Occupancy, Spatial Variance, and the Abundance of Species

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A notable and consistent ecological observation known for a long time is that spatial variance in the abundance of a species (σ^2) increases with its mean abundance (μ) and that this relationship typically conforms well to a simple power law (Taylor 1961):

$$\sigma^2 = a\mu^b, \tag{1}$$

where a and b are constants. Indeed, such models can be used at a spectrum of spatial scales to describe spatial variance in the abundance of a single species at different times or in different regions and of different species across the same set of areas (Taylor et al. 1978; Taylor and Woiwod 1982).

A second general pattern that has come to prominence more recently is that the proportion of areas occupied by a species (p, its probability of occurrence in a sample) increases with its average abundance (μ) among those areas and again that this is manifest from micro- to macrospatial scales both for a given species at different times or in different regions and for different species across the same set of areas (Brown 1984; Gaston and Blackburn 2000). While a number of models have been developed to describe this pattern, most are special forms of the general model (Wright 1991; Hanski et al. 1993; He and Gaston 2000)

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$$p = 1 - \left(1 + \frac{\mu}{k}\right)^{-k}, \tag{2}$$

where k is a spatial aggregation parameter defined in the domain of $(-\infty, -\mu)$ or $(0, \infty)$ and takes the form

$$k = \frac{\mu^2}{\sigma^2 - \mu}. \tag{3}$$

When $k < -\mu$, model (2) is derived from the positive binomial distribution that describes spatial regularity, and when $k > 0$, it is derived from the negative binomial distribution for spatial aggregation (He and Gaston 2000).

Variance-mean and occupancy-abundance patterns characterize the spatial distributions of species and share a common currency of abundance, but there has been little attempt in ecology to explore the connection between the two. The existence of such a connection for specific models of spatial variation in species abundance (e.g., Poisson) is not difficult to understand, but it has long been recognized that at different mean densities, the distributions of species conform best to different such models (Perry and Taylor 1986), limiting the utility of this insight. However, substituting equation (3) into model (2) and recognizing that σ^2 is defined by model (1) gives a general model unifying occupancy (p) and spatial variance (σ^2):

$$p = 1 - \left(\frac{\mu}{\sigma^2}\right)^{\mu^2/(\sigma^2 - \mu)}, \tag{4}$$

where $\sigma^2 \neq \mu$ but can infinitely approach μ, resulting in $p = 1 - e^{-\mu}$, which is occupancy for the Poisson distribution.

Note that model (4) has also been used in agricultural entomology for estimating pest levels of individual species from binomial sampling data (Wilson and Room 1983; Yamamura 2000). However, the unification of the two general ecological patterns of variance-mean and occupancy-abundance implied by the model is novel and has not apparently been reported and investigated before. Indeed, this model is arguably of much wider ecological significance from the perspective of pattern unification than that

of estimating population levels and, as such, it may help in fundamental understanding of spatial variation in abundance. The first objective of this study is to show that these two formerly independently documented patterns are able to predict each other and hence are just different expressions of the same phenomenon (i.e., the distribution of species). In doing so, the study does not consider the variance-mean and the occupancy-abundance as competing models but two complementary mathematical forms. The second objective is to provide mechanistic interpretations for the unification of the two patterns, with an emphasis on theories of metapopulation dynamics. The study further discusses the importance in investigating spatial variability (in contrast to temporal stochasticity) in abundance for understanding population persistence in landscapes.

Methods

Data

We compiled eight empirical data sets (four intraspecific and four interspecific), reflecting a spectrum of spatial scales, to examine how well the variance-mean and occupancy-abundance patterns can predict each other.

The four intraspecific data sets are as follows: first, the number of striped ambrosia beetle (*Trypodendron lineatum* Olivier) caught in each of 12 traps in 32 periods (dates) from 1993 to 1998 in a lodgepole pine (*Pinus contorta* Doug. ex Loud.) plantation in British Columbia, Canada. On each date, the mean of the beetle abundance and its variance was calculated for the 12 traps (see app. A in the online edition of the *American Naturalist*). Four periods of samples were ignored when no individuals were caught in any of the 12 traps; second, the number of aphids *Acyrthosiphon pisum* (Harris) caught in each of 22 suction traps distributed across Britain for seven 4-wk periods (ignoring two periods when no individuals were caught in any trap; see Woiwod et al. 1988); third, the number of ticks *Ixodes ricinus* L. on each sheep for 10 groups of sheep (of 20–86 individuals; Milne 1943); and fourth, the number of eggs of the chrysomelid *Altica oleracea* (L.) on each leaf for each of 49 stems of the host plant *Oenothera biennis* (L.) (Yamamura 1990).

The four interspecific data sets are as follows: first, the number of individuals of each of 30 moth species caught in each of 53 light traps distributed across Britain over a 1-yr period (Taylor and French 1973); second, the number of individuals of each of 14 benthic infaunal species caught in each of 10 quadrats in a subtidal marsh creek in Rhode Island (Heltshe and Forrester 1983; see app. B in the online edition of the *American Naturalist*); and finally, the number of individuals of each of 814 tree species counted at

two quadrat sizes, 12.5 m × 12.5 m and 25 m × 25 m, respectively, in a 50-ha tropical rain forest plot censused in 1987 in the Pasoh Forest Reserve of Malaysia (He et al. 1997; Manokaran et al. 1999). The area of occupancy of a species was the number of the occupied quadrats multiplied by quadrat size.

Two of the data sets, one intraspecific and one interspecific, are shown in appendixes A and B as examples.

Model Fitting and Prediction

Because variance-mean data are typically heteroscedastic, the simple linear regression method has been widely used as a standard method for fitting the log-transformed model (1) to each of the eight sets of variance-mean data. The appropriate method for fitting model (2) to occupancy-abundance data is the maximum likelihood method by assuming binomial errors (He et al. 2002). The parameter k was estimated by minimizing the log-likelihood function $l = \sum_{i=1}^{s} [y_i \log(p_i) + (n_i - y_i) \log(1 - p_i)]$, where the notation is slightly different for intraspecific and interspecific data. For intraspecific data, s is the total number of trapping dates (e.g., app. A), while for interspecific data, s is the total number of species (e.g., app. B); n_i is the number of empty and occupied traps on the ith date for appendix A data or the number of empty and occupied quadrats for the ith species for appendix B data, y_i is the number of occupied traps or quadrats, and p_i is given by model (2) in which density μ_i can be read, for instance, from the tables in appendix A for the ith trapping date or species.

The prediction of the variance-mean pattern was then made using the fitted occupancy-abundance model (2) by substituting it into the unified model (4), in which the relationship between variance (σ^2) and mean (μ) is then determined. To be more specific, the prediction involves three steps. First, we fitted the occupancy model (2) to the observed occupancy-abundance data. We then substituted the fitted occupancy p (for each abundance μ) into model (4) so that the variance (σ^2) in the model now became the only unknown variable. We finally numerically solved the model (4) for the variance (σ^2), given the observed abundance (μ). Likewise, the prediction of the occupancy-abundance pattern was made using the fitted variance-mean power model (1) by substituting it into model (4); that is, given the observed abundance, the occupancy (p) was solved by substituting the fitted variance into model (4).

Model Assessment

Two statistics were used to assess how far (or close) the fitted model departs from the predicted results. The ratio of the squared roots of the residual sums of squares is

RSSE1, and RSSE2 is the same ratio but applied to log-transformed data:

$$RSSE1 = \frac{\sqrt{\sum (y_p - y_o)^2}}{\sqrt{\sum (y_f - y_o)^2}},$$

$$RSSE2 = \frac{\sqrt{\sum [\log(y_p) - \log(y_o)]^2}}{\sqrt{\sum [\log(y_f) - \log(y_o)]^2}},$$

where y_o is the observed variance (σ^2) or occupancy (p), y_p is the predicted variance or occupancy from the unified model (4), and y_f is the fitted variance or occupancy using model (1) or (2); RSSE = 1 indicates that model (1) or (2) describes the data as well as the relationship predicted by the unified model (4), RSSE > 1 indicates model (1) or (2) describes the data better than the relationship predicted by the unified model (4), while RSSE < 1 suggests that the prediction from the unified model (4) is superior to the individual model (1) or (2). To statistically judge how far RSSE departs from 1, we generated the sampling distribution of RSSE by bootstrap resampling and obtained a 95% confidence interval for the RSSE based on 500 resamples. If the confidence interval contains the value 1, we conclude that model (1) or (2) and model (4) describe the data equally well; otherwise, either the individual models or the unified model describes the data better.

Although our primary interest in this study is to investigate how well one pattern can predict the other, not to test how well these models could fit data (this is well established), we include an approximate assessment of how much variation in the data can actually be explained by the individual model (1) or (2) and by the unified model (4). This can be done, by analogy to the method in linear regression, by partitioning the total sum of squares (SST) into the sum of regression (or prediction) squares (SSR) and the sum of residual squares (SSE). The proportion of variation explained by a model is measured by SSR/SST, where $SST = \sum (y_o - \bar{y}_o)^2$ and $SSR = \sum (\hat{y} - \bar{y}_o)^2$, in which $\bar{y}_o$ is the mean of observed data y_o and $\hat{y}$ is the estimate (or prediction) of either y_p or y_f as notated in RSSE. The assessment of variation was done for the log-transformed data. In this study, all computation (including bootstrapping) was carried out using program S-Plus 2000 (MathSoft 1999).

Results

The numerical examples in figure 1 illustrate the predictive relationships between the variance-mean power law model (1) and the occupancy-abundance model (2). Figure 1a and 1b show how an occupancy-abundance pattern is predicted by a variance-mean model. This was done by inserting model (1) (e.g., $\sigma^2 = 5\mu^2$ as for curve 1 in fig. 1a) into model (4) and then solving for the p-μ relationship. Similarly, for a given occupancy (p), model (4) predicts the log-linear variance-mean relationship of model (1) (fig. 1c). Note that in producing figure 1c, model (1) did not participate but was the result of the prediction. The relationships among occupancy, variance, and abundance are shown in figure 1d. It is clear that for a given abundance (μ), occupancy-variance forms an inverse relationship, and the concavity of the curve becomes flatter with the increase in abundance (fig. 1d). This is consistent with expectation because for a very abundant species, few sites will be left unoccupied while abundance still varies considerably from site to site.

To further confirm the prediction of model (4) for the occupancy-variance relationship and the numerical results in figure 1, we tested the unified model using the eight data sets described above. The estimated parameters for models (1) and (2) are shown in table 1. The prediction of variance from occupancy and the prediction of occupancy from variance are rather impressive (figs. 2, 3; table 2). Although the statistics used to compare the component models against the unified model are not always consistent, there is no systematic bias toward the fitted patterns or those predicted from the unified model (4) (table 2). Some data may be more closely described by the unified model (e.g., occupancy data for *Acyrthosiphon pisum* measured by RSSE1; table 2), whereas others are better fitted by the component model (1) or (2) (e.g., the variance data for *Altica oleracea*). However, there seems to be a systematic pattern in the cases where the component models and the unified model do differ (i.e., the eight footnoted cases in table 2). In the four variance cases where the component model (1) appears to fit the data better than the unified model (4) (i.e., the RSSE > 1), we suspect that this may simply reflect the fact that the R_f^2 of the component model (1) is higher than the R_p^2 of the unified model in the four cases (table 2), while in the footnoted occupancy cases, the R_p^2 of the unified model is higher than the R_f^2 of the component model (2) except for *A. pisum*.

While caution is needed in interpreting the RSSE bootstrap confidence intervals for some data sets because of small sample size (e.g., *A. pisum* has only seven data points to resample), nevertheless, the RSSE criteria in table 2 show that the predicted variances and occupancies are little different from the fitted models (1) and (2). These results suggest that the component models (variance-mean and occupancy-abundance) and the unified model both can describe the two patterns equally well. In other words, the mean-variance pattern can indeed predict the occupancy-abundance pattern and vice versa. Even though the predicted variance-mean relationships do not exhibit a straight line on a log-log scale, the predictions and the
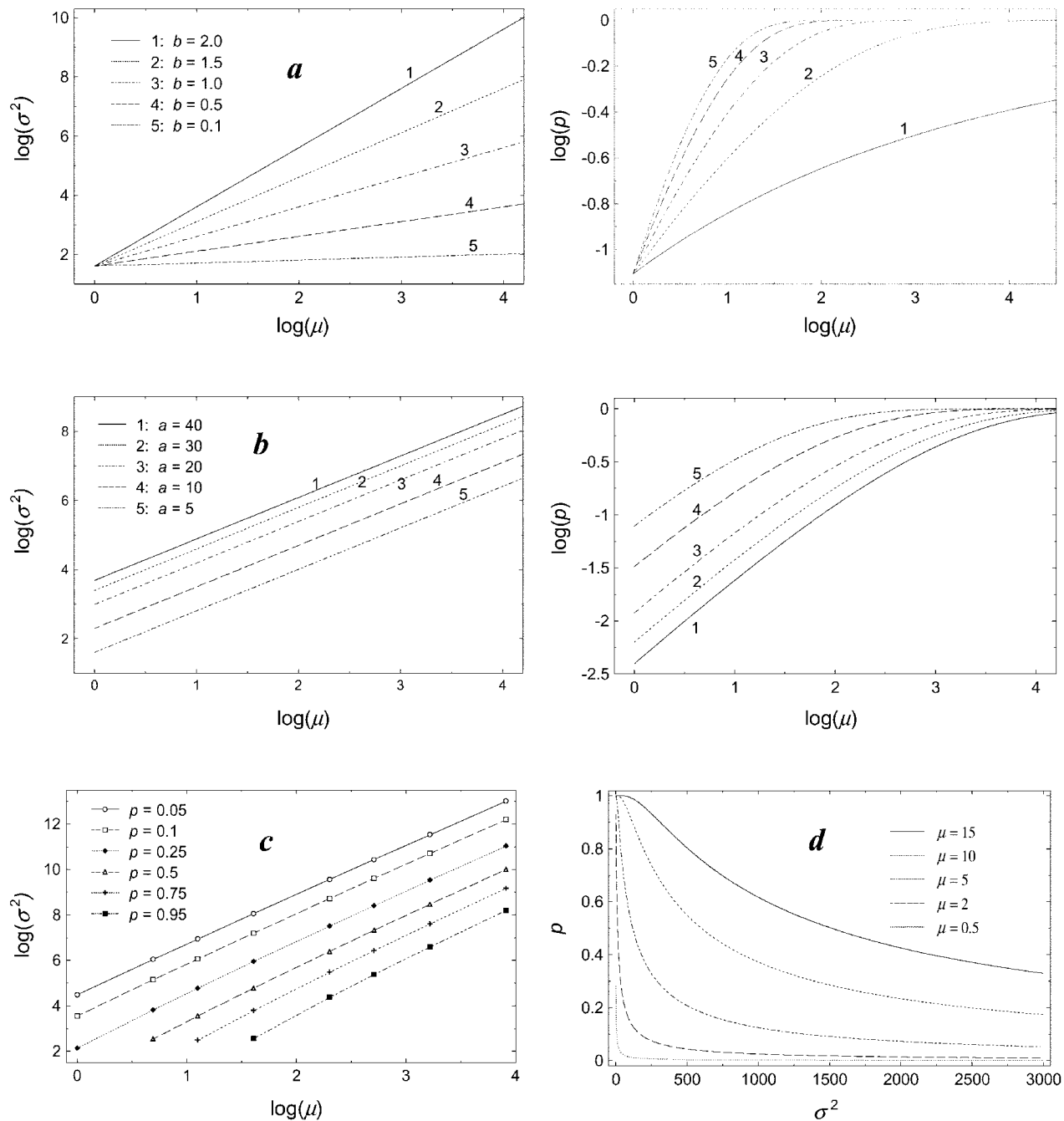
Figure 1: *a*, *b*, Variance-mean power models (*left column*) and their corresponding occupancy-abundance curves predicted from model (4) (*right column*). *a*, Power model for *a* = 5 with *b* varying from 2 to 0.1. *b*, Model for *b* = 1.2 with *a* varying from 40 to 5. *c*, Variance-mean relationships solved from model (4) for various occupancy *p*'s. The slopes of the lines approximately equal 2.25. *d*, Occupancy-variance relationships solved from model (4) for various abundance *μ*'s.

Table 1: Parameters for the estimated variance-mean model (1) and occupancy-abundance model (2) for the eight data sets

		Variance-mean model (1)		Occupancy-abundance model (2)
Data	n	$\log(a)$ (SE)	b (SE)	k (SE)
Intraspecific:				
Trypodendron lineatum	28	.991 (.131)	1.575 (.075)	.883 (.196)
Acyrthosiphon pisum	7	1.586 (.209)	1.730 (.075)	.472 (.089)
Ixodes ricinus	10	.545 (.321)	1.462 (.114)	2.525 (.541)
Altica oleracea	49	1.049 (.039)	1.300 (.025)	.683 (.051)
Interspecific:				
Moth species	30	1.932 (.196)	1.769 (.086)	.319 (.018)
Infaunal species	14	.333 (.058)	2.054 (1.106)	1.473 (.671)
Pasoh tree species 1	814	.528 (.023)	1.077 (.006)	.807 (.009)
Pasoh tree species 2	814	.807 (.025)	1.150 (.009)	.907 (.008)

Note: Model (1) was fit to the log-transformed data using simple linear regression method, while model (2) was parameterized using the maximum likelihood method.

fitted variance-mean models are practically indistinguishable according to the RSSE in table 2.

Discussion

As expected given their ubiquity and generality across spatial scales, a variety of statistical and ecological processes can and do give rise to variance-mean and occupancy-abundance relationships, although their role in generating both patterns in the same study system has not empirically been demonstrated (Perry 1988; Gaston et al. 1997). It has been shown that the negative binomial distribution on which model (2) is based can be generated from a wide range of statistical processes including several types of birth-death processes (Boswell and Patil 1970). From an ecological perspective, the mechanisms that result in the variance-mean and occupancy-abundance patterns have been argued to be rooted in demographics, behavior, niche structure, or even sampling artefact (Taylor et al. 1983; Brown 1984; Downing 1986; Perry 1988; Gaston 1994). A significant implication of the unification is that it suggests that interpretations for one pattern can also be used for interpreting the other pattern because of the mutuality of the two.

A simple but elegant interpretation for the two linked patterns can be found in theories of metapopulation dynamics. In part because of the significance for conservation and management issues, the theories of metapopulation dynamics, in which species dispersal is assumed to be a fundamental process in maintaining local populations in different habitat patches, have been widely used to interpret occupancy-abundance relationships (Hanski 1991; Hanski et al. 1993; Gonzalez et al. 1998). From the prediction of the unified model (4), such a metapopulation process should also lead to a positive variance-mean relationship. Indeed, the variance-mean pattern is inevitably produced by metapopulation dynamics through immigration of individuals from high-density sites to lower-density or vacant ones (the rescue effect; Hanski 1991). For instance, assume a metapopulation with abundances = 5, 10, 0, and 0 in four sites and that, due to the rescue effect, the third vacant site is now rescued through immigration from the second site so that the abundances become 5, 8, 2, and 0. This effect increases the chance of colonization and reduces spatial variation, conforming to the prediction of the unified model (4). These theoretical results are not only supported by empirical field experiments (Kruess and Tscharntke 1994; Gonzalez et al. 1998) but also demonstrated by stochastic cellular automaton simulations, which show that spatial aggregation is an unavoidable outcome of poor colonization and dispersal ability, from which the negative variance-occupancy correlation as shown in figure 1d will result (Tilman et al. 1997).

In addition to metapopulation dynamics, a fractal model of species distributions has been explored, which typically stipulates a power law relationship between occupancy and abundance (Kunin 1998; Harte et al. 2001). Although it is not immediately clear what kind of spatial pattern in abundance variability is implied by such a model, a result of Harte et al. (2001), which proposes to link variance in abundance to the probability of species presence in bisected areas in a study, may provide the first step in making such a connection.

The neutral theory of Hubbell (2001) has shown that a parsimonious set of demographic parameters (e.g., dispersal, mortality, fecundity, and speciation) that are assumed to be probabilistically identical on a per capita basis can predict many prominent ecological patterns with high accuracies (Bell 2001; Hubbell 2001). As we have shown earlier, from the theory of metapopulation dynamics, dis-
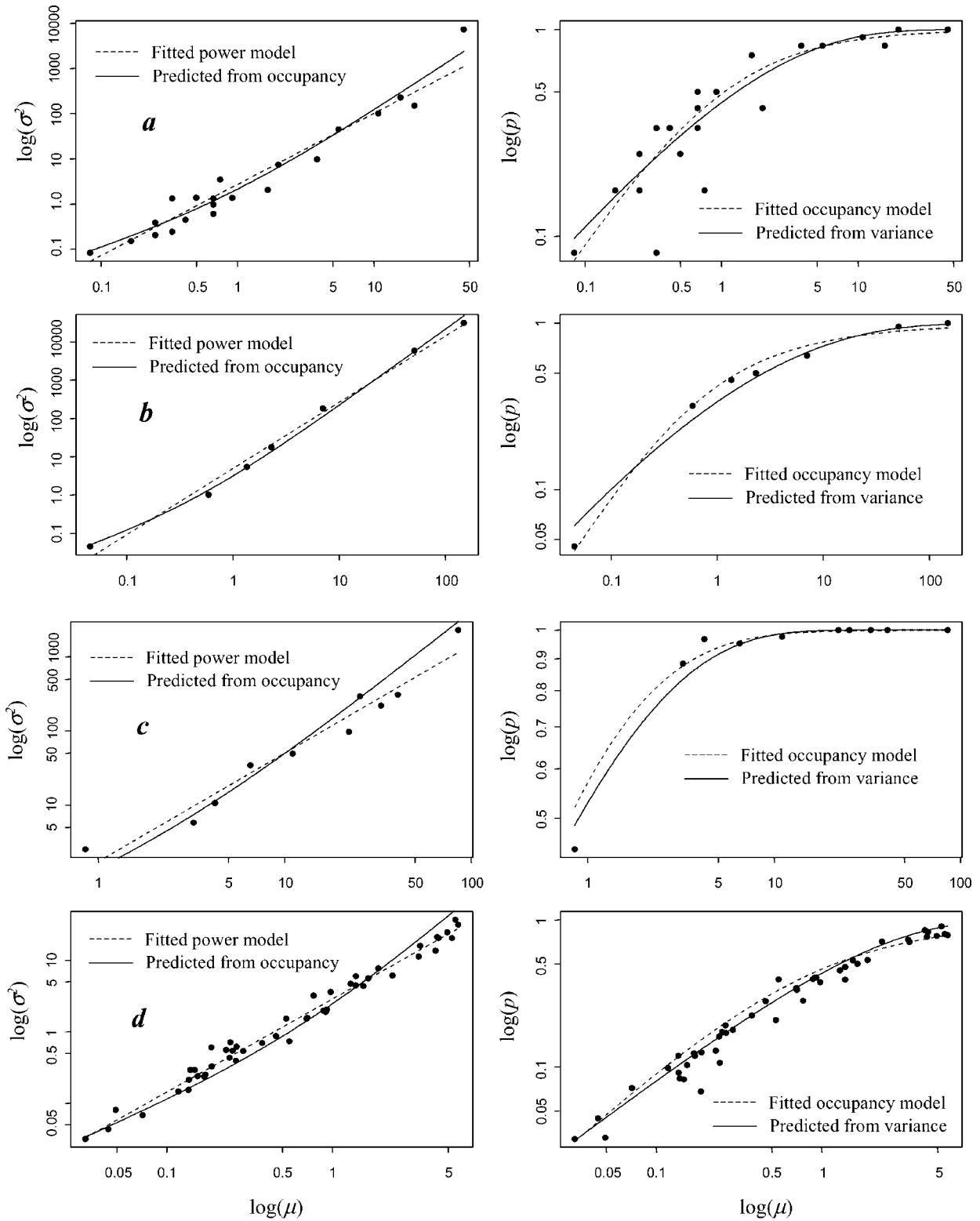
Figure 2: Intraspecific variance-mean and occupancy-abundance relationships for (*a*) *Trypodendron lineatum*, (*b*) *Acyrthosiphon pisum*, (*c*) *Ixodes ricinus*, and (*d*) *Altica oleracea*. The dashed curves are the power model (1) and the occupancy model (2) fitted to the respective data. The solid curves are the predictions of model (4) given by the opposite patterns.
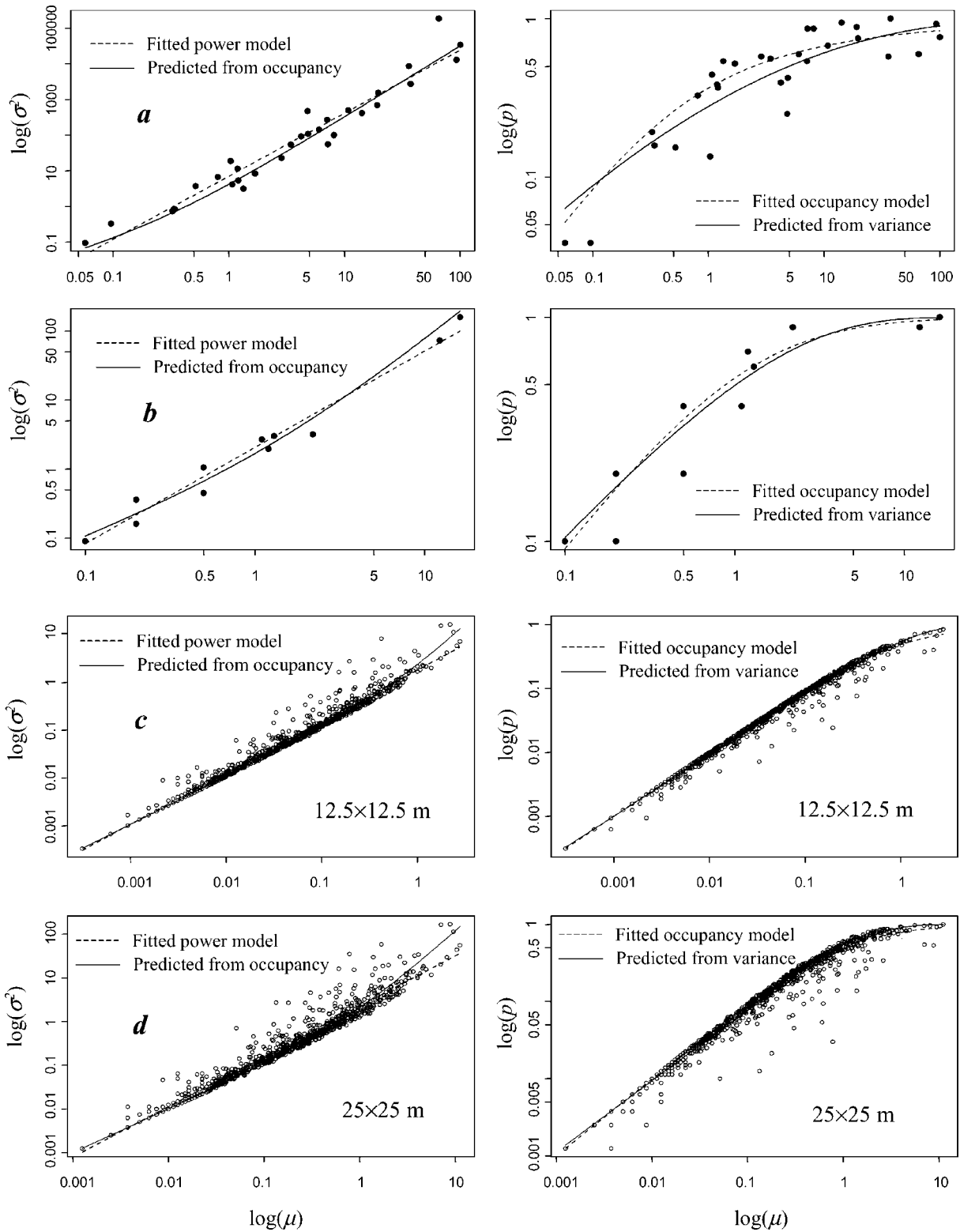
Figure 3: Interspecific variance-mean and occupancy-abundance relationships for (*a*) moths, (*b*) benthic infauna, and (*c, d*) Pasoh tree species at two spatial scales. The dashed curves are the power model (1) and the occupancy model (2) fitted to the respective data. The solid curves are the predictions of model (4) given by the opposite patterns.

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Table 2: Comparison of the fitted variance and occupancy to the predictions from the unified model (4)

Data	n	Variance				Occupancy			
		RSSE		R^2		RSSE		R^2	
		RSSE1 (95% CI)	RSSE2 (95% CI)	R_f^2	R_p^2	RSSE1 (95% CI)	RSSE2 (95% CI)	R_f^2	R_p^2
Intraspecific:									
Trypodendron									
lineatum	28	.79 (.73, 1.09)	.89 (.79, 1.23)	.944	.956	.99 (.82, 1.08)	.98 (.90, 1.05)	.799	.807
Acyrthosiphon pisum	7	5.66 (.38, 8.40)	.67 (.58, 1.50)	.991	.996	.72[a] (.62, .90)	1.77 (.61, 2.19)	.993	.977
Ixodes ricinus	10	.73 (.56, 1.49)	1.24 (.88, 2.84)	.953	.928	1.13 (.55, 1.56)	.84 (.42, 1.57)	.950	.965
Altica oleracea	49	3.41[a] (1.82, 5.85)	1.62[a] (1.33, 1.85)	.983	.956	.90 (.71, 1.15)	.76[a] (.67, .89)	.941	.966
Interspecific:									
Moth species	30	.99 (.57, 2.97)	.97 (.80, 1.09)	.939	.942	1.09 (.95, 1.32)	1.02 (.82, 1.32)	.821	.812
Infaunal species	14	.92 (.26, 2.03)	.99 (.67, 1.20)	.980	.980	1.04 (.87, 1.51)	.97 (.85, 1.27)	.926	.929
Pasoh tree species 1	814	.88 (.68, 1.25)	1.09[a] (1.02, 1.13)	.977	.973	1.10 (.94, 1.30)	.93[a] (.90, .97)	.989	.990
Pasoh tree species 2	814	.90 (.62, 1.68)	1.08[a] (1.02, 1.13)	.957	.950	1.01 (.97, 1.07)	.94[a] (.91, .97)	.970	.974

Note: The individual models describe the data better than the unified model if the lower bound of the 95% bootstrap confidence interval (CI) is larger than 1, whereas the unified model is superior if the upper bound of the CI is smaller than 1. The bootstrap CIs were generated from 500 resamples. R_f^2 is the proportion of variation explained by the fitted model, whereas R_p^2 is the proportion of variation explained by the prediction of the unified model, all measured in terms of log-transformed data.

[a] Indicates that the fitted individual variance or occupancy model describes the data significantly differently from the unified model.

persal, which is also a critical underpinning process in neutral theory, can play a key role in linking the variance-mean and occupancy-abundance patterns. A question of particular interest is thus what other neutral processes (e.g., birth, death, and speciation rates) could tell us more about the connection between the two patterns.

It is well known in ecology that, all else being equal, the greater the temporal variation of a population, the greater the likelihood of extinction (Leigh 1981; Goodman 1987). However, how spatial variation affects population persistence is poorly understood. This study underlines the importance of studying spatial variance for understanding species persistence in metapopulation systems and biological conservation. According to model (4), for a given level of abundance, high spatial variability is associated with a small range size (fig. 1*d*), making a population more susceptible to environmental change and habitat loss and therefore increasing its risk of extinction. This is supported by much empirical evidence showing that landscape fragmentation or environmental stochasticity, which promotes spatial variability, results in lower occupancy (i.e., "shallow incidence function"; Hanski 1992) and is a possible cause of population extirpation (Pimm 1991; Kruess and Tscharntke 1994; Gonzalez et al. 1998). Such a negative impact of greater spatial variability on species persistence can, however, be alleviated by the rescue effect, which both reduces the likelihood of local extinction and lowers spatial variation. Rare species are typically found to be less aggregated than common species, which, sampling artefacts aside, might suggest that low aggregation could be a means by which they persist.

Important applications of variance-mean models are in sampling design and in stabilizing variance for data analysis (Taylor 1961; Kuno 1990; Hayek and Buzas 1997). The unified model (4) suggests that data on occupancy, which are more readily obtained, can also be used for these purposes. For example, in the interspecific case, variance for an assemblage of species can be derived using models (2) and (4) if occupancy-abundance data for just some of the species are available. This is achieved by first fitting the occupancy model (2) to those species whose occupancy-abundance data are available. The abundance (μ) of other species whose occupancies are known can be estimated using the parameterized model (2). The variances of those species can then be obtained through the unified model (4).

Another application, again owing to the readiness of garnering occupancy data, is to use information on occupancy and variance for biological monitoring and conservation purposes. Model (2) helps provide data on occupancy-abundance relationships, whereas model (4) permits the derivation of information for assessing spatial variability in species distribution. When using these models to derive occupancy data or variance for monitoring and conservation programs, however, a sampling problem that has not explicitly been addressed here but must be kept in mind is that of species detectability. The presence of a species in a study site may or may not be observed in the field. The nondetection may mean that the species is truly absent or is missed because of insufficient survey efforts. The latter scenario will inevitably lead to underestimation of occupancy rates. This problem may also exist to some degree in some of the data sets used in this study, but it should clearly not be a problem for others such as

the census data of the Pasoh forest. Incorporation of this sampling bias into occupancy-abundance models is challenging, but the problem must be solved to provide unbiased occupancy rates useful for practical applications. Some constructive approaches to the problem can be found in Heikkinen and Högmander (1994) and MacKenzie et al. (2002) for two common sampling designs. The issue is further complicated by the fact that detectability often varies over time and space due to the dynamic change and nonstationary spatial distribution in abundance. This study assumed occupancy to be temporally and spatially invariant, although future improvement may be made by considering abundance (μ) in model (2) to be temporally or spatially dependent. We suggest that development in this direction will inevitably advance the understanding of spatiotemporal dynamics of metapopulations.

There is growing evidence that ecology is progressing from searching for bivariate ecological patterns (e.g., species-area, species-abundance, productivity-richness, variance-mean, occupancy-abundance, body size-richness) toward the study of multivariate patterns between the same sets of variables (Hanski and Gyllenberg 1997; Ritchie and Olff 1999; Pachepsky et al. 2001; He and Legendre 2002). The current study is another step in this process suggesting that ecology may be on the verge of a significant period of pattern unification.

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