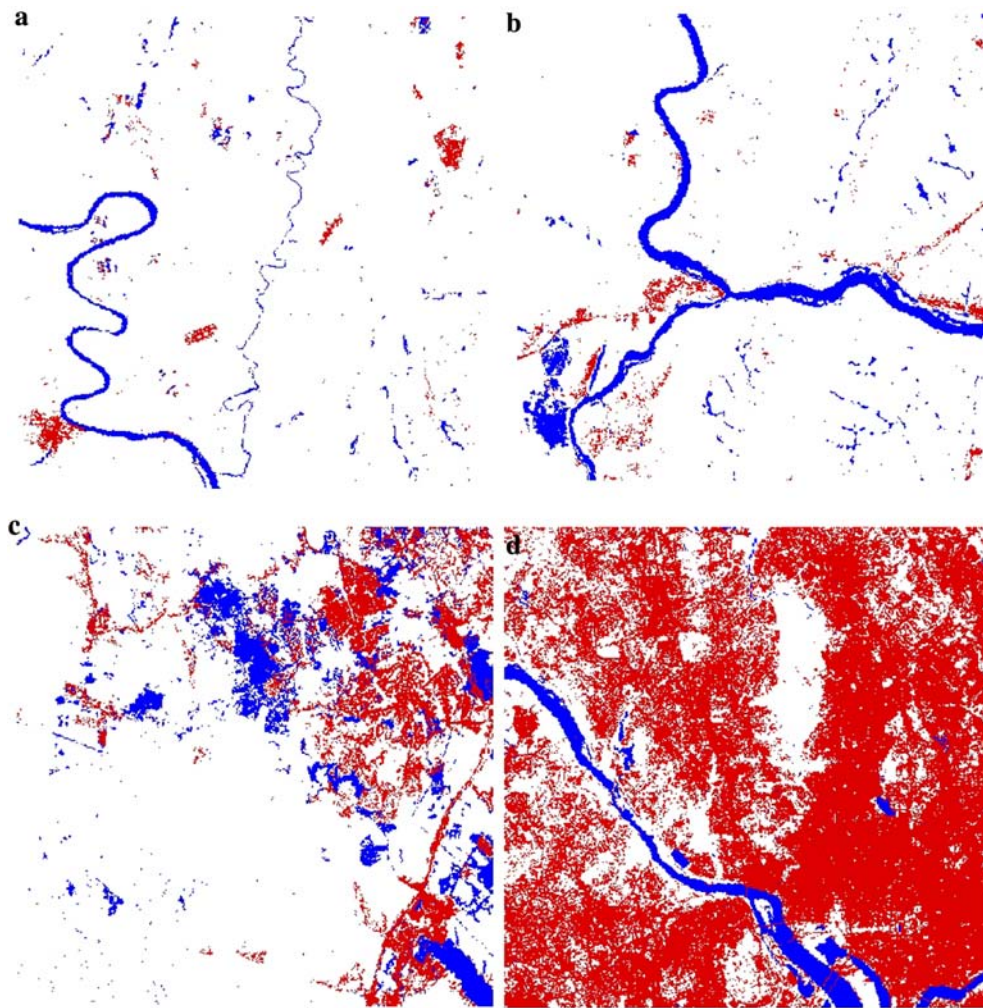
<sup>b</sup>The four maps were extracted from the NLCD land-cover mapping data (see text for details)

<sup>c</sup>These analyses were performed with QRULE. See Appendix for details on obtaining the QRULE execution, script and log files for these simulations

pixel types using the nearest-neighbor rule. The diagonals of the matrix represent the probability of self-association, the off-diagonals represent the probability of association with other land-cover types, with the columns summing to 1.0 (i.e., all associations accounted for). The  $\chi^2$ -test of this matrix is the familiar statistical procedure of estimating a departure from the “expected” random matrix, providing statistical rigor for testing neutral models. Because the method uses the marginal frequencies (i.e., the values of *p* for each cover type), it provides a test consistent with that employed by QRULE. QRULE calculates the association matrices for each landscape and estimates their departure from that expected by a purely random process using the  $\chi^2$ -test.

A new method for neutral models was used to test the second hypothesis. A Masked-Constraint Algorithm (MCA) was included in QRULE to randomly generate forest pattern constrained by the fixed patterns of aquatic and urban land cover types. This approach presumes that human land use decisions are effectively constrained by proximity to water (and hence, by topography). This method was implemented in three steps: (1) The observed landscape served as an input to define the cover types used to form the map

constraints. The user supplied the usual input values required by RULE (e.g., number of replicates, which metrics to compute), but also specified which cover type(s) to serve as fixed constraints (the aquatic and urban land cover, in this example) and which cover type should be randomly generated (i.e., forest). (2) The association matrix for the observed landscape was estimated by QRULE. (3) A random map was initiated by creating a map of identical size and resolution, and then applying a mask extracted from the land cover types defined as the constraints of the observed system (Fig. 2). The process of forest cover generation was initiated by random placement of “seeds” along the margins of the mask. The diagonal element of the association matrix for forest cover was then used to define the probability of growth into adjacent non-forest sites. Growth of forest patches continued until the overall proportion of forest, *p*, of the actual landscape was achieved. The remaining habitat was set to the background matrix value (i.e., agriculture). The process was repeated until 12 MCA maps were generated and analyzed. The data produced from the analysis of MCA maps was then compared to the observed landscapes and the simple random maps.



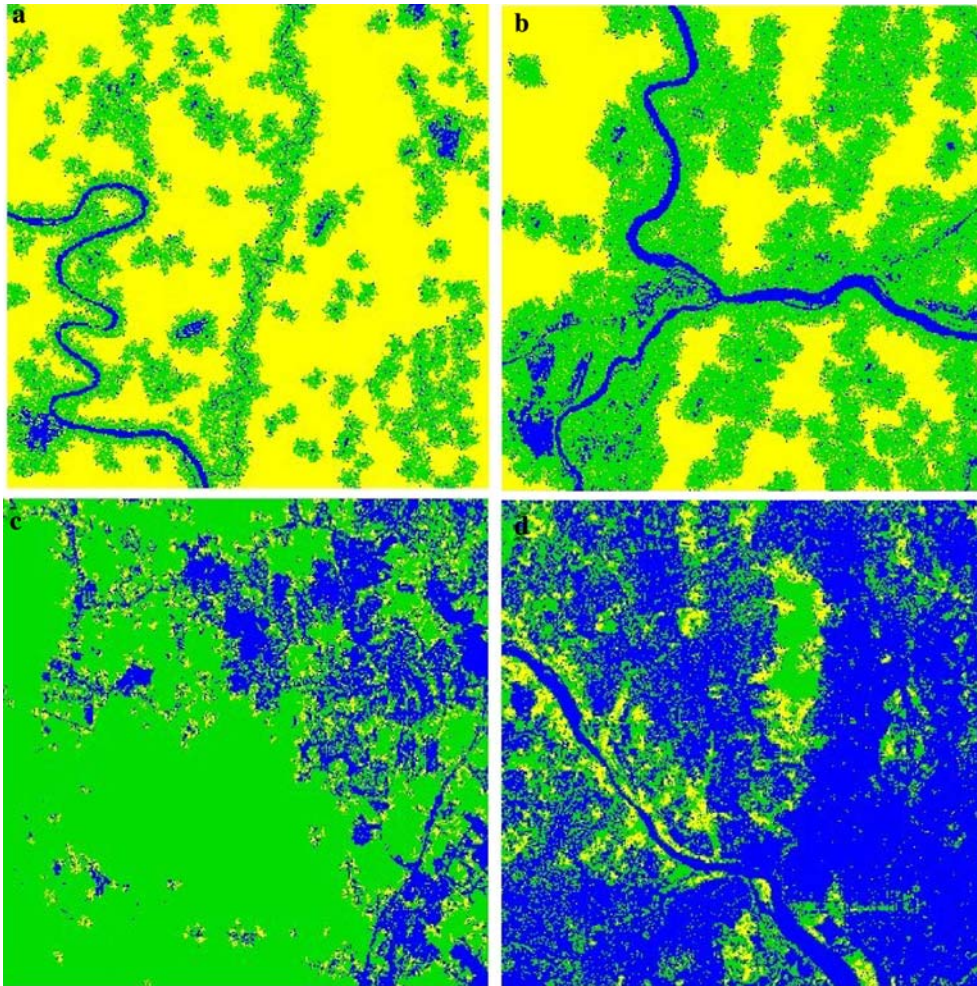
**Fig. 2** The masks created for the four mid-Atlantic landscapes: (a) Antietam, Md.; (b) Harpers Ferry, Va.; (c) Prince William, Va; and (d) Rock Creek, Washington,

DC. The masks are composed of 2 land-cover types: rivers (blue) and urban (red)

## Results

Within the constraints of the land cover mask, random forest patches are generated. This was especially evident for Antietam and Harpers Ferry where the landscape constraints and the proportion of forest cover was lowest (Fig. 3). A comparison of the cfd of the number of forest patches for the four landscapes (Fig. 1) is illustrated in Fig. 4. The cfd of the simple random maps were not significantly different from the actual maps in three of the four cases (Table 3). The cfd for the simple random map was significantly different from the Prince William

landscape due to the greater frequency of small, isolated patches in the random maps. Further examination of cfd for the random maps showed that, except for Prince William, random maps deviated from the observed landscapes in one important way: the largest patch size of the random maps was several orders of magnitude smaller than the largest patch for the actual landscapes. Because the KS test measures the degree of difference between two normalized distributions, it was insensitive to cumulative differences in the tails of the distribution where the probability of occurrence is relatively small. The random map for Prince William was an



**Fig. 3** Representative simulations of the four mid-Atlantic landscapes: (a) Antietam, Md.; (b) Harpers Ferry, Va.; (c) Prince William, Va.; and (d) Rock Creek, Washington, DC. These simulations used the MCA neutral model (see

Fig. 2 and text for details). Forested areas (green) and agricultural lands (yellow) were simulated around the mask (blue) composed of river and urban land-cover types

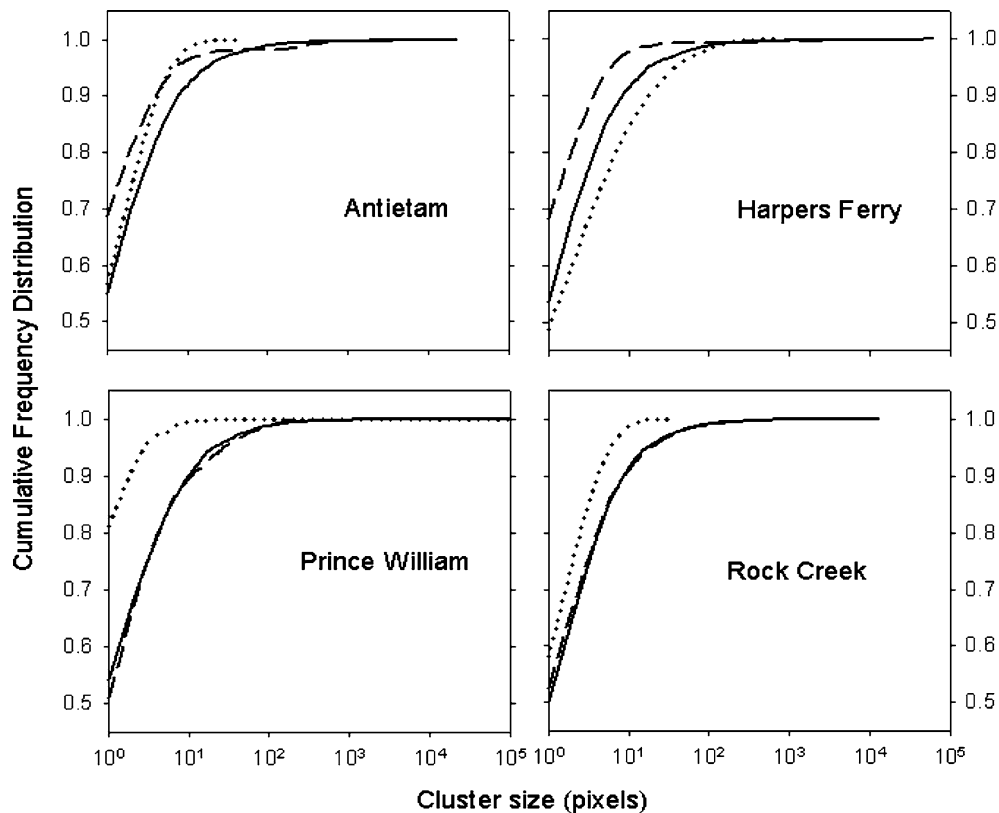
exception because  $p$ , the proportion of area that was forested, was equal to 0.7426—far above the critical threshold of  $p_c=0.5928$  (four neighbor rule, Gardner et al. 1987; Plotnick and Gardner 1993). When  $p > p_c$  random maps display the well-known percolation phenomena (Stauffer and Aharony 1992) where large spanning patches are formed by simple random processes.

The cfd for the MCA maps (dashed lines in Fig. 4) gave an excellent fit for observed patterns of Prince William and Rock Creek (Table 2), the two landscapes where the high value of  $p$  and the limits imposed by urban land cover dominated pattern formation. However, the cfd for the MCA

maps deviated significantly from the Antietam and Harpers Ferry landscapes where the topography of the ridge and valley province dominated pattern formation.

Examination of Table 2 shows that, except for Prince William, the random maps also tended to overestimate the number of patches ( $N_c$ ) and underestimate the characteristic patch size ( $S_{av}$ ) and the correlation length ( $Cl_g$ ) of patches of forest habitat. The estimates of  $S_{av}$  were particularly poor, often differing by three orders of magnitude. The Prince William case was again an exception because, as noted above, percolation processes ensure that large patches were formed.





**Fig. 4** The cumulative frequency distribution of patch sizes for the four mid-Atlantic landscapes (solid line) are contrasted with two neutral models: the simple random maps (dotted line) and MCA maps (dashed line)

Because the pattern metrics estimated from the random maps had a relatively small variance (CV ranging from  $<0.1$  to 5%) even small differences between random and actual maps were statistically significant.

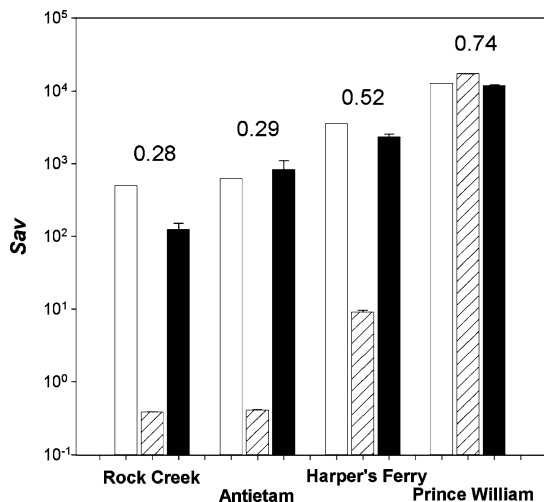
The pattern metrics for the MCA maps (Table 2) were much closer to the actual maps with the exception of Prince William where  $N_c$  for the random maps provided the better estimate than  $N_c$  for the MCA maps. The characteristic patch size,  $S_{av}$ , was more accurate for all MCA maps (Fig. 5). In fact, estimates of  $S_{av}$  for the actual maps for both the Antietam and Harpers Ferry landscapes did not significantly differ from the MCA maps. The estimates of  $Cl_g$  for the MCA maps were of the same magnitude while the random maps produced estimates that were orders of magnitude less than three of the four landscapes (Table 2).

The observed frequency of association of habitat types between neighboring pixels provides a

different perspective on spatial patterns because this information can characterize non-random association between different habitat types. This matrix, as constructed by QRULE, is always symmetrical with dimensions of  $c \times c$ , where  $c$  is the number of habitat types being considered. A  $\chi^2$ -test of the association matrix of an unconstrained map has  $df = c(c - 1)/2$  (Zar 1996).

**Table 3** Kolmogorov–Smirnov test of the cumulative frequency distribution of predicted forest patches from two neutral models compared against the four mid-Atlantic landscapes

Landscape	df	KS		Critical value ( $\alpha=0.05$ )
		Random	MCA	
Antietam	118	0.075 (NS)	0.133 (0.05)	0.122
Harpers Ferry	99	0.094 (NS)	0.159 (0.02)	0.134
Prince William	92	0.316 (0.001)	0.027 (NS)	0.139
Rock Creek	127	0.108 (NS)	0.024 (NS)	0.119



**Fig. 5** Histogram and error bar ( $\pm 1$  standard deviation) of the area-weighted average patch size ( $S_{av}$ ) for forested regions of the four mid-Atlantic landscapes (open bar), random (cross-hatched) and MCA (solid) maps. The number above each set of bars is  $p$ , the fraction of the landscape that is forested

Table 4 reports the  $\chi^2$  values for the four landscapes ( $c=5$ ,  $df = 10$ ). The average  $\chi^2$  values for the 12 iterations of the MCA neutral model are also reported with  $c=3$ ,  $f$  (the number of constrained habitat types) = 1, and consequently  $df = (c(c-1)-f(f-1))/2 = 2$  reduced due to the constraints of the habitat mask. The  $\chi^2$  values for the actual landscapes were larger than the MCA maps, indicating a greater deviation from a random pattern, but both types of maps differ by roughly five orders of magnitude from that due to random processes alone.

The third column in Table 4 highlights an interesting result. The 95th percentile for 10,000 maps was estimated using QRULE (each map had four habitat types with the same proportions and map dimensions as the actual maps). One might expect the 95th percentile to be approximately equal to the tabulated  $\chi^2$  of 12.592 (four habitat types, 6 df, Zar 1996). However, the observed value was larger than the tabulated value because random selection of pixels occurs within a finite spatial context making the completely random, independent selection of neighbors (required by  $\chi^2$ ) impossible. Although this is an important consideration affecting statistical inferences from map comparisons, the relatively

large  $\chi^2$  values observed for both actual maps and MCA maps clearly show that the neighborhoods of these maps were structured rather than random.

## Discussion

Most observations of the natural world will quickly reveal the intrinsic variability of a wide variety of physical and biological phenomena. It is the local variation in topography, soils, climate and history that shapes our landscapes, producing the distinctive patterns that make each location recognizable (Nassauer 1997). Because each landscape is unique, the determination of processes responsible for observed patterns has proven to be difficult (Turner et al. 2001). Nevertheless, a wide variety of statistical methods are available to test the adequacy of our understanding of pattern-process relationships at landscape scales. The first step in hypothesis testing is to define what would be expected in the absence of the process being considered. This “expectation” may be a landscape that lacks that process (e.g., fire, road development, or invasive species), or, as presented here, a model capable of defining the expected pattern from a more elaborate set of pattern-generating rules. Once the “expected pattern” is defined, a variety of statistical tests may be applied. The illustration we present

**Table 4** A  $\chi^2$ -test of the hypothesis that the matrix of habitat association was random

Landscape	$\chi^2$		
	Observed landscape <sup>a</sup>	MCA <sup>a, b</sup>	Simple random <sup>c</sup>
Antietam	17.5e5	9.39e5	24.89
Harpers Ferry	21.5e5	11.5e5	25.12
Prince William	17.2e5	7.1e5	25.08
Rock Creek	17.4e5	7.1e5	25.17

<sup>a</sup>The critical value ( $\alpha = 0.05$ ) for the observed landscape with five habitat types (10 df) was 18.307; the critical value for MCA with three habitat types (2 df) was 5.991 (Zar 1996)

<sup>b</sup>Average  $\chi^2$  value from 12 iterations

<sup>c</sup>The 95th percentile of  $\chi^2$  values from 10,000 iterations of a simple random map with four cover types (6 df with a critical value of 12.592)

examines only a few possibilities, but raises some general issues in making inferences about landscape pattern.

### Landscape pattern and “ $p$ ”

As with simpler random landscapes, our analyses underscored the crucial importance of  $p$ , the proportion of the landscape occupied by a focal cover type, as an index of pattern. Comparisons of landscape metrics are only meaningful if the landscapes have similar values of  $p$ . At high values of  $p$ , the landscape is composed of a few large patches that may “percolate” from edge-to-edge; in these cases, simple random landscapes often provide a reasonable model of real landscapes. This implies that inferences about landscape pattern and process will not be very satisfying at high values of  $p$ . There are two possible responses to this general result. The first option is to focus inferential studies on landscapes with lower values of  $p$  because the maximum number of patches in random landscapes occurs at  $p \sim 0.3$  (Gardner et al. 1987), far below the critical threshold of 0.6. It seems likely that we can learn more about patches by studying landscapes with larger numbers of patches. The second option is to accept that patchiness declines at high values of  $p$ , making these cover types the dominant components of pattern. For example, a landscape comprised of a few large forest patches may not be as interesting as the non-forested patches embedded within the forest matrix (i.e., agriculture or development) or other community and ecosystem attributes of the forests (e.g., compositional or structural variation generated by environmental gradients). Thus, in the high- $p$  case, we might reverse the focal cover types and characterize patterns of the lower- $p$  cover types. Alternatively, we may redefine forest patches, subdividing large, contiguous areas into finer categories or subtypes (e.g., stand ages, community types, or disturbance histories).

### Pattern metrics

While the imperfect link between pattern metrics and pattern-generating processes has been widely recognized (Neel et al. 2004; Tischendorf et al.

2003; Wu and Hobbs 2002), it is worth emphasizing here that some intuitive and popular metrics of pattern—especially average patch size—are simply not very effective indicators. In part this is because the distribution of patch sizes is typically highly asymmetric, and so the mean is a poor descriptor of the distribution (Figs. 4 and 5). It is well known from percolation theory that the largest patch size is a better index (Stauffer and Aharony 1992) because of the threshold-like behavior of so many phenomena relative to  $p$  (Gardner 1999; Turner et al. 2001). In the analyses illustrated here, we have found the cfd to be much more informative about landscape pattern. This invites the use of distributional statistics such as the Kolmogorov–Smirnov (KS) test. Unfortunately, the KS test is insensitive to differences between distributions in the extremes where pattern may be most ecologically relevant. Clearly, there is a great deal of research that still needs to be done to develop more sensitive and ecologically meaningful tests of landscape pattern.

### Inferential models of pattern generation

While most of us would agree that landscapes are probably not generated by random processes, we have been remarkably slow to pose more interesting alternative models. Thus, we have taken only the first step in an iterative process toward explaining landscape pattern. Therefore, it is appropriate that we begin with randomness as the simplest null model (Gotelli 1996). When this model is rejected, we are free to move on to more interesting, and probably more complicated, explanatory models. Presumably, we would continue to successively pose more complicated models until we failed to reject one, leaving us with the most parsimonious explanatory model consistent with measurements from real landscapes.

From the perspective of statistical inference, it seems obvious that we can make stronger inferences about landscape processes by invoking and exploring models that are more narrowly constrained in terms of explanatory processes. A focused explanatory model allows us to highlight each process, forming layers that may or may not

be merged into a final explanatory model. This procedure is analogous to a multiple regression model that is fit in a “stepwise forward” fashion (or more generally, a set of nested models compared formally in terms of their incremental explanatory power using, e.g., AIC methods). The aim of this approach is to select the best from a set of competing models, where each of the competitor models is itself ecologically plausible (and more compelling than simple randomness). This model-selection approach to inference is rapidly gaining momentum in ecology (e.g., Burnham and Anderson 1998; Anderson et al. 2000; Johnson 2002; Robinson and Wainer 2002; Di Stephano 2004).

Understanding the relationship between pattern and process requires the development of the most compelling explanatory models of landscape pattern. Landscape pattern has long been attributed to the combination of abiotic constraints (climate, terrain, soils: the physical template), biotic processes (competition, dispersal), and natural or anthropogenic disturbance regimes (Delcourt et al. 1983; Urban et al. 1987, 2000), but we have not made much progress in elaborating how these agents of pattern vary regionally and interact in time to produce measurable change. Significant challenges lie ahead in specifying models that relate these agents to observed patterns in ways that allow convincing statistical tests.

The examples we have presented illustrate the approach we wish to pursue. The adjacency matrix, which may be unique for each landscape, can be used to constrain the random location of cover types to produce more realistic landscape patterns. However, the adjacency matrix is itself a pattern metric—the result of some unspecified generating processes—and it is ultimately these processes we wish to uncover. If the adjacency matrix provides a “better explanation” of landscape pattern, then we must ask what processes acting within these landscapes have generated the observed pattern of adjacencies in land cover? Certainly the specific processes will depend on the particular landscape and cover type considered, but the likely candidates will include aspects of the physical template, biotic processes, and disturbance regimes. It remains for us to devise methods to identify and isolate these candidate

explanatory variables in ways that allow results to be objectively evaluated.

#### Explanatory models and Monte Carlo methods

It is obvious that complex, multi-layered explanatory models of landscape pattern are much more cumbersome than their statistical analogues (e.g., a KS or  $\chi^2$ -test). However, any explanatory model, whether simple or complex, can be implemented as computer simulations and generated patterns can be statistically characterized via Monte Carlo methods. These methods have been well developed (Manly 1997) but have yet to be fully explored in landscape ecology (Fortin et al. 2003).

Although the process may be awkward, the procedure for testing potential relationships between pattern and process at landscape scales is conceptually simple and straightforward. First, a candidate model is posed; this model is then used to generate a distribution of expected values and associated statistics; and the distribution of results is then compared to actual landscapes. This model–data comparison is neither new nor revolutionary, but opens the door to many new possibilities both statistical and inferential.

Within this framework, there are a spectrum of approaches. The simplest is the original neutral landscape model where pattern is generated from simple random processes constrained only by map grain and extent and the number of land cover types. At the other end of the spectrum, spatially explicit landscape simulators might be used to generate patterns from detailed ecological mechanisms. For example, Urban (2005) used the heuristic forest landscape model METAFOR to illustrate feedbacks between environmental gradients and local seed dispersal mediated by competitive hierarchies in tree species growth rates and tolerances to drought and cold. These feedbacks generated qualitatively contrasting spatial patterns in simulated forests. Urban (2005) did not test these patterns against actual forest patterns, simply because these data were not available (we do not yet have the capability to remotely sense species composition for these forests, although this capability might not be far

off, given developments in hyperspectral sensors and other techniques). This example underscores two important issues in using such models to generate hypothesis tests for landscape pattern. First, if the model is data-intensive, there is a substantial empirical cost as compared to simpler random landscapes. Second, the data needed to test the models can be similarly expensive, requiring measurements with fine grain and broad extent. Although continued advances in remote sensing technology continues to reduce these costs, significant investments in time and effort might never be entirely eliminated. Nevertheless, we expect a model-intensive approach to be a promising direction for future efforts. Several models now available might be applied in this way (Mladenoff and Baker 1999).

As an intermediate approach, the constrained random method we have illustrated here bridges the purely random methods with the more complex simulators. The constraints of the MCA infuse, via the adjacency matrix, the consequence of ecological processes without the undue expensive of model development and parameterization. However, this approach requires that there be an explicit link between the ecological explanation and the mask or constraint used to generate the statistical expectations. Here, the adjacency matrix offers itself as a useful focus, because we can posit ecologically reasonable explanations for the tendency for some land cover types to occur next to others (e.g., residual forest next to water; also see Taverna et al. 2005). We hope that wider adoption of these approaches will ultimately result in general, parsimonious models capable of explaining and predicting landscape change. QRULE provides a useful platform for such developments.

## Conclusion

Relatively simple models can often ‘explain’ complicated patterns. Indeed, as Gardner et al. (1987) have noted, real landscapes are sometimes indistinguishable from purely random maps. This result does not argue that real landscapes are generated by simple, random processes, but merely defines the conditions where more complicated

explanations are not required. However, the failure of this simple model indicates where a more complicated explanation is required—explanations that may invoke specific agents of pattern formation from the physical template (environmental gradients), biotic processes, and disturbance regimes (including human actions). We have illustrated one method for exploring a more complicated explanatory model, an extension of simple neutral models, with the hope that the general approach will be extended to richer and more useful explanatory models of landscape pattern and process.

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## Appendix

The development of RULE (Gardner 1999) has been an evolutionary process. The current incarnation of this program, QRULE, involves extensive changes to the format of the output, data files for statistical summaries, and the inclusion of the neutral model described in this manuscript. Program documentation, example input and output files, and the Fortran source code for QRULE may be obtained from <http://www.al.umces.edu/QRule>. It is hoped that the release of the source code will allow alternative neutral models to be suggested and tested to better understand the relationship between pattern and process at landscape scales. The Open Software License (<http://www.opensource.org/licenses/index.php>) applies to the distribution, use, and possible alteration of QRULE.

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