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# On the generality of stability-complexity relationships in Lotka-Volterra ecosystems

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**Abstract**

Understanding how complexity persists in nature is a long-standing goal of ecologists. In theoretical ecology, local stability is a widely used measure of ecosystem persistence and has made a major contribution to the ecosystem stability-complexity debate over the last few decades. However, permanence is coming to be regarded as a more satisfactory definition of ecosystem persistence and has relatively recently become available as a tool for assessing the global stability of Lotka - Volterra communities. Here we document positive relationships between permanence and Lotka - Volterra food web complexity and report a positive correlation between the probability of local stability and permanence. We investigate further the frequency of discrepancy (attributed to fragile systems that are locally stable but not permanent or locally unstable systems that are permanent and have cyclic or chaotic dynamics), associate non-permanence with the local stability or instability of equilibria on the boundary of the state-space, and investigate how these vary with aspects of ecosystem complexity. We find that locally stable interior equilibria tend to have all locally unstable boundary equilibria. Since a locally stable boundary is inconsistent with permanent dynamics, this can explain the observed positive correlation between local interior stability and permanence. Our key finding is that, at least in Lotka - Volterra model ecosystems, local stability may be a better measure of persistence than previously thought.

Key words: community persistence; permanence; local stability analysis; non-equilibrium dynamics; boundary equilibria

## Introduction

Ecologists aim to understand the conditions under which a community of interacting species survives as a whole and in the long term. In practice, much of the research into the question of long term coexistence of species has regarded this as an equilibrium problem. From a theoretical perspective it has been the tractability of local (also known as asymptotic or neighbourhood) stability analysis that has ensured the pervasiveness of the equilibrium view point: ‘even if other definitions of stability are more attractive, if they are not tractable then the ecologist cannot adopt them with profit’ (Hutson and Schmitt, 1992). The deficiencies of local stability analysis are numerous and well known (Anderson et al., 1992; Berlow et al., 2004; Haydon, 1994; Jansen and Sigmund, 1998) and there is little reason to believe that the natural world is in equilibrium. A more satisfactory definition of ecosystem stability is a global property called permanence, which requires only that densities of rare species tend to increase. The analysis of permanence was, however, intractable until recent attention from mathematicians (reviewed in Hofbauer and Sigmund, 1988) enabled Law and colleagues (Anderson et al., 1992; Law and Morton, 1993; Law and Morton, 1996) to provide a non-technical description of a method for Lotka-Volterra (LV) communities that has made permanence analysis accessible as a tool to ecologists.

Despite permanence analysis being made tractable to ecologists for more than a decade, there are only a handful of theoretical community studies in which permanence has been used as well as, or in place of, local stability (Chen and Cohen, 2001; Emmerson and Yearsley, 2004; Kristensen, 2008; Vandermeer, 2006). One area where permanence will contribute to theoretical community ecology is in the ongoing debate over the relationship between stability and complexity of ecosystems. In the 1970s, theoreticians reported that three measures of complexity, species richness, connectance (the frequency of species interactions) and the mean strength of those interactions, decreased the probability of local stability in randomly parameterised large complex systems (Gardner and Ashby, 1970; May, 1972). Recently, Chen & Cohen (2001) were the

first to systematically explore permanence in a similar framework. They studied two of the measures of complexity, connectance and species richness, and found that increases in both reduced the probability of permanence in ecosystem models. However, they made some potentially restrictive assumptions that could lead to ecologically implausible model ecosystems (with equal equilibrium species abundances assumed when each species' interaction strengths are sampled from the same uniform distribution, whilst the presence of autotrophs was not ensured), and did not explore the third dimension to complexity: interaction strength. Thus the effect of enhanced ecological plausibility on permanence-complexity relationships in model ecosystems remains an open question.

The mean interaction strength is a traditional measure of ecosystem complexity (May, 1972) and we relate it here to permanence for the first time. However, taking the average neglects the natural variability of interaction strengths. In real ecosystems the range of interaction strengths can span nine orders of magnitude (Wootton, 1997) and the distribution is commonly observed to be skewed towards weak interactions (De Ruiter et al., 1995; Fagan, 1997; Goldwasser and Roughgarden, 1993; Paine, 1992; Wootton, 1997). Such variability has been identified as an important determinant of stability under some conditions. In competitive communities, greater variance in strengths of competitive interactions can increase the probability of stability (Jansen and Kokkoris, 2003). The non-random patterning of weak interactions in omnivorous loops increases the probability of local stability in empirical food webs (Neutel et al., 2002; Neutel et al., 2007) and permanence in special sets of trophic relations (Emmerson and Yearsley, 2004). Further, non-equilibrium dynamics were stabilized when complexity was added via a species (consumer) with weak interactions (McCann et al., 1998). It is unclear however whether the skew towards weak interactions will influence permanence in more generally structured ecosystem models.

How much do predictions differ between local stability and permanence? Using two examples of simple communities Anderson et al. (1992) found the parameter space for community coexistence measured

by local stability was substantially smaller than that under permanence. Permanent but locally unstable communities represent those which must have some form of non-equilibrium asymptotic behaviour e.g. cyclical or chaotic orbits. Communities may also admit locally stable behaviour in the absence of permanence (Chen and Cohen, 2001; Hofbauer and Sigmund, 1988), which we characterise as ‘fragile’ ecosystems. If the match and discrepancy between local stability and permanence can be understood, then we may be able to attempt to answer an important question for ecology which was posed by Anderson et al. (1992): ‘how much confidence should we have in a theoretical ecology based on asymptotic stability analysis?’.

In discussing complexity, we will examine the properties of the Jacobian matrix: order (species richness), frequency of non-zero elements (frequency of interactions between species) and magnitude of elements (strength of interactions). The Jacobian governs the local dynamics around a specified equilibrium point and thus we will use ecosystem complexity to refer to the properties of the Jacobian at the interior equilibrium. The criterion of permanence rests on the boundary: densities of rare species will tend to increase if the boundaries of the positive orthant repel the ecosystem dynamics away into the interior (Law & Blackford 1992). For clarity, we stress here the distinction between permanence and global asymptotic stability: permanence applies to all orbits and initial conditions where all species are present, but does not require that all orbits converge on the interior equilibrium point.

The results presented in this paper are arranged around three sets of questions. The first set of questions is on permanence-complexity relationships: (1.1) because there are some questions regarding the ecological plausibility of models generated under the assumptions of Chen & Cohen (2001) we ask whether using algorithms for constructing more flexible ecosystems with enhanced plausibility (variation in equilibrium species abundances and the presence of autotrophs is ensured) affect permanence-complexity relationships? (1.2) What is the relationship between mean absolute interspecific interaction strength and

permanence? and (1.3) What is the effect of skew towards weak interspecific interaction strengths on permanence? The second set is on the match and discrepancy between predictions from local stability and permanence: (2.1) Are local stability and permanence correlated? (2.2) Does the proportion of permanent ecosystems with non-equilibrium dynamics change with complexity? and (2.3) Does the probability of fragility change with complexity? The third set is based on the boundary equilibria: (3.1) Is non-permanence associated with boundary equilibria which are locally stable or unstable? and (3.2) Do the probabilities of at least one locally stable boundary and of a locally stable interior follow the same relationships with ecosystem complexity?

## Methods

### *Model ecosystems*

We constructed model ecosystems using the LV equations which describe the population dynamics of  $n$  interacting species,

$$\frac{dN_i}{dt} = N_i \left( b_i + \sum_{j=1}^n a_{ij} N_j \right) \quad \text{for } i = 1, \dots, n. \quad \text{eqn 1}$$

The equations were adopted as the global dynamics of the ecosystem *sensu* Volterra (1926), rather than the more general but locally applicable formulation of Lotka (1925). This means we can define the parameters in eqn 1 with unambiguous ecological interpretations:  $b_i$  is the intrinsic growth rate of the  $i$ th species and  $a_{ij}$  is the per capita effect of the  $j$ th species on the  $i$ th species and are the elements of the per capita interaction matrix  $\mathbf{A}$ . At the interior equilibrium point,  $\mathbf{AN}^* = -\mathbf{b}$  and the Jacobian matrix  $\mathbf{G}$  has a simple form:



$$\mathbf{G} = \begin{bmatrix} a_{11}N_1^* & a_{12}N_1^* & \cdots & a_{1n}N_1^* \\ a_{21}N_2^* & a_{22}N_2^* & \cdots & a_{2n}N_2^* \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}N_n^* & a_{n2}N_n^* & \cdots & a_{nn}N_n^* \end{bmatrix}. \quad \text{eqn 2}$$

The elements of the diagonal of the Jacobian matrix ( $g_{ij}$  where  $i = j$ ) represent intraspecific interaction strengths and the off-diagonal elements ( $g_{ij}$  where  $i \neq j$ ) represent interspecific interaction strengths in the vicinity of the equilibrium point ( $\mathbf{N}^*$ ). It is the off-diagonal elements of the Jacobian ( $g_{ij}$ ), rather than the per capita interactions ( $a_{ij}$ ), which we refer to in the subsequent analyses as interspecific interaction strengths.

Model ecosystems were generated that contained paired interactions of consumer and resource species, i.e. food webs. All food webs were checked to ensure they did not contain discrete subwebs. The food webs were given a cascade trophic structure to ensure species lower in the web could not feed on higher species (no loops). The cascade trophic structure was implemented by placing negative effects of consumers on resource species ( $g_{ij}$ ) above the diagonal of the Jacobian matrix, and positive effects of resource species on consumers ( $g_{ji}$ ) below.

There are two approaches to generating the Jacobian matrix at the interior equilibrium point under Volterra's formulation of eqn 1. Given the per capita interaction matrix  $\mathbf{A}$ , they differ in whether the equilibrium values ( $\mathbf{N}^*$ ) or the intrinsic growth rates ( $\mathbf{b}$ ) are assigned. In this study  $\mathbf{N}^*$  was assigned and  $\mathbf{b}$  ( $=-\mathbf{AN}^*$ ) calculated in order to maintain control over the species abundance relationships contained within  $\mathbf{N}^*$ . We used four algorithms for constructing model ecosystems:

1. The first algorithm assigned equilibrium abundances ( $N_i^*$ ) to be the same value, 0.5, for consistency with subsequent parameterisation. The non-zero elements of the per capita interaction matrix  $\mathbf{A}$  were drawn from a uniform random distribution in the interval (-1,0) for each  $a_{ii}$  and  $a_{ij}$  ( $i < j$ ) and in the interval (0,1) for each  $a_{ij}$  ( $i > j$ ). Under the same model ecosystem construction (except they assigned a unity

equilibrium point  $N_i^* = 1$ ), Chen and Cohen (2001) showed that the probability of an ecosystem being permanent decreased with increasing species richness and connectance.

2. The second algorithm ensured feasibility of intrinsic growth rates by defining a quarter of all species as autotrophs ( $b_i > 0$ ) and the remaining as heterotrophs ( $b_i < 0$ ). Intrinsic growth rates could not equal zero ( $b_i \neq 0$ ). Other parameterisation as for algorithm 1.
3. The third algorithm ensured the feasibility of intrinsic growth rates and relaxed the assumption of equal  $N_i^*$  by allowing the  $N_i^*$  to vary uniformly in the interval (0,1). In this algorithm the per capita interactions were drawn from a uniform random distribution in the interval (-1,0) for each  $a_{ii}$ , (-2,0) for each  $a_{ij}$  ( $i < j$ ) and (0,2) for each  $a_{ij}$  ( $i > j$ ). The intervals were chosen to ensure the mean of the intraspecific interaction strengths ( $\overline{g_{ii}}$ ) and mean of the absolute values of non-zero interspecific interaction strengths ( $\overline{|g_{ij}|_{i \neq j}}$ ) remained constant across all algorithms.
4. Modelling ecosystems by assigning  $\mathbf{N}^*$  also permits specification of the off-diagonal elements of the Jacobian ( $g_{ij}$  where  $i \neq j$ ) as independent random variates, allowing direct manipulation of the interspecific interaction strengths. Model ecosystem construction was equivalent to that for the third algorithm as described above, except the non-zero interspecific interaction strengths were assigned using a random uniform distribution in the interval (-1,0) for each  $g_{ij}$  ( $i < j$ ) and (0,1) for each  $g_{ij}$  ( $i > j$ ). In an Electronic Appendix we investigate the effect of including reduced ecological efficiency (using algorithm 4 to model ecosystems but this time multiplying the interspecific interaction strengths by 0.1, corresponding to the effect of prey on predators of an efficiency of 10%).

### *Varying ecosystem complexity*

The complexity of each model ecosystem was defined by the properties of the Jacobian at the interior equilibrium point: species richness ( $n$ ); connectance ( $C$ ) which measures the proportion of actual interactions between species relative to all topologically possible interactions (excluding intraspecific trophic interactions); and the mean and variance of the absolute interspecific interaction strengths (MAIIS and VAIIS for brevity). Unless otherwise stated, the default parameterisation of ecosystems was the following: six species ( $n=6$ ) for computational tractability; and a connectance ( $C=0.4$ ) and mean absolute interspecific interaction strength (MAIIS=0.5), to match that used by Chen & Cohen (2001).

To generate skew towards weak interaction strengths, off-diagonal elements of the Jacobian matrix representing interspecific interaction strengths were modelled as gamma distributed variates. Absolute values of non-zero interaction strengths ( $|g_{ij}|$ ) were assigned using a random gamma distribution with variance (VAIIS) from  $10^{-2}$  to  $10^{1.5}$  with steps of  $10^{0.25}$ . In this way, the greater the VAIIS, the greater the skew towards weak interactions (Fig 2a). Absolute values were multiplied by -1 for each  $g_{ij}$  ( $i < j$ ) and +1 for each  $g_{ij}$  ( $i > j$ ). A gamma distribution that fulfils the condition  $(\text{mean}^2 / \text{var}) > 1$  has a modal peak in the probability distribution, thus in this case the distribution from which the (non-absolute) interspecific interaction strengths are drawn is effectively bimodal (Fig 2b). The effect of the modality of the interspecific interaction strength distribution on the probability of permanence was investigated in relation to variation in MAIIS and VAIIS.

### *Stability analyses*

Local stability of the equilibrium point is determined by the eigenvalues of the Jacobian matrix. At the interior equilibrium the Jacobian has the form shown in eqn 2, whilst at the boundary equilibria the diagonal elements have the form

$$g_{ii} = b_i + \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij} M_j$$

if the  $i$ th species is missing ( $M_i = 0$ ). The abundances of the remaining subcommunity at  $\mathbf{M}$  need to be determined and checked for feasibility ( $M_i > 0$  for all  $i$  where  $M_i \neq 0$ ). Throughout this paper, by 'local stability of boundary equilibria' we mean the stability of the full community including all missing species rather than stability of the associated subcommunity with missing species removed. All the boundary equilibria of non-permanent communities were evaluated using local stability analysis to determine whether non-permanence was associated with either all unstable boundary equilibria, or at least one stable boundary equilibrium.

An ecosystem was defined as permanent if it satisfied two conditions: an average Lyapunov function existed near the boundary of the state space, and the system was dissipative (Anderson et al., 1992). If an average Lyapunov function exists the boundary repels all trajectories into the positive orthant of state space, and if a system is dissipative then trajectories cannot tend to infinity. Therefore the system is permanent because it is bounded within the positive orthant. The dissipativity condition is satisfied here because our LV model ecosystems have all self-regulating species ( $a_{ii} < 0$ ) and only consumer-resource interactions (Anderson et al., 1992). To test our model ecosystems for the existence of an average Lyapunov function we used Jansen's (1987) sufficient condition as laid out by Law & Blackford (1992), solved as a linear programming problem in MATLAB (version 7 release 14, The MathWorks Inc.).

Based on permanence and local stability analysis of boundary and internal equilibria, we were able to identify the following characteristics of model ecosystems: permanent with a locally stable interior equilibrium point; permanent and locally unstable interior; fragile (non-permanent and locally stable interior); non-permanent; non-permanent with at least one stable boundary equilibrium; and non-permanent

with all boundaries unstable. The probability of stability (permanence/local stability) is defined as the proportion of our model ecosystems that were stable (permanent/locally stable).

## Results

### PERMANENCE-COMPLEXITY RELATIONSHIPS

#### *1.1 The effect of relaxing assumptions made by Chen & Cohen (2001) on permanence-complexity relationships*

Chen & Cohen (2001) selected a scaling such that all equilibrium abundances were equal when each species' interaction strengths were sampled from a uniform distribution and did not check for the presence of autotrophs ( $b_i > 0$ ) in their model ecosystems. With these two assumptions intact we started by reconstructing Chen & Cohen's (2001) negative permanence-complexity relationships for species richness (Fig 1a line with circles) and connectance (Fig 1b line with circles). Ensuring the feasibility of intrinsic growth rates did not affect the qualitative results (Fig 1a,b lines with stars). Randomly generating the equilibrium abundances ( $N^*$ ) as well as ensuring the feasibility of intrinsic growth rates (Fig 1a,b dotted lines) generated results very close to those of Chen and Cohen (2001). We conclude that relaxing assumptions made by Chen & Cohen (2001) does not qualitatively affect permanence-complexity relationships.

Directly assigning the interspecific interactions ( $g_{ij}$  where  $i \neq j$ ) also had no qualitative effect on the trends (Figs 1a, b solid line with no marker). Directly assigning the interspecific interactions has the advantage of permitting direct control over the strengths of those interaction. Subsequent analyses (§1.3-3.2, Figs 2-5) are based only on algorithm 4 model ecosystems where the assumptions of Chen & Cohen are relaxed and interspecific interactions are directly assigned.

### *1.2 The relationship between mean absolute interspecific interaction strength (MAIIS) and the probability of permanence*

For a connectance of 0.4, increasing MAIIS had no clear effect on the probability of permanence, with all probabilities close to one. We tested whether this was the case for a higher connectance ( $C=0.9$ ), and found a non-linear increase in the probability of permanence with MAIIS (Fig 1c). However we also identified conditions under which the relationship would reverse: when interaction strengths are drawn from a unimodal distribution (§1.3), and when the variance and mean vary together (§1.3) which may be induced by reducing ecological efficiency (Electronic Appendix Fig 1).

### *1.3 The effect of skew towards weak interspecific interaction strengths on the probability of permanence*

The relationship between the probability of permanence and variance in absolute interspecific interaction strength (VAIIS) was U-shaped: at low VAIIS the relationship with the probability of permanence was negative, whilst at greater VAIIS the relationship with the probability of permanence was positive (Fig 2c solid line, for  $C=0.9$  and  $n=6$ , MAIIS = 0.5). We examined the robustness of this U-shaped pattern across other values of complexity (Fig 2c-e). Increased species richness (Fig 2c) and connectance (Fig 2d) increased the depth of the U-shaped curve, whilst increased MAIIS increased the depth and shifted the trough of the U-shaped curve to greater VAIIS values (Fig 2e). The presence of a peak in the gamma distribution from which the absolute interaction strengths were drawn (Fig 2a) and the corresponding modality of the distribution of (non-absolute) interaction strengths (Fig 2b) was found to correspond to the inversion from a negative to a positive relationship between VAIIS and probability of permanence (Fig 2e). Thus the probability of permanence increased with skew in unimodal distributions of interaction strengths, and decreased with skew in bimodal distributions (Fig 2e). In contrast, the probability of permanence increased with MAIIS in

bimodal distributions of (non-absolute) interaction strengths and decreased with MAIIS in unimodal distributions (Fig 2e).

## PERMANENCE AND LOCAL STABILITY

### *2.1 Correlation between local stability and permanence*

The probabilities that model ecosystems had a locally stable interior (dotted lines), were permanent (solid lines) and were both permanent and locally stable (dashed lines) with increasing complexity were all correlated (Fig 3) although there were differences in their probabilities (Fig 3). Not all ecosystems that were locally stable were permanent, and not all permanent ecosystems were locally stable. The difference between the dashed lines and the solid lines gave the probability that model ecosystems were permanent but without a locally stable interior equilibrium point (studied further in section 2.2). The difference between the dashed lines and the dotted lines gave the probability of finding model ecosystems which were locally stable but not permanent (studied further in section 2.3).

### *2.2 The relationship between the proportion of permanent ecosystems with non-equilibrium dynamics and ecosystem complexity*

A permanent ecosystem with an unstable interior equilibrium has non-equilibrium dynamics. The relationship between the proportion of ecosystems with non-equilibrium dynamics and species richness depended on the species richness (Fig 4a solid line): for smaller ecosystems, the relationship was positive, whereas for larger ecosystems the relationship was negative with larger permanent ecosystems tending to be locally stable. The relationship between connectance and the proportion of ecosystems with non-equilibrium dynamics was positive at relatively low connectance (below about  $\frac{3}{4}$  connected) (Fig 4b solid line). At higher connectance levels (Fig 4b solid line) and all values of MAIIS (Fig 4c solid line), the proportion stayed

roughly constant. The relationship between the proportion of ecosystems with non-equilibrium dynamics and VAIIS depended on the level of VAIIS: when VAIIS was low, the relationship was positive, whereas when VAIIS was high the relationship was negative (Fig 4d, solid line).

### *2.3 The relationship between the probability of fragility and ecosystem complexity*

Ecosystems which are locally stable but not permanent are unlikely to be robust to large perturbations, and described here as ‘fragile’. However, it is necessary to bear in mind that the permanence method used here is only sufficient for systems with more than three species (Anderson et al., 1992) and there may be undetected permanent ecosystems. Larger ecosystems were increasingly likely to be fragile (Fig 4a dotted line), as were more connected ecosystems (Fig 4b dotted line). The probability of fragility stayed roughly constant with increasing MAIIS (Fig 4c dotted line) and did not show a consistent trend with VAIIS (Fig 4d dotted line).

## THE BOUNDARY EQUILIBRIA AND PERMANENCE

### *3.1 Non-permanence and local stability of boundary equilibria*

Non-permanence was associated with two types of boundary: either a boundary with one or more locally stable boundary equilibria, or a boundary with all unstable boundary equilibria (Fig 5). The decrease in the probability of permanence with species richness and connectance (Fig 1a,b black solid lines redrawn in Fig 5a,b) was associated with increases in both types of boundary (Fig 5a,b shaded areas). In contrast, the increase in the probability of permanence with increased MAIIS (Fig 1c black solid line redrawn in Fig 5c) was associated with a decreased probability of at least one locally stable boundary (Fig 5c light gray area), since there was a roughly constant probability that all boundaries would be locally unstable (Fig 5c dark grey area). The probability of permanence decreased initially then increased with skew towards weak interspecific interaction strengths (measured as VAIIS, Fig 2c black solid line redrawn in Fig 5d). The initial decrease was



associated with changes in both types of boundary (Fig 5d shaded areas) while the increase was mostly associated with a decrease in the probability of at least one locally stable boundary (Fig 5d light grey area).

### *3.2 The relationship between ecosystem complexity and the probabilities of a locally stable boundary and of a locally stable interior*

The probability that an ecosystem had at least one locally stable boundary equilibrium point and the probability that the same ecosystem had a locally stable interior equilibrium point had opposite relationships with complexity of the interior equilibrium point (compare solid grey lines in Fig 3 with corresponding light grey shaded areas in Fig 5). In the model ecosystems studied here (Figs 3-5) the mean probability of finding a locally stable ecosystem that had all locally unstable boundary equilibria was 0.94 (SD 0.04). Thus, locally stable ecosystems tended to have all locally unstable boundary equilibria. Since permanent ecosystems must have repelling boundary equilibria, local stability increased the probability that an ecosystem was also permanent.

## **Discussion**

In this paper we use permanence and local stability analysis as tools to examine three aspects of the ecosystem stability-complexity debate. The first explored permanence-complexity relationships in more ecologically plausible and generally structured ecosystems than previously. We showed that relaxing assumptions made by Chen and Cohen (2001) had no qualitative effect on permanence-species richness or permanence-connectance relationships, that increasing mean absolute interaction strength and the skew towards weak interactions may increase the probability that an ecosystem is permanent. The second aspect considered how predictions differed between local stability and permanence, what causes those differences

and how they vary with complexity. While, in general, model ecosystems were more likely to persist than would have been expected by local stability analysis alone, the probabilities of local stability and permanence were correlated. The discrepancy was associated with both fragile (locally stable but not permanent) ecosystems and those which were permanent with non-equilibrium dynamics (permanent but locally unstable). The probability of finding these types of model ecosystems changed with complexity, and did not show the same patterns. The third aspect focused on the boundary of the state-space. We found that non-permanence could either be associated with locally stable boundary equilibria or all unstable boundary equilibria, and that changes in the probability of a locally stable boundary could not simply be attributed to changes in ecosystem complexity. In fact, locally stable ecosystems tended to have all locally unstable boundary equilibria, meaning that local stability increased the probability of permanence. Below we discuss these simulation results with respect to the eight questions posed at the end of the introduction, discuss the implications of these findings and draw conclusions about their generality for theoretical ecology.

The first question asked whether increasing ecological plausibility by including obligate autotrophs and variation in the equilibrium species abundances affected permanence-complexity relationships. Permanence is an ecosystem property that confers global stability by requiring only that the densities of rare species must increase (Anderson et al., 1992). The first systematic study of the permanence of ecosystems in relation to changes in ecosystem complexity was by Chen & Cohen (2001). They increased the complexity of ecosystems as measured by the species richness and connectance and found that the probability of permanence declined. We have shown that this pattern is robust to the inclusion of obligate autotrophs and variation in the equilibrium species abundances. It seems that larger, more connected ecosystems are generally less likely to be permanent than smaller, sparsely connected ecosystems.

Second, we asked how the mean strength of interactions between species (abbreviated to MAIS here) affected the probability of permanence. Unlike for species richness and connectance, we found the

probability of permanence could increase with mean interaction strength. The probability of local stability behaved similarly, a result which is consistent with recently reported positive relationships across mean interaction strengths for LV competitive communities where the variance in interaction strengths was held constant (Jansen and Kokkoris, 2003), as was done here. This result is intriguing because it is contrary to analytical arguments based on the distribution of eigenvalues in the complex plane (May, 1972; Haydon, 1994). It would appear that these arguments do not apply to Jacobian matrices with substantial forms of skew symmetry (unpublished results) and that here a tendency to skew symmetry is introduced by increasing the mean of interaction strengths whilst keeping their variance constant. Further investigation is required to link this particular Jacobian construction to restricted eigenvalue variance.

In the final question on the effect of model ecosystem construction on permanence-complexity relationships we asked whether skew towards weak interspecific interactions affected the probability of permanence. We found that increasing the skew towards weak interactions initially decreased but then increased the probability of local stability and permanence. Our results agree with the analysis of LV competitive communities by Jansen & Kokkoris (2003) who also observed a U-shaped curve for the probability of local stability with increasing mean interaction strength. The inversion point (from a negative to positive relationship) was found here to correspond to a change in the modality of the non-absolute interaction strength distribution (from bimodal to unimodal). The bimodal distribution has relatively high variance such that there are few weak but more strong interactions, whereas the unimodal distribution has mostly weak interactions. Many empirical studies agree that a skew towards weak interaction strengths (few strong, many weak) is a feature of large, real ecosystems (Bascompte et al., 2006; Berlow, 1999; De Ruiter et al., 1995; Paine, 1992), and therefore this study implies this characteristic is both locally and globally stabilising. Frequently the stabilising effect of weak interactions is attributed to patterning of the relative interaction strengths within the ecosystem (e.g. De Ruiter et al., 1995; Emmerson and Raffaelli, 2004;

Haydon, 2000; Neutel et al., 2002; Neutel et al., 2007; Yodzis, 1981). As in Jansen & Kokkoris (2003), no patterning in the magnitudes of the interaction strengths was specified in our model ecosystem algorithms, suggesting that skew towards weak interactions can be stabilising (both locally and globally) in more generally structured ecosystems.

The second set of questions considered how predictions differed between local stability and permanence. First we asked whether the probabilities of local stability and permanence were correlated. Our numerical results showed the probability of local stability and permanence were strongly correlated: as complexity changed both responded in the same way. The quantitative correspondence was good at some parameterisations (e.g. few species, low connectance, low VAIIS), whilst at others it was poor (e.g. mid VAIIS). More importantly they showed the same qualitative changes with ecosystem complexity, and the reason for the numerically-based correlation is discussed in context of the boundary equilibria below.

Although the probability of local stability and permanence were correlated, local stability analysis did consistently classify some permanent ecosystems as unstable, and some locally stable ecosystems were not permanent. In questions five and six we investigated further those ecosystems which possessed one form of stability but not both. Those that were locally stable but not permanent were characterised as fragile ecosystems. Those ecosystems that were permanent but not locally stable must have had non-equilibrium attractors e.g. limit cycles or chaotic attractors. In this study we asked how the proportion of permanent ecosystems with non-equilibrium dynamics, and fragile ecosystems changed with complexity. The probability of fragility was influenced by ecosystem species richness, connectance and variance of interaction strengths. In large LV ecosystems local stability may be less likely to imply permanence than in the smaller model ecosystems studied here because the probability of fragility increased linearly with species richness. The probability of non-equilibrium dynamics was influenced by ecosystem species richness,

connectance and variance of interaction strengths. Extrapolation of the results shown here for relatively small ecosystems ( $\leq 12$  species) suggests that permanence implies local stability in large LV ecosystems.

The boundary of the state-space was the focus of the seventh and eight questions in this paper – the association between the local stability of boundary equilibria and non-permanence, and how the local stability of interior and boundary equilibria vary with ecosystem complexity. Non-permanent ecosystems must result from attractors, equilibrium or non-equilibrium, on the boundary. Whilst we did not ascertain the types of attractors on the boundary responsible for non-permanence, we did assess whether non-permanence was associated with at least one locally stable boundary equilibrium or whether all boundaries were locally unstable. The probability that an ecosystem had at least one locally stable boundary equilibrium point and the probability that the same ecosystem had a locally stable interior equilibrium point had opposite relationships with complexity of the interior equilibrium point. The reason for the numerically-based correlation between local stability and permanence can therefore be explained as follows: if an ecosystem is locally stable then there is a high probability it has unstable boundaries (94% for the ecosystems studied here) and, since stable boundaries are detrimental to permanence, a locally stable ecosystem is a strong candidate for permanence. Returning to the question posed by Anderson et al. (1992): ‘how much confidence should we have in a theoretical ecology based on asymptotic stability analysis?’, we have found numerical results that provide good evidence that suggest ecologists should be confident in qualitative findings from local stability analysis of LV ecosystems, at least as far as the parameters used to create algorithms for this paper are concerned.

While here we increased the generality of the model ecosystems for which permanence-complexity relationships have been studied, the models on which this study is based are at the simpler end of the continuum, from May’s random matrices (May, 1972) to empirical ecosystems. In real systems there is likely to be some order that restricts the combinations of parameter values and equilibrium densities. Numerous studies have revealed that community and interaction matrices reflecting the structure of real communities

have a special internal configuration which, when randomised, has detrimental effects on stability (De Ruiter et al., 1995; Emmerson and Raffaelli, 2004; Yodzis, 1981). Some promising structures which confer stability have been identified as common features of real food webs, such as slow and fast energy channels (McCann et al., 1998; Rooney et al., 2006) and low biomass ratios in long trophic loops (Naeem, 1999; Neutel et al., 2002; Neutel et al., 2007). It remains an open question still as to what form permanence-complexity relationships take when models of ecosystems are made closer to natural systems, and whether the non-random patterning identified in empirical systems that increases local stability also enhance the probability that an ecosystem is permanent.

Further studies are necessary on permanence properties of more general or empirically parameterised LV ecosystems. These could adopt more sophisticated approaches than used here to create food web topologies (e.g. the niche model (Williams and Martinez, 2000)) and parameterise food webs (e.g. body-size relationships (Brose et al., 2006)) which allow interaction strengths and/or species abundances to vary systematically throughout an ecosystem. However, some food web models are still limited in their ability to predict observed patterns in natural food webs (Fox, 2006). Alternatively, LV ecosystems could be assembled using sequential assembly rules (Fowler, 2010; Petchey et al., 2008), or empirical parameterisations of LV ecosystems could be analysed. Neutel et al. (2002) parameterised LV model ecosystems using empirical data, but rather than assign all the elements of the Jacobian matrix and analyse stability of the full system, they filled the off-diagonal elements and then determined how much intraspecific interaction (determined by the size of diagonal elements) was required for the Jacobian matrix to become locally stable. Potentially, a similar approach could be developed for assessing the intraspecific interactions required to ensure permanence.

### *Conclusion*

Permanence is a more satisfactory definition of ecosystem stability than local stability because it is a global criterion and is more empirically tractable than local stability (Anderson et al., 1992; Berlow et al., 2004). The adoption of permanence as a measure of ecosystem stability by both empiricists and theoreticians would facilitate the translation of data into model coefficients (Berlow et al., 2004) and aid alignment between empirical and theoretical contributions to the stability-complexity debate. However, the application of permanence in ecology is currently restricted to LV equations and only as a sufficient criterion when communities contain more than three species (Anderson et al., 1992). Furthermore, all species modelled in LV equations are assumed to have a linear (type I) functional response. This special stipulation means LV communities have a unique equilibrium point. The introduction of plausible non-linearities may result in multiple interior equilibria and it is unclear how robust our findings would be to this form of increased generality. Nonetheless the LV framework underpins much community dynamical theory and here we have generalised results on permanence in LV ecosystems with enhanced ecological reality and report positive permanence-interaction strength relationships without the requirement for special ecosystem architecture. Our key finding is numerical evidence that ecologists can be more confident in qualitative findings from local stability analysis of LV ecosystems.

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**Figure 1. The probability of permanence with increasing complexity under the four algorithms for model ecosystem construction**

The probability of permanence with increasing ecosystem complexity: (a) species richness  $n$ , (b) connectance  $C$  and (c) mean absolute interspecific interaction strength, MAIIS. In (c)  $C$  was fixed at 0.9 because when  $C=0.4$  the probability of permanence across MAIIS values was  $\sim 1$ . There was no qualitative effect of the different algorithms on the relationships between permanence and ecosystem complexity. Circles represent Jacobians structured as in Chen & Cohen (2001) with equal equilibrium abundances (here  $N_i^* = 0.5$ ) and no criteria on feasibility of intrinsic growth rates ( $\mathbf{b}$  vector). Stars represent Jacobians with criteria on the feasibility of  $\mathbf{b}$  included (the number of autotrophs was calculated as  $\text{round}(n/4)$ ). Dotted lines represent Jacobians with a feasible  $\mathbf{b}$  and randomly generated equilibrium abundances ( $N_i^*$ ). Solid lines with no marker represent Jacobians with criteria on  $\mathbf{b}$ , randomly generated equilibrium abundances ( $N_i^*$ ) and directly assigned Jacobian off-diagonal elements ( $g_{ij}$  where  $i \neq j$ ). Each point was based on a minimum of 1000 ecosystems and where not varied or specified  $n=6$ ,  $C=0.4$ , MAIIS=0.5 and variance in absolute interspecific interaction strengths (VAIIS) was 0.08. All Jacobians were not diagonally dominant.

**Figure 2. The probability of permanence with increasing skew towards weak interspecific interactions.**

(a) Gamma distributions were used to vary variance in absolute interspecific interaction strengths (VAIIS) in order to generate skew towards weak interaction strengths. Three distributions of the absolute interspecific interaction strengths are shown here for

$\log(\text{VAIIS}) = -1.5$  (thin line), 0 (mid-weight line) and 1.5 (thick line). (b) The corresponding (non-absolute) interspecific interaction strength distributions. (c-d) The relationship between the probability of permanence and increasing skew towards weak interspecific interactions (increasing VAIIS) was U-shaped. We tested the generality of the U-shaped relationship for ranges of (c) species richness  $n$  (4 black dotted line, 6 black solid line, 8 grey solid line) and (d) connectance  $C$  (0.5 black dotted line, 0.9 black solid line, 1 grey solid line). (e) Contour plot of the probability of permanence (bar scale) as a function of MAIIS and  $\log(\text{VAIIS})$ . The black dotted line marks the threshold  $[(\text{mean}^2/\text{var}) > 1]$  between parameters which generate a gamma distribution of absolute interaction strengths with a peak. Each point in (c-e) was based on a minimum of 1000 ecosystems, and where not specified  $n=6$ ,  $C=0.9$  and  $\text{MAIIS}=0.5$ . No Jacobians were diagonally dominant.

**Figure 3. The probability that ecosystems were permanent, had a locally stable interior equilibrium point or were both permanent and locally stable, with increasing complexity**

The probability that ecosystems were permanent (black solid lines), had a locally stable interior equilibrium point (grey solid lines) or were both permanent and locally stable (black dotted lines), as ecosystem complexity was increased: (a) species richness  $n$ , (b) connectance  $C$ , (c) mean absolute interspecific interaction strength (MAIIS) and (d) variance of absolute interspecific interaction strengths (VAIIS). Parameters as for Figs 1 and 2b. Each point was based on 10000 model ecosystems.

**Figure 4. The probability an ecosystem had non-equilibrium dynamics (locally unstable and permanent) and the probability an ecosystem was fragile (locally stable but not permanent) with increasing complexity**

The probability an ecosystem was permanent but locally unstable (solid lines) and the probability an ecosystem was locally stable but not permanent (dotted lines) as ecosystem complexity was increased: (a) species richness  $n$ , (b) connectance  $C$ , (c) mean absolute interspecific interaction strength (MAIIS) and (d) variance of absolute interspecific interaction strengths (VAIIS). Parameters as for Figs 1 and 2c black solid line. Each point was based on 10000 model ecosystems. Note scale on y-axis is different from other figures.

**Figure 5. Attractors on the boundary that are associated with non-permanence**

The probability of non-permanence is one minus the probability of permanence (solid line). The area above the line was shaded to indicate the likelihood that non-permanence was associated with one or more locally stable boundary equilibria (light gray area) or one or more non-equilibrium attractors on the boundary (dark gray area) as ecosystem complexity was increased: (a) species richness  $n$ , (b) connectance  $C$ , (c) mean absolute interspecific interaction strength (MAIIS) and (d) variance of absolute interspecific interaction strengths (VAIIS). Parameters as for Figs 1 and 2c black solid line. Each point was based on 10000 model ecosystems.

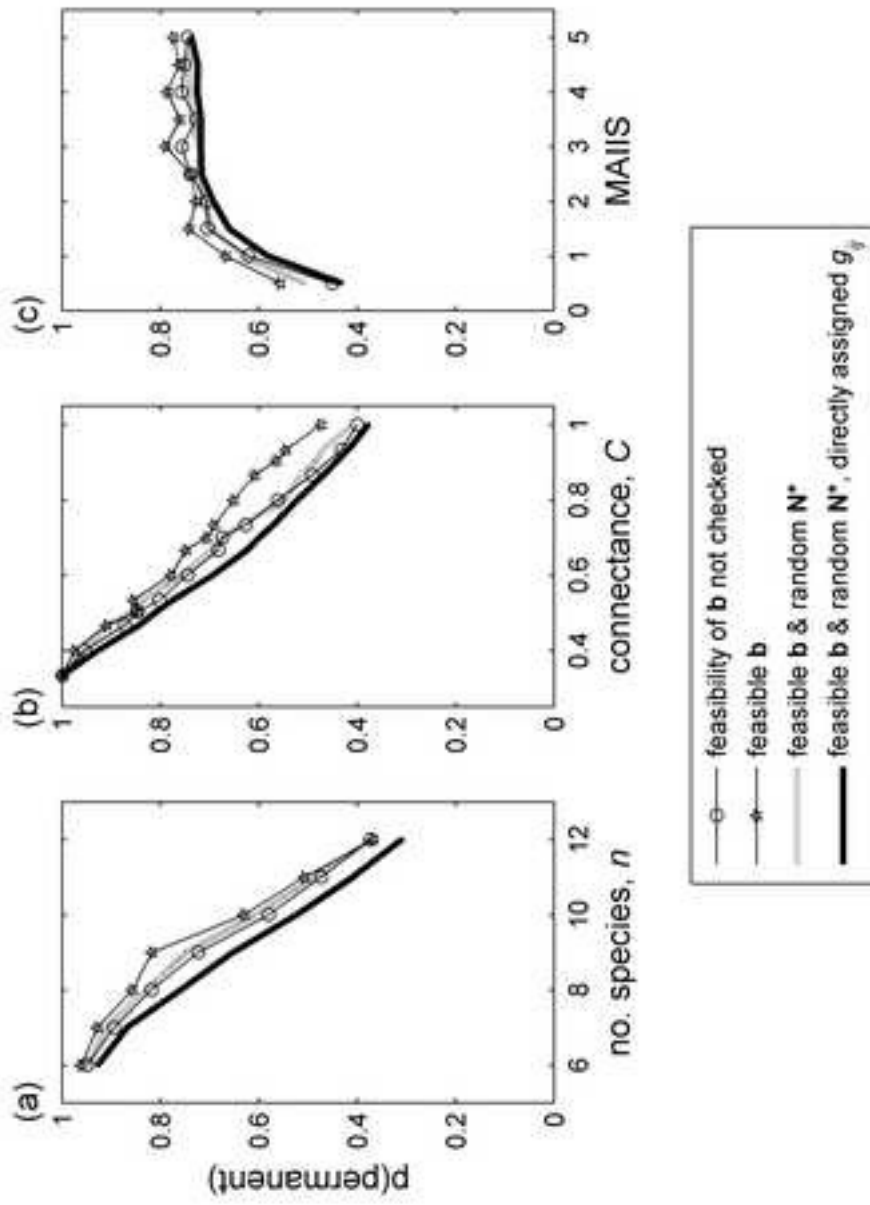
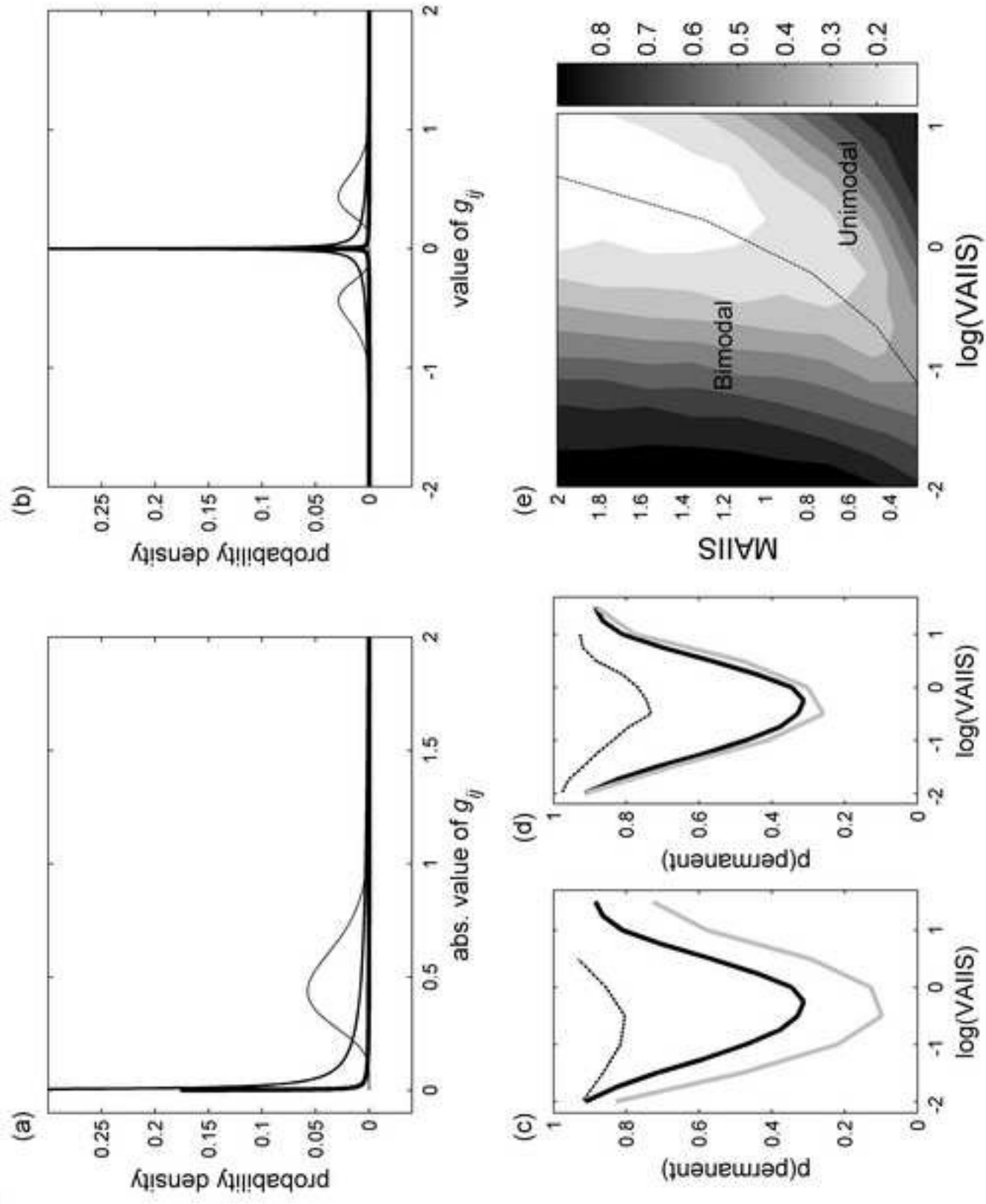


Figure 1

Figure 2





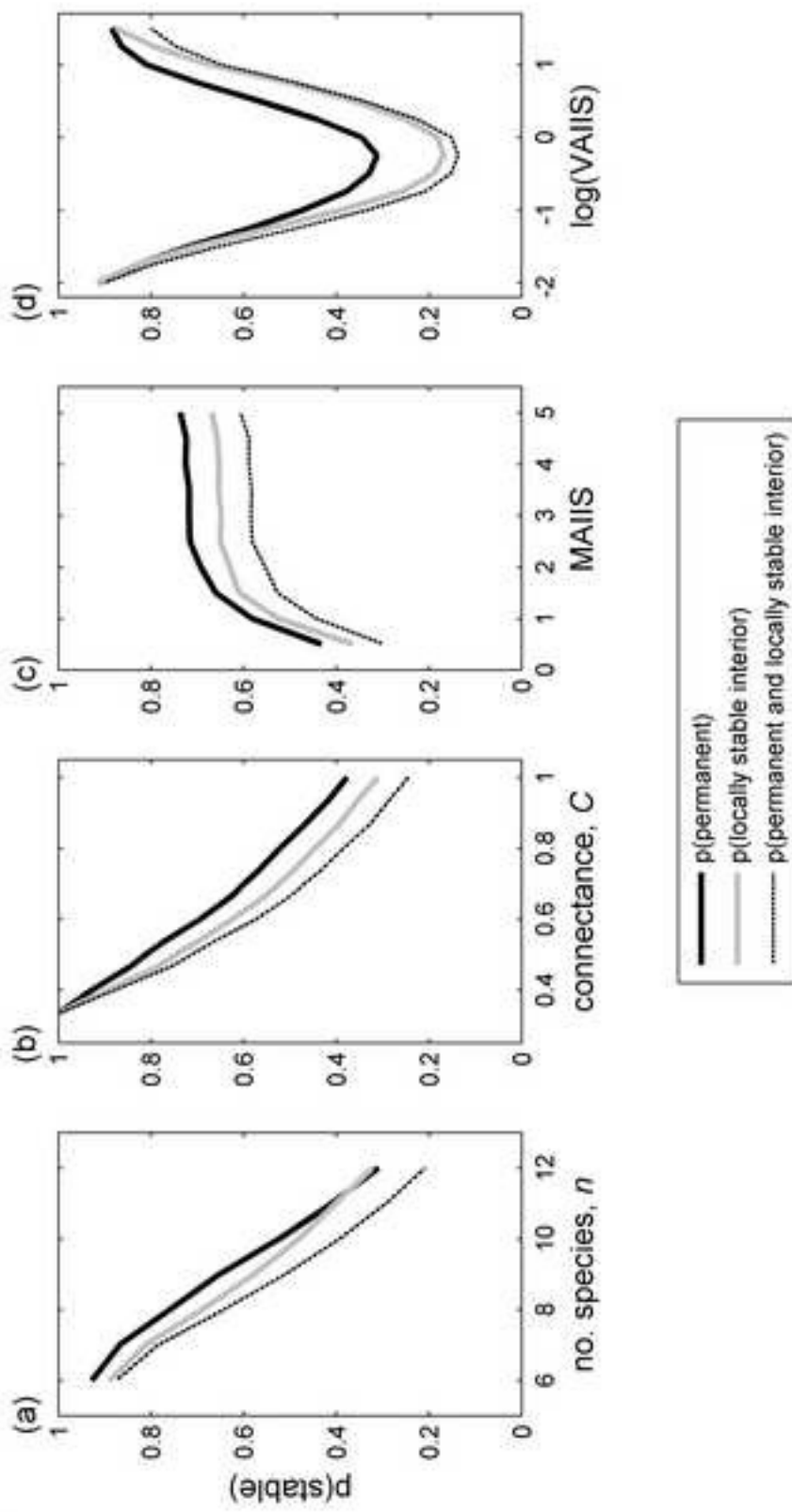


Figure 3

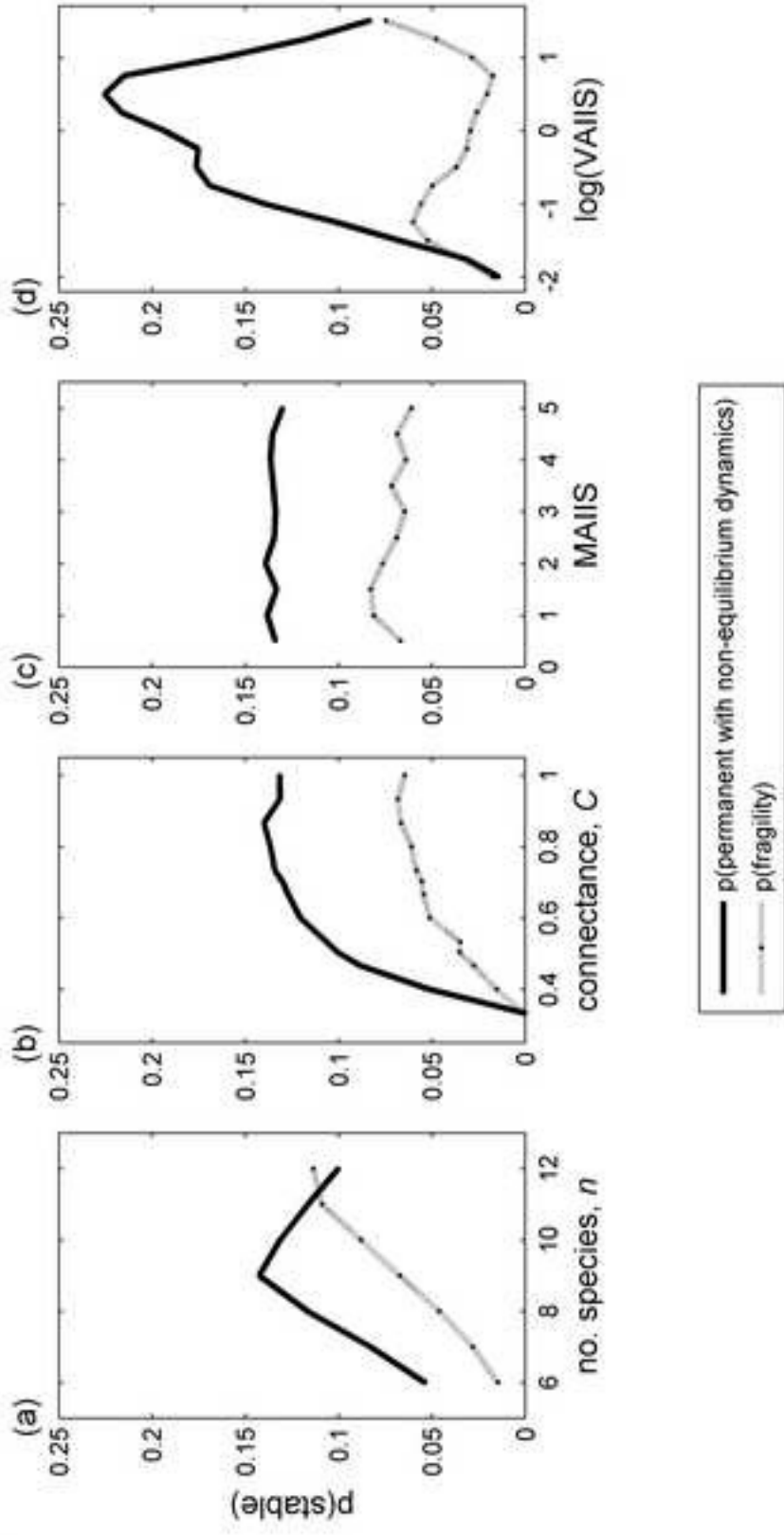


Figure 4

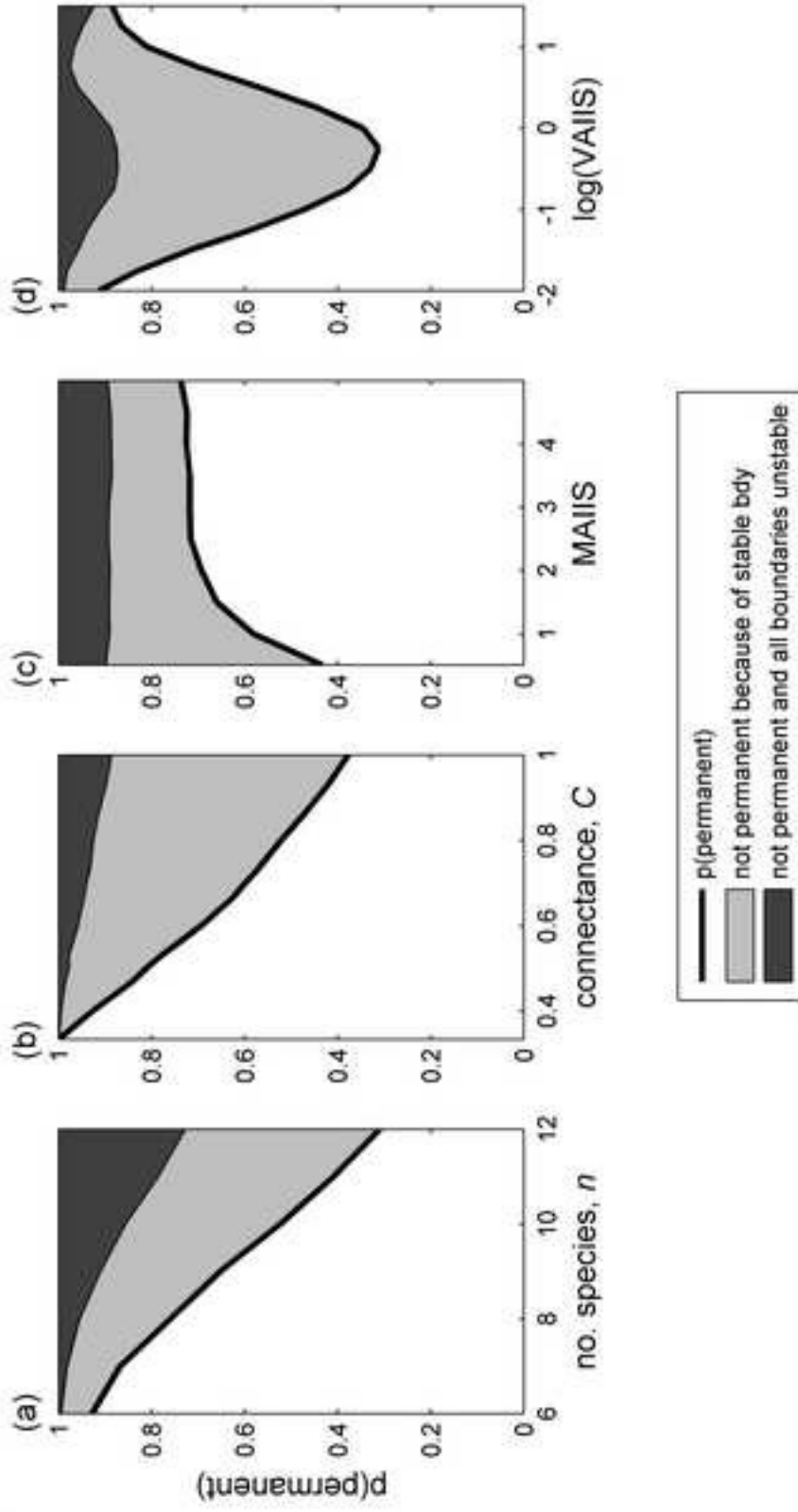


Figure 5