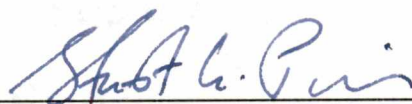


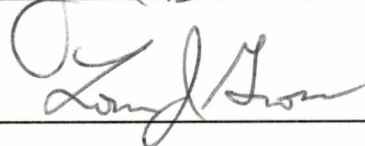
To the Graduate Council:

I am submitting herewith a dissertation written by Hang-Kwang Luh entitled "Historical Processes in Ecology and Evolution". I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.



Stuart L. Pimm, Major Professor

We have read this dissertation  
and recommend its acceptance:



Accepted for the Council:



Associate Vice Chancellor and  
Dean of The Graduate School

**HISTORICAL PROCESSES IN ECOLOGY AND  
EVOLUTION**

A Dissertation  
Presented for the  
Doctor of Philosophy  
Degree  
The University of Tennessee, Knoxville

Hang-Kwang Luh  
December 1993

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## ABSTRACT

This research attempts to address the importance of historical perspective in ecology and evolution. The first section is an overview. The rest focuses on two topics: 1) reconstructing historical processes in ecological communities, and 2) removing historical components from the ecological and evolutionary data.

In Parts 2 and 3 I use a directed Boolean hypercube (a self-organizing system) to simulate the process of community assembly. This system of assembly has a varying degree of restriction. With more restriction, the system displays disorderly dynamic behavior, and the assembly trajectory is determined by certain critical states (past accidents). Part 2 was published in *Journal of Animal Ecology* (see Literature Cited in Part 3). Part 3 will be submitted soon.

In Parts 4 and 5 I use simulation to compare two comparative methods, *independent contrasts* and *phylogenetic autoregression*, under a variety of evolutionary models (amount of phylogenetic information, accuracy of phylogeny). Phylogenetic information plays a crucial role in the comparative method. Forcing comparative methods to filter out non-existing phylogenetic correlation may introduce statistical bias. Biologists must take historical processes (as described by phylogenetic correlation) into account when they analyze comparative data over the broad range of taxa. Part 4 will appear in Phylogenetics and Ecology (see Literature Cited in Part 5). Part 5 will appear in *Journal of Theoretical Ecology*.

## TABLE OF CONTENTS

| CHAPTER                                                                    | PAGE |
|----------------------------------------------------------------------------|------|
| PART 1: GENERAL INTRODUCTION                                               |      |
| 1. Introduction .....                                                      | 2    |
| 2. Modeling the past.....                                                  | 3    |
| 3. Synthesis.....                                                          | 5    |
| Literature Cited .....                                                     | 6    |
| PART 2 : THE ASSEMBLY OF ECOLOGICAL COMMUNITIES -<br>A MINIMALIST APPROACH |      |
| 1. Introduction .....                                                      | 8    |
| Dynamic Models.....                                                        | 9    |
| The community transition graph.....                                        | 10   |
| The community transition graph is a Boolean network.....                   | 14   |
| Possible topologies for community assembly.....                            | 15   |
| What do these questions mean ecologically?.....                            | 16   |
| 2. Methods: three recipes .....                                            | 17   |
| Recipe 1 .....                                                             | 17   |
| Recipe 2 .....                                                             | 18   |
| Recipe 3 .....                                                             | 20   |
| 3. Analysis .....                                                          | 22   |
| 4. Results I: Random transition graphs.....                                | 23   |
| Configuration .....                                                        | 23   |
| Dynamics.....                                                              | 24   |
| 5. Results II: Adaptive landscape assembly graphs .....                    | 26   |
| Configuration .....                                                        | 26   |
| Dynamics.....                                                              | 27   |
| 6. Results III: Minimal community transition graphs .....                  | 27   |
| Configuration .....                                                        | 28   |
| Dynamics.....                                                              | 28   |

|                                     |    |
|-------------------------------------|----|
| 7. Conclusions.....                 | 30 |
| A synopsis of the results .....     | 30 |
| Ecological implications .....       | 32 |
| On building minimalist models ..... | 35 |
| Literature Cited .....              | 38 |

### PART 3: THE ASSEMBLY OF ECOLOGICAL COMMUNITIES - A FOOD - WEB APPROACH

|                                                                                |    |
|--------------------------------------------------------------------------------|----|
| 1. Introduction .....                                                          | 58 |
| Community transition graphs .....                                              | 59 |
| Different community transition graphs.....                                     | 61 |
| 1. Community transition graphs without any loops.....                          | 61 |
| 2. Predators' sink hypercube .....                                             | 63 |
| 3. Predator is removed if there is no prey .....                               | 63 |
| How to include these ecological criteria in a community transition graph ..... | 64 |
| 1. Rugged landscape transition graph.....                                      | 64 |
| 2. Predators' sink hypercube .....                                             | 64 |
| 3. Predator is removed if there is no prey .....                               | 65 |
| Statistical properties of community assembly.....                              | 65 |
| 2. Method.....                                                                 | 66 |
| Simulation of the food web .....                                               | 66 |
| Simulation of ecologically sensible transition graphs .....                    | 67 |
| Simulation of community assembly on community transition graphs.....           | 67 |
| 3. Analysis .....                                                              | 69 |
| 4. Results.....                                                                | 70 |
| Configurations of community transition graphs .....                            | 70 |
| Dynamics.....                                                                  | 71 |
| 5. Discussion.....                                                             | 73 |
| A comparison of the results .....                                              | 73 |
| Ecological constraints increase complexity of community assembly.....          | 75 |
| Literature Cited .....                                                         | 77 |

PART 4: PHYLOGENY, EVOLUTIONARY MODELS, AND  
COMPARATIVE METHODS: A SIMULATION STUDY

|                                                                                |     |
|--------------------------------------------------------------------------------|-----|
| 1. Introduction .....                                                          | 94  |
| 2. Methods .....                                                               | 98  |
| Phylogenetic trees .....                                                       | 98  |
| Trait evolution and evolutionary models.....                                   | 100 |
| Simulated comparisons .....                                                    | 101 |
| Statistical analysis .....                                                     | 102 |
| 3. Results.....                                                                | 104 |
| 4. Discussion.....                                                             | 108 |
| Comparing independent contrasts and autoregression: selecting a<br>method..... | 108 |
| Literature Cited .....                                                         | 111 |

PART 5: TRUTH OR CONSEQUENCES - EFFECTS OF PHYLOGENETIC  
ACCURACY ON TWO COMPARATIVE METHODS

|                                                  |     |
|--------------------------------------------------|-----|
| 1. Introduction .....                            | 129 |
| Some assumptions of the methods .....            | 129 |
| 2. Methods .....                                 | 133 |
| Generating the truth .....                       | 133 |
| Generating what comparative biologists see ..... | 134 |
| 3. Comparative tests.....                        | 135 |
| 4. Results.....                                  | 137 |
| 5. Discussion.....                               | 139 |
| Literature Cited .....                           | 143 |
| Vita.....                                        | 150 |

## LIST OF TABLES

| TABLE                                                                                                                         | PAGE |
|-------------------------------------------------------------------------------------------------------------------------------|------|
| <b>PART 3: THE ASSEMBLY OF ECOLOGICAL COMMUNITIES -<br/>A FOOD - WEB APPROACH</b>                                             |      |
| Table 1. Binary and decimal descriptions of the ten 'nearest neighbors' of the state 27 in a ten-species assembly model. .... | 79   |
| Table 2. Summary of construction recipes and assembly methods.....                                                            | 80   |
| <b>PART 4: PHYLOGENY, EVOLUTIONARY MODELS, AND<br/>COMPARATIVE METHODS: A SIMULATION STUDY</b>                                |      |
| Table 1. Condition for simulating comparative methods. ....                                                                   | 114  |
| Table 2. Percentage of cases in which significant phylogenetic correlation was detected using the Moran's I statistics.....   | 115  |
| Table 3. Statistical results of comparing independent contrasts and autoregressive methods.....                               | 116  |
| <b>PART 5: TRUTH OR CONSEQUENCES - EFFECTS OF PHYLOGENETIC<br/>ACCURACY ON TWO COMPARATIVE METHODS</b>                        |      |
| Table 1. Results of the tests of validity.....                                                                                | 145  |
| Table 2. Results of the tests of power. ....                                                                                  | 146  |
| Table 3. The amount of phylogenetic autocorrelation.....                                                                      | 147  |

## LIST OF FIGURES

| FIGURE                                                                                                                                                 | PAGE |
|--------------------------------------------------------------------------------------------------------------------------------------------------------|------|
| PART 2 : THE ASSEMBLY OF ECOLOGICAL COMMUNITIES -<br>A MINIMALIST APPROACH                                                                             |      |
| Figure 1. The simplest transition graph.....                                                                                                           | 41   |
| Figure 2. Examples of two-species transition graphs.....                                                                                               | 42   |
| Figure 3. Examples of three-species transition graphs.....                                                                                             | 43   |
| Figure 4. More examples of three-species transition graphs. ....                                                                                       | 44   |
| Figure 5. The frequencies of number of persistent communities present in<br>each model. ....                                                           | 45   |
| Figure 6. The frequency of route lengths.....                                                                                                          | 46   |
| Figure 7. Percentages of models that do not pass through loops.....                                                                                    | 47   |
| Figure 8. Hypercube with a simple loop and a complicated loop.....                                                                                     | 48   |
| Figure 9. Distribution of route lengths for models with different numbers of<br>species. ....                                                          | 49   |
| Figure 10. Number of persistent states in landscape transition graphs.....                                                                             | 50   |
| Figure 11. Route lengths and the number of species in the landscape<br>community assembly models. ....                                                 | 51   |
| Figure 12. The total number of persistent states and the total number of<br>reachable persistent states in models of landscape community assembly..... | 52   |
| Figure 13. Distribution of number of persistent communities for the minimal<br>community transition graphs with four, five, and six species. ....      | 53   |
| Figure 14. Distribution of route lengths for minimal community transition<br>graphs.....                                                               | 54   |
| Figure 15. The percentage of models that passes through different number of<br>loops.....                                                              | 55   |
| Figure 16. Distribution of loop lengths for the minimal community transition<br>graphs with four, five and six species. ....                           | 56   |

## PART 3: THE ASSEMBLY OF ECOLOGICAL COMMUNITIES - A FOOD - WEB APPROACH

|                                                                                                                                            |    |
|--------------------------------------------------------------------------------------------------------------------------------------------|----|
| Figure 1. This is a four dimensional hypercube, where each vertex is a community state. ....                                               | 81 |
| Figure 2. Landscape transition graphs.....                                                                                                 | 82 |
| Figure 3. Community transition graph constructed by recipe I.....                                                                          | 83 |
| Figure 4. Community transition graph constructed by recipe II.....                                                                         | 84 |
| Figure 5. Restricted assembly. ....                                                                                                        | 85 |
| Figure 6. One or two persistent states are the most common in both recipes. ....                                                           | 86 |
| Figure 7. The frequencies of unattainable communities in the models.....                                                                   | 87 |
| Figure 8. The average percentages of transition pathways are pre-determined by the recipes. ....                                           | 88 |
| Figure 9. The frequency of route lengths.....                                                                                              | 89 |
| Figure 10. The frequency of loop lengths.....                                                                                              | 90 |
| Figure 11. The percentages of community states that are attainable in theory, but which were not attained in 100 assembly simulations..... | 91 |
| Figure 12. Percentage of transition graphs that the community can not reach all persistent states. ....                                    | 92 |

#### PART 4: PHYLOGENY, EVOLUTIONARY MODELS, AND COMPARATIVE METHODS: A SIMULATION STUDY

|                                                                                          |     |
|------------------------------------------------------------------------------------------|-----|
| Figure 1. Illustration of simulated random traits A and B.....                           | 117 |
| Figure 2. Three simulated evolutionary conditions for examining comparative methods..... | 118 |
| Figure 3. The independent contrasts with no evolutionary model.....                      | 121 |
| Figure 4. The independent contrasts with punctuational evolutionary model. ....          | 122 |
| Figure 5. The independent contrasts with gradual evolutionary model.....                 | 123 |
| Figure 6. The autoregressive methods with no evolutionary model.....                     | 124 |
| Figure 7. The autoregressive methods with punctuational evolutionary model. ....         | 125 |
| Figure 8. The autoregressive methods with gradual evolutionary model.....                | 126 |

|                                                                                                                                                                                                                |     |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| Figure 9. Flow diagram representing various comparative conditions and associated decisions for selecting an appropriate comparative method with either the independent contrast or autoregressive method..... | 127 |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|

## PART 5: TRUTH OR CONSEQUENCES - EFFECTS OF PHYLOGENETIC ACCURACY ON TWO COMPARATIVE METHODS

|                                                                     |     |
|---------------------------------------------------------------------|-----|
| Figure 1. The true phylogeny used in data generation.....           | 148 |
| Figure 2. The nine working phylogenies used in the simulations..... | 149 |

## **PART 1: GENERAL INTRODUCTION**

## Introduction

Every living system, even the simplest, is the result of a history that includes not only a sequence of events, but also a succession of configurations. One important consequence is that current biological systems may not be considered independent. Over the last decade, biologists have increasingly considered such historical processes in their own disciplines.

Fossils provide evidence of the distribution of species in space *and* time. On the horizontal plane of stratification that is the earth's crust, the same types of organic remains are not spread over wide areas, but restricted to particular zones. In vertical sections through rocks, we see that the same species have not existed throughout the entire history of life. The theory of evolution has already shown that *organisms* can only be understood by consideration of both the space which surrounds them and the time that has led to their current forms. The same should be true for any biological system. Time provides a necessary fourth dimension for our understanding of nature (Jacob 1973).

Since every current living system is a product of its past and/or the past of other systems, paleontologists and paleoecologists study phylogeny and community assembly respectively. They collect evidence of past events and relate them to obtain a conceptual view of history. The study of biological systems benefits from a historical perspective because this can: 1) enable the investigation of important biological processes that are difficult to address in a short time-frame, 2) show the interactions among organisms over a range of temporal scales, 3) compare the characteristics of biological systems under disturbances of different periods, and 4) link the "unstable conditions" that organisms have been living with in the past. Historical studies in

ecology and evolution provide information on the behavior and organization of biological systems, changes in this organization, and the link between these elements.

### **Modeling the past**

Reconstructing historical processes is affected by: 1) how we view the past and 2) how we treat past events. To those who are determinism, the entire history of nature is seen as a consequence of organismal interactions, and living systems have self-equilibrating power. Outside disturbances might push the system temporarily away from equilibrium, but eventually the system will return. This idea is influenced by Newtonian deterministic laws of motion (given every initial condition precisely, one can determine past and future). Influenced by the idea of determinism, Clement viewed plant communities as "complex organisms" (Kingsland 1991). He suggested that under the same environment, all successional pathways lead to a single common climax. All these routes are both directional and pre-determined, which suggests the plant community undergoes a life cycle and evolutionary history similar to that of an individual organism. Past events are not important because the system has a pre-determined end-point.

It follows that the historical processes of nature can sometimes be reconstructed by deterministic models. One can predict the consequences given particular initial conditions and compare the predictions with empirical observations. Unfortunately, models simplify and narrow the field of vision. The predictions sometimes only hold over a certain range of initial conditions. The unpredictable domain is completely

deterministic models is due either to human ignorance of initial conditions or to the use of an inappropriate model.

At the other extreme, the history of nature can be interpreted as periods of stasis interrupted by catastrophes or events of unusual significance, where these events entirely control the direction of historical flow. Thus, there can be no deterministic models which describe the whole historical process. Such historical *accidents* can be described only by a probabilistic model, i.e., as a stochastic process.

Stochasticity and determinism are logically opposed. However, either can be applied to historical events. Leopold (Leopold 1949) viewed the ecological succession in Kentucky as a deterministic process. During the period of The United States Revolutionary War, the dominant plant in Kentucky was canebrake, which prevented newcomers from settling in this area. When the cane was burned and grazed out, it was replaced by bluegrass that expanded widely. Leopold thought that the land itself had something to do with the succession of bluegrass that turned formidable land into good homestead. On the other hand, Worster argued that the formation of grassland in Kentucky was more complicated than in Leopold's view (Worster 1992). He pointed out that the Kentucky bluegrass was not a native species, but was introduced from Europe by immigrants. Its seed spread as a result of their travels and grew in newly disturbed land like the fields of Kentucky. The success of the Kentucky bluegrass was thus based on several chance events. Kentucky might now be dominated by other plants if one of these events had not occurred.

## Synthesis

The forms and patterns of living things are the result of neither the diminishing perturbations of stable systems, nor the probabilistic behavior of unpredictable systems. These viewpoints can only describe part of our world. If one looks at the system from the deterministic viewpoint, one sees an organized, patterned world. However, if one takes a stochastic view, one sees the world as disorganized.

Living systems must be the result of something more than deterministic trajectories and critical accidents. This may be self-organization, an emergent property of complex systems (Kauffman 1991, 1993). Self-organizing systems can be viewed as a spectrum, running from simple systems such as a laser beam, through more complex systems such as those of gene regulation, to highly complex systems such as ecosystems. Self-organizing systems are paradoxical. On the one hand, they are highly ordered and can maintain themselves through a precise activity, e.g., the genetic regulation in reproductive systems. On the other hand, they are embedded in and merged with their environment, which may be highly variable. On the temporal scale, each self-organizing system has a unique history, but its history is tied to the history of other self-organizing systems and the larger environment.

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**PART 2 : THE ASSEMBLY OF ECOLOGICAL  
COMMUNITIES - A MINIMALIST APPROACH**

## Introduction

Ecological communities did not spring into existence fully formed. Rather they developed through a process that we call community assembly. In this process, individual species invaded, persisted, or became extinct, sometimes repeatedly. Yet most community ecology focuses on current ecological processes, rather than on the community's history. There is a parallel here to the process of evolution. While not denying the importance of current adaptations, we cannot ignore the long and apparently capricious pathways taken by evolutionary lineages. There is now a considerable body of literature on community assembly that includes a theoretical development, which we discuss below. There are compilations of empirical patterns (Diamond 1975; Cole 1983; Kneidel 1983), and experimental studies (Robinson and Edgemon 1988; Drake 1991; Drake, et. al., 1992). Drake (1989) is a review.

The theoretical models embody dynamics that are difficult to produce, often stretch computational resources to their limits, and produce complex results. In this paper, we strip the detailed population dynamics from the models of community assembly. We examine the topological properties of extremely simple models of assembly. In doing so, we produce a guide to the special features of assembly models and predictions of patterns that we might see in nature.

The models are by intent as free from ecological assumptions as we can make them. We hope that they will yield insights into both theoretical issues and such pressing practical concerns as the restoration of damaged ecological communities. We expect that building such simple models will generate criticism. At the end of this paper we try to address some likely concerns. We draw parallels with more familiar

models of one or two species. Here ecologists build both simple, analytical models and complex simulation models to understand population processes.

We start by briefly reviewing the essential features of detailed dynamic models of assembly and then introduce our simplified versions of them.

## **Dynamic Models**

**General features.** Recipes for making models of community assembly take static food web structures or a sequence of food web structures. The recipes add population dynamics to the structures and so create dynamic models of community composition. Examples of such modeling efforts are Post and Pimm (1983); Drake (1985, 1988, 1990); Mitchen and Lawton (1986); Robinson and Dickerson (1987); Robinson and Valentine (1979); and Tregonning and Roberts (1978, 1979). The recipes require the choice of the equation form, rules for choosing which species interact, ways of generating interaction coefficients, and numerical methods for integrating the equations as the community adds and loses species. The details of the models are many and involve many assumptions. Extended discussion of them appear in Drake (1990), Post and Pimm (1983) and Pimm (1991). The models contain many random elements in both the choice of the interaction parameters and the sequence in which species are tested for their ability to invade. Consequently, the programme must repeat the simulations many times to deduce average dynamical patterns. The many assumptions of the models need to be tested to evaluate their effects on these patterns.

**Specifics.** Dynamic models begin by choosing an equation form (often Lotka-Volterra) to describe the rate of change of the density of the community's component species. There is one equation for each species present in the community. Each

equation contains parameters such as the species' intrinsic growth rate and the specifications of the interactions (predation, competition etc.) with the other species present in the community. Next, the models must create a new species potentially capable of invading the community by specifying its growth rate and its interactions with the species already present. This new species must be tested to see if it can invade the community. If it cannot, the species is rejected and another species tested. The test involves calculating whether or not the new species can increase in density when it is rare. If the new species can invade, then by definition its population will grow. The growth will change the densities of some, and probably all, of the species in the community. The models must calculate what are the new equilibrium densities of the species. New species may simply add on to the community. Or they can cause the extinction of one or more of the species already present. The assembly process then creates another potential invader, tests it, and adds it if appropriate. This continues until some predetermined end point is reached. With a finite species pool this end point might be when no more species can invade.

In the models that follow, we remove these detailed population dynamics. We examine what features of community assembly are likely to be independent of them.

### **The community transition graph.**

Community assembly is a sequence of different community states; each state being a unique combination of species' presence. (We consider equal all species' abundances greater than zero.) We can arrange different community states in graphical form by constructing the directed graph of the transitions. The graph we call the

community transition graph. Figure 1 is the simplest community transition graph. It shows a community with no species in it; then species A invades.

In general, transition graphs have a finite set of states (vertices) representing all the possible communities one can create with the available species. In the example, there are two communities with one species. For each pair of adjacent states, there is only one difference in the composition, that is, a species' presence or absence. There is no information about each species' density. The relations among different community states appear as directed pathways connecting one community state to its neighbours. The transition pathway between each pair of adjacent states is in one and only one direction.

Time,  $T$ , is modelled as a discrete step:  $T = 1, 2, 3 \dots$ . Each community state at  $T+1$  depends only upon the previous one at time  $T$ . We make one assumption for analyzing these models. It is that the community cannot make two movements at each step. There are no diagonal movements. Two (or more than two) species cannot invade or become extinct at the same time. We shall return to this assumption at the end of this paper.

Every community develops from the empty state and passes along a sequence of states. Eventually, the process will end at a single state or be confined within some kind of loop or cycle. A community state with directed transition pathways only going in to it we call a persistent state. If there is not even one persistent state, the assembly is considered unstable. Suppose a community has passed a state and later the community goes back to that state again. Then the pathways that the community has passed through form a loop. A closed loop in which every state has only one arrow going out and which eventually re-enters the same state we call a persistent cycle. The

number of transitions from the start of the assembly until the persistent state gives the route length. Finally, there may be situations where the transitions may move repeatedly through a set of states using several alternative pathways. Now consider some examples.

Figure 2 provides four examples of community transition graphs where two species invade the community. The community transition graph is a square. There are four community states: one empty state, one two-species state, and two one-species states.

The directions of transitions depend upon what the two species are ecologically. Not all the transition graphs are ecologically sensible — an observation that is central to this paper. Suppose that the two species are a species of prey A and a species of predator B. The prey A can invade without the predator. The predator B, however, can invade only when the prey A is present (Figure 2a). There is only one persistent state and in it prey A and predator B coexist. For two more examples, suppose that the two species compete. The dynamics may allow both species to coexist (Figure 2b.). In this case, there is only one persistent state, regardless of which species invades first. Or, there might be two persistent states. The first species to invade always excludes the later one (Figure 2c).

The final situation (Figure 2d) is ecologically implausible; A and B can neither exist individually nor coexist. Thus, A invades the empty state, B then invades A, A becomes extinct, then B becomes extinct. The graph is unstable in our definition. The graph forms a persistent cycle that includes the state with no species present. We said "implausible" not "impossible." We recognise that a prey species might invade, followed by a predator that then drives the prey to extinction, and then becomes extinct

itself. At the level of a patch, this may be likely. It will be much less so over the entire arena in which the prey and predator interact. Later, we will consider this situation unlikely enough to justify dropping such cycles from assembly models. This creates a reasonable way of adding some ecological reality to otherwise ecology-free models.

In three-species systems, the community transition graphs are cubes. Figure 3 provides examples. Suppose there are two predators and one prey. As with the two-species model, suppose that neither of the predators (B,C) can invade unless the prey (A) is present. Hence, the states with only predators are never reachable. Given this restriction, consider three possibilities. First, all three species may coexist, so there is only one persistent state (ABC: Figure 3a). Second, one predator always replaces the other and there is one persistent state, with only one predator and one prey are present (AC: Figure 3b).

Third, whichever predator invades first has the advantage and can exclude the second predator. There are two persistent states (AC, AB Figure 3d). Which state the community reaches depends on which species of predator invades first.

For a final set of examples, suppose that the three species compete with each other. All three species may coexist (Figure 4a). One species (B) may exclude the other two (Figure 4b). Two species (BC) may exclude the third (Figure 4c). Also, there can be a cycle; species A replaces B that replaces C that replaces A, and so on (Figure 4d).

Even here, the cycle of A replaces B, B replaces C, C replaces A, may be improbable. Suppose the species compete for resources, such as space, food, or enemy-free space. Then if A is a better competitor than B, B better than C, then surely A will be better than C too! The cycle might be possible if the competitors were directly

interfering with each other: A can poison B, B poison C, but C poison A. Many real examples of cycles appear to involve direct interference. For example, the overgrowth of one coral-encrusting species by another in the work of Buss (1986) and Buss and Jackson (1979).

The final possibilities we must introduce involve unreachable persistent states and the Humpty-Dumpty effects they may create. In the three-species models, it is possible that the ABC state is persistent. Yet it may not be reachable because all the adjacent states (AB, BC, and AC) repel transitions from their neighbours (A and B, B and C, A and C, respectively.) Humpty-Dumpty effects (see Drake 1990; Pimm 1991) are a possible result of this arrangement. A community may assemble with A, B, and C present, only via pathways that involve a fourth species (or even more species), that become extinct in the process. Without that fourth species, the three species state would be unreachable. Any attempt to re-assemble the community by the sequential addition of its component species would fail. Even with all the "pieces" (species) we cannot put the community "back together again."

### **The community transition graph is a Boolean network.**

Technically, the community transition graph is a Boolean N-dimensional hypercube, where the community states are variables whose values are only 0 and 1, i.e. the species' presence and absence. Each transition pathway connecting a pair of community states is a Boolean function because the direction is either in or out. A community graph with N species has  $2^N$  different community states and  $N \cdot 2^{N-1}$  transition pathways to connect those states. Each pathway has two possible directions (outgoing or incoming), so there are  $2^{N \cdot 2^{N-1}}$  community transition graphs. Thus, a

two-species community has four community states, four directed transition pathways and twelve possible community transition graphs. With a three-species community, there are eight community states, sixteen directed transition pathways and 4096 alternative community transition graphs. In short, just add one species to a system, and the possible combinations of transition graphs will increase dramatically.

### **Possible topologies for community assembly**

The properties of community assembly depend upon the configurations of community transition graphs. Simple transition graphs with two and three species are easy to deal with, both analytically and computationally. When the number of species increases, the community transition graphs rapidly become complicated. We ask several questions about the statistical distribution of different community transition graphs.

(1) How often is the transition graph unstable? When there is no persistent state in the graph, the community assembly process will never stop.

(2) How many persistent states does the graph contain?

(3) How common are graphs with persistent cycles?

(4) When graphs have persistent states, how many steps does it take the community to reach those states?

(5) Suppose persistent states and cycles coexist within the same graph. How often can the community reach the persistent states and how often is the assembly confined within the persistent cycles?

(6) When there is more than one persistent state in the community transition graph, how often can the community reach one persistent states yet cannot reach the others?

(7) How do the answers to these questions vary with the number of species in the community?

### **What do these questions mean ecologically?**

These questions about the statistical properties of food web assembly translate into some straightforward ecological questions. First, does the species composition of a community persist? Or does it cycle, and, if so, in a simple manner through a few recognisable states or through a complex sequence that might appear superficially random? Our impression is that the conventional wisdom about communities is that they have persistent composition. Ecologists have long recognised that the end point of succession may not be a persistent, single state. Yet such an assumption underlies most studies that explore the factors that allow competitors or predators and their prey to coexist. (The topic of "coexistence" appears frequently and at length in ecology text books.)

If persistence is the norm, is it the most probable circumstance in the simplest assembly models? Or does it require the addition of special constraints and, if so, what is their significance? If constantly cycling compositions were easy to get and hard to eliminate even with the addition of special constraints, then we might want to re-examine the conventional wisdom.

Second, although the idea of alternative persistent states is not new, our impression is that it is not the most popular explanation for the wide diversity of

communities we see. Rather, the obvious differences in the physical and chemical environments between locations, combined with inevitable differences between species in their adaptation to those environments, lead to an explanation of the diversity of communities that seems to enjoy a logical primacy. Thus, ecologists appear only to accept evidence for alternative persistent states when differences in the environment can be ruled out. Such is the case in laboratory studies. Yet suppose alternative persistent states are a ubiquitous and inevitable feature of assembly models. It would be equally reasonable to explain the diversity of communities, — from small-scale patchiness in composition to larger scale patterns — from the inevitable differences in their history.

Third, how long does it take for communities to achieve persistent states, if indeed these are the end points? Persistent communities might only develop after a long and complicated assembly. So when we damage communities, the results may be not only communities that do not persist. The communities may change their composition with further invasions and extinctions for the foreseeable future. Suppose we are restoring communities: can we duplicate the original process? Will it be possible to re-assemble the community from its constituent species? Or will we lack essential species that are now absent from the community or possibly extinct world-wide? Perhaps we will assemble a persistent community, but if alternative persistent states are common, it may not be the community we want.

### **Methods: three recipes**

#### **Recipe 1**

To answer these questions, we employ three recipes to construct community transition graphs. In the first, the direction of transition pathways are specified entirely

at random to explore a sample of all the possible community transition graphs. We call these models the random community transition graphs. All graphs are possible. There are no exclusions of transitions that appear ecologically impossible or implausible. We do not try to use the interpretations we provided for Figures 2 to 4 to restrict the transitions. These graphs are entirely ecology-free.

## **Recipe 2**

In the second recipe, we exclude all cycles. As we discussed above, it is the cycles that appear ecologically implausible. We found no cycle we thought likely (at least at a community-wide scale) until we had three species. Moreover, we constrained them to be three species of competitors. Even then, this cycle requires special circumstances. What happens if we prohibit cycles of any kind?

To do this, we employ Kauffman's (Kauffman and Levin 1987; Kauffman 1993) model of evolution: the assembly of a phenotype. In his simple case, there are  $N$  pairs of traits. Which of each pair will be expressed depends on an assembly process where traits are switched on and off during the phenotype's evolution. The obvious difference between community assembly and evolution is that species have a fitness. For each combination of traits, there is value that is often thought of metaphorically as the height of a place in a landscape. Adaptation pushes the species' phenotype higher, until it reaches a peak. Cycles are impossible: one cannot have the realisation of Escher's visual paradox of water constantly flowing downwards around a canal atop a castle's ramparts.

In a similar way, we can create models of community assembly that lack cycles. Each community state in the graphs is assigned a "height" — a fitness value, in you

like. The community transition graph always moves from a "lower" state to one of its "higher" neighbours. We call this sort of transition graph the landscape transition graph. Such a model clearly has too much ecology in it! The model moves as if the community is behaving like some super-organism ever driven to greater perfection. We do not consider this model because we think in these terms. Rather, we recognise that this model represents the limiting case that prohibits cycles and there might be ecologically sensible circumstances where cycles are unlikely. The models not only have the advantage of being a limiting case, but they are easy to simulate.

There are many ways of organising the states on a landscape. The landscape might resemble Mount Fuji in Japan — a single prominent peak. If so, the assembly would move towards a single persistent state from every other possible state. The other limiting case is for the heights of each state to be selected at random. The metaphorical landscape then resembles the Alps — a very rugged terrain with many peaks and valleys. In Kauffman's models of adaptation, the ruggedness of the adaptive landscape has to do with the connectedness of the traits. If the presence and absence of each trait does not change the fitness of the others, then the landscape will have a single peak. As epistatic effects increase, the change in one trait alters the contribution of more and more traits, each of which alters the fitness contribution of yet other traits. The result is a very rugged fitness landscape.

We have no idea if we should model community assembly graphs by landscapes, let alone what kind of landscape is the correct one. A random and hence rugged landscape is the simplest assumption and it is the only landscape we investigate in this paper. It also may be closest to nature. We are reminded of Yodzis' (1988) exploration of the effects that the change in the density of one species should have on

the density of the other species in a community when the species are embedded in the complex food webs we see in nature. Yodzis' results suggest that these effects are hard to predict in direction, let alone size. Many prey species are actually harmed when we remove their predators, because the predators also prey on the species' competitors. We suspect that this uncertainty translates into assembly. Whether species A can invade when species B, C, D... are present, is likely to depend on whether or not another species X is present or absent. We find at least an analogy here to the discussion of epistatic effects, where it is the system's complexity that generates the rugged landscape.

### **Recipe 3**

In the third recipe, we add one ecological constraint to the random assembly models. We argue that the simplest loops are ecologically impossible and so we remove them. Since these loops are of the form: A invades the empty community, B then invades A, B drives A to extinction, then B becomes extinct (Figure 2d), we remove all four-pathway loops that exist around the faces of the hypercube. We call the results the minimal community transition graphs. Producing such models is computer-intensive. This limits how many species we can include in our investigations. At least we can compare some of these models with the two limiting cases explored in more detail.

We produced these models in one of two ways. As in the first set of simulations, we created random transition graphs. We then discarded those that had the simple cycles. Because these cycles are very common in the random community transition graphs (see below), we found only few graphs that lacked them. With more

than four species, we never found models without the simple cycles in our samples of 100,000 graphs. We could have increased the number of simulations. Unfortunately, checking the simple cycle on each surface of the hypercube would have taken more computer time than was available to us.

The second approach employs a useful property of hypercubes. Each  $n$  dimensional hypercube is constructed from two  $n-1$  dimensional hypercubes. One of the  $n-1$  hypercubes is the community transition graph without the  $i$ th species at every node. The other  $n-1$  hypercube is the community transition graph with the  $i$ th species at every node. By connecting each node of the first  $n-1$  hypercube to the node of the second, we get an  $n$ -species community transition graph.

Our simulation started from the fourteen possible two-species transition graphs that lack cycles. Two of these transition graphs were selected at random from the fourteen and were connected to form a three-species transition graph. We gave these additional connections random directions. We know that two lower dimensional hypercubes were free of simple cycles, so we need only check the surfaces connecting these two lower dimensional hypercubes to see if they contained the simple cycles. This approach still creates models with some simple cycles. We discarded the models with simple cycles until we found one model that completely lacked simple cycles. The search then returned to the beginning to pick two more of the fourteen two-species cycle-free graphs. Though this process does create models with cycles, it produces a much smaller percentage of them than the first approach. Because of its greater efficiency, we can extend this method to models with more species.

By simulation, we found 1894 transition graphs free of simple cycles in the three-species models. We connected random pairs, as above, to form the four-species

models. For four or more species, it is impossible practically to catalogue all the possible transition graphs free of simple cycles. So, we randomly selected two lower-dimensional, simple-cycle-free transition graphs to make the higher dimensional graph. We continued this process to explore the higher dimensional hypercubes without the simple cycles until the number of species was six. Checking the simple cycles on the connected surfaces saved much computer time. When the number of species is above six, however, the time taken still exceeds our computing resources.

### Analysis

Our analyses involve a two-stage process. We first create a graph and look at its static properties. (Henceforth, we label these results, configuration). Second, we simulate how the assembly can proceed from an initial community with no species in it. (These results, we label dynamics.) The program first constructs the hypercube of  $N$  species. A binary random number generator specifies the direction of each transition pathway. For each number of species, we generated 100,000 randomly-selected community transition graphs and checked the configuration of each. For example, did the community transition graph have persistent states? If so, how many does it have? Did the community transition graph have persistent cycles? Did it have both persistent cycles and states?

The second stage of the analysis explores the dynamics of the assembly process itself. For each number of species in the model, we randomly choose one hundred transition graphs with at least one persistent state from the sample of 100,000 graphs. Then, we simulated the community assembly process from the initial state of no species, to the final persistent state or persistent cycle. At each state there could be

zero, one, or more than one choice for the next state. The first case represents a persistent state, of course. The second allows only one choice. For the other cases, we chose one of the possible pathways with equal probability. For each transition graph, we repeated the entire process one hundred times.

For each of the one hundred repetitions, we recorded:

- (1) How often the community could not reach one of its persistent states.
- (2) How many steps it took the community to reach the persistent states.
- (3) How often the community state transition sequences had loops.
- (4) If there were loops in the route, how many loops were there in each random walk, and
- (5) how long were those loops.

## **Results I: Random transition graphs**

### **Configuration**

(1) The percentage of unstable models (models with no persistent states) changes little with the number of species in the model. For two-species models, it is easy to show that two out of the sixteen possible (12.5%) are also unstable. From simulation, this percentage rises to 29% for four-species models. It remains between 33% and 36% for models with five to ten species.

(2) When transition graphs have persistent states, only one persistent state per community is the most frequent event. This is regardless of how many species are present in the community (Figure 5). Communities with different numbers of species have different maximal numbers of persistent community states, however. So what should this maximum be?

Two persistent states cannot be next to each other. Thus, the maximum number of the persistent states is half of the total number of possible community states. The theoretical maximum number of persistent states increases very rapidly with increasing numbers of species in the community. The chance of achieving this number, however, is very small. Only two of the possible graphs have the theoretical maximum number of the persistent states. Our simulations confirm that many coexisting persistent states in the community transition graphs are very rare. For instance, in the ten-species models, there are 1024 different community states. A maximum of 512 persistent states are thus theoretically possible. The maximum number of persistent states that we found coexisting in the ten-species models was eight. Only four out of the total of 100,000 had even this many persistent states (Figure 5). Unlike the theoretical maximum number of persistent states, the maximum number of persistent states actually found in the sample of 100,000 random graphs increases approximately linearly with the number of species.

(3) Persistent cycles are extremely rare in the random community transition graphs. Only 0.177% of the four-species had such cycles, and we found none in the eight-, nine-, and ten-species systems. The frequencies of persistent cycles and persistent states coexisting is also small. Only 1.01% of the four-species models had such coexistence, and we found no such graph in the six- to ten-species models.

## **Dynamics**

Recall that to explore the dynamical properties of the groups we randomly selected one hundred graphs from each of the 100,000 produced for the four- to ten-species models. Only in the sample of four-species graphs, did we find a transition

graph that had both persistent states and cycles. The community reached the persistent state forty-eight times. It was restricted in the persistent cycles fifty-two times. Within our statistical error, the cycle and the state were equally probable. Also, in the four-species graphs, there were three transition graphs that had persistent states, but the assembly process could not find pathways to reach them from the initial, empty community. In all the other samples of one hundred graphs, no transition graph ever had persistent cycles, and the community could always reach persistent states.

Figure 6 presents the distributions of the route lengths for each number of species. It is the shortest route lengths that are most common. The most frequent route lengths are less than ten steps, but there are very small probabilities of very long route lengths in each assembly. The frequency distributions of route lengths for few species are dominated by the shortest route lengths. With more species, the most common pathways can be long ones.

This result may be sensitive to our assumption of adding or subtracting one species at a time. We have yet to explore quite what happens to path lengths when several species invade simultaneously.

Although there may be loops, the community could still reach the persistent states without passing through them. We classified each of the one hundred graphs according to the percentage of the one hundred random assemblies that passed through loops. For example, if the assembly passed through loops 28% of the time, then that particular graph would be a 72% no-loop graph. Graphs in which the assembly avoids loops completely are always uncommon (Figure 7). They are absent when there are more than six species. Typically, the assembly will pass through some loops some times and at others go directly to a persistent state.

Loops may be very simple or very complicated. The simplest loop is a square cycle on the surface of the hypercube. The previous data do not distinguish between loops of different lengths. For example, a route length of twelve, could involve three passes through the loop at the left of Figure 8, or two passes through the longer loop of six states.

We also calculated the length of loops. Figure 9 shows the histograms of loop lengths from four to ten species. Species-rich community transition graphs not only have longer loop lengths but also many more loops in each random walk. Even so, for all models, most loops are four steps. That is, the loops are the simple cycle on the surface of hypercube.

## **Results II: Adaptive landscape assembly graphs**

### **Configuration**

In the second set of simulations, we explored models that completely lacked loops. We arranged the community states on a landscape, and, as explained above, a very rugged one, where each state had a random height. Such landscape community transition graphs are known to have a very large number of persistent states (Figure 10; Kauffman and Levin 1987).

Compare Figure 10 to Figure 5. The graphs are so different, that it is hard to do so! For the random graphs, the most common number of persistent states is always one. For the landscape graphs, the most common number of persistent states is larger and, moreover, this number increases dramatically as the number of species increases. To make matters even more difficult, the frequencies in Figure 5 are on a logarithmic scale, while those in Figure 10 are on an arithmetic scale. This is because the

frequencies of persistent states drop very rapidly for the random graphs of Figure 5, and very slowly for the landscape graphs of Figure 10.

## **Dynamics**

Given the many persistent states in these graphs and the prohibition of any kind of loop from the graph, one would expect the route lengths from initial state to persistent state to be very short. Indeed, they are (Figure 11). You should compare Figure 11 with Figure 6. Again it is difficult to present the results in the same form. With the random graphs, route lengths can often be very long. On average, they increase rapidly with increasing numbers of species. For these rugged landscape models, the route lengths are short and vary little with increasing numbers of species.

Finally, because the landscape is so rugged, most persistent states are unattainable because there is no transition route available (Figure 12). (This, too, may be a result that may be altered if several species can invade simultaneously. Again, we have yet to investigate such an effect.)

## **Results III: Minimal community transition graphs**

The random transition graphs have very few persistent states, take many steps to reach those states and have many loops. These circumstances arise because the communities pass over many of the simple, four-step cycles that we consider ecologically implausible. Conversely, the landscape transition graphs have no loops, they have many persistent states and they reach states quickly. Many of these states, however, cannot be reached. In the third recipe of community assembly, we removed

all community transition graphs with the simplest and most common kind of cycle from the simulations.

## **Configuration**

In the minimal community transition graphs, the percentage of unstable models (models with no persistent states) is very small. It decreases with the number of species in the model, 0.63%, 0.32% and 0.12% for models with four, five, and six species.

The frequency distribution of persistent states in the minimal community transition graphs (Figure 13) is more similar to the landscape transition graphs than to the random transition graphs. (You should compare Figure 13 with the figures for random transitions, Figure 5, and landscape transition graphs, Figure 10.) The modal number of persistent states is greater than one. The mode increases with the number of species in the model and the distribution of numbers of states becomes more symmetrical as the number of species increases. The increase in the modal number of persistent states in the minimal community transition graphs is not as fast as that in the landscape transition graphs, however.

## **Dynamics**

Investigations of the dynamics of assembly of minimal community transition graphs shows that they are also similar to the landscape graphs. We found no persistent cycles in the simulations of these models. Most route lengths are less than ten steps and the chance of passing through a longer route is very small. (You should compare Figure 14 with Figures 6 and 11). The difference between Figures 6, 11, and

14 is that the longest route lengths for the minimal community transition graphs (Figure 14) are less than that of the random community transition graphs (Figure 6) and slightly longer than those for the landscape transition graphs (Figure 11).

Figure 15 shows the frequency with which the assembly passed through no loops at all. These frequencies are much higher than those of the random community transition graphs shown in Figure 7.

Figure 16 shows the histograms of loop lengths from the assemblies of the minimal community transition graphs. After we removed the simple cycles (loop length = 4) from the hypercube, the lengths of the loops and the number of loops in each model dramatically decrease. Most loops are six steps long in the four-species models, and eight steps long in the five- and six- species models.

As in the landscape community transition graphs, not all persistent states are attainable in some minimal community transition graphs. Our simulations showed that about 80% of the possible persistent states were reachable in the four-species models. This percentage dropped slightly to about 70% in the six-species models. You should compare this result with the data in Figure 12. In the landscape models, most persistent states were reachable when there were six or fewer species. The reachable proportion dropped quickly as the number of species in the models exceeded six. We are unable to investigate minimal community transition graphs with more than six species because of computational limitations.

## **Conclusions**

### **A synopsis of the results**

First, let us contrast the two simplest recipes for building models that describe how communities may assemble: random assembly and assembly on random

landscapes. Then we will consider the third recipe in which we add a minimal amount of ecological realism to the first recipe. We will then ask whether the resulting models more closely resemble those in the first or the second recipe.

In the first recipe, the transitions between different adjacent community states — communities that differ in the presence or absence of one species — are chosen at random. In the second recipe, we constrain those transitions in a way that recalls the metaphor of an adaptive landscape in evolutionary theory. When cyclical changes in composition are forbidden, each state has a metaphorical equivalent of height. The height of each state is chosen randomly, and the metaphorical landscape is very rugged as a result.

The features of the models and their dynamics are these:

(1) The first recipe is ecology-free. We know there are restrictions on the transitions that follow from the nature of simple ecological processes. We ignore the restrictions to understand a limiting case. These restrictions exclude some simple cyclical changes in composition though not complex cycles. The second recipe has too many constraints in it, for it prohibits all cycles.

(2) Random transition graphs most commonly have one persistent state, the frequencies of more than one persistent state decrease approximately exponentially. Landscape transition graphs commonly have many more persistent states and the number increases rapidly with the number of species in the system.

(3) Persistent cycles are rare in the random transition graphs and are impossible in the landscape transition graphs.

(4) The persistent states are nearly always reachable from the empty community in the random transition graphs. While the number of reachable persistent states

increases rapidly with the number of species in the landscape transition graphs, the relative proportion drops quickly. That is, the total number of persistent states increases even more quickly than the number of reachable states.

(5) While persistent cycles are never common, cyclical changes in composition on route to a persistent state are a dominant feature of the random transition graphs. Particularly when there are more than a few species in the model, the path length to a persistent state of a random transition graph is often very long. The community states cycle, often many times, through a sequence of states. Escape is possible, and thus eventually inevitable, but not probable on any single occasion. The most common cycle is the simplest one around four states: with species P,Q, R,... always present, the cycle goes from A and B absent, only A present, A and B present, only B present, A and B absent. In contrast, the path lengths to a persistent state in the landscape transition graphs are very short.

Next, let us contrast the features of the third recipe (minimal transition graphs) with the first two, numbering the results in a comparable fashion.

(1\*) This third recipe excludes only the simple cycles that we consider ecological implausible. Ecologically sensible models may have even more exclusions — a point to which we will return.

(2\*) Minimal graphs have more than one persistent state and the number of persistent states increases rapidly with the number of species in the model.

(3\*) We did not find persistent cycles.

(4\*) Persistent states were usually reachable, but computational limitations meant that we could not investigate models with many species in them. There is the

chance that as with the landscape transition graphs, the proportion of reachable states may decrease rapidly with increasing numbers of species.

(5\*) The path lengths to the persistent states are typically short, though they can involve cyclical changes through loops more complex than in the random transition graphs.

In short, these models with even minimal ecological constraints appear very similar to the landscape transition graphs.

### **Ecological implications**

Before this study, it was our impression that ecologists viewed persistent communities as the norm and communities where composition cycled repeatedly to be unusual. This view might be incorrect. The apparent constancy of community composition might be a trivial result of how short-term are our observations of nature. We conclude that the traditional view of communities is correct. It is a result of the statistics of community assembly graphs. Persistent cycles are not very common (results 3,3\*).

While community composition may cycle on the way to a persistent state, most of these cycles are the simple ones that are ecologically unlikely (result 5). Even minimal assumptions make cycles uncommon (result 5\*). More stringent assumptions — such as preventing two predators coexisting on a single species of prey, or rankings of species according to their efficiencies at exploiting space or nutrients — would prevent even more cycles. This rarity of cycles has an interesting result. Even when we know that the community states cannot be placed on a metaphorical landscape by theory alone, simple ecological constraints create community assemblies that appear as if the

states are on a landscape. Thus, assembly looks like the process of evolution. It looks as though there is something that pushes the assembly towards peaks in the landscape and as though there is something akin to fitness. The community behaves like a super-organism. Wilson and Sober (1989) provide an extended discussion of the debate about super-organisms.) Descriptions of ecological community assembly, including Odum's (1969) well-known paper on succession, often appear to suggest goal-seeking behaviour by the community. Such behaviour cannot be axiomatic — there really isn't a goddess Gaia — but it may be a result of simple, ecologically plausible axioms. We show that even minimally realistic models of assembly consist of communities that move towards persistent states, often with a minimum of cyclical distractions.

Another feature of our models should be plain when we see what happens when we partially destroy communities, by causing extinctions. Unlike natural communities, which have had time to reach their persistent states, these damaged communities are new ones. Over time, we should expect to watch them change in composition, as they admit some species, lose yet other species. These changes may be prolonged if the transitions graphs are essentially random. In short, the persistent composition of natural communities should contrast with the ephemeral composition of damaged communities.

Next, we suggest that those responsible for restoring ecological communities may face rival difficulties. First, if random transition graphs best describe community restoration, then the restoration might eventually reach its desired persistent community (result 2). It would do so only after a long period of intermediate cycling (result 5). The second alternative is when community restoration is best described by landscape or minimal transitions graphs. The restoration would quickly reach a persistent

community (results 5, 5\*). Unfortunately, this persistent community may not be the desired community, but rather another of the many possible communities reachable on the very rugged landscape (results 2,2\*). Even with all the species, we can re-assemble the community only if luck is on our side and the assembly, by chance, follows its original path.

The problem gets worse. Because most of the persistent states are not reachable, it is possible that the desired community was achieved by a pathway or pathways involving species that are no longer present. Even with all the species, we cannot re-assemble the community. Leopold's famous remark that the "first precaution of intelligent tinkering" is to "keep every cog and wheel" (Leopold 1966; p190) is a necessary but not sufficient condition. (All these arguments about restoration suppose that we have followed Leopold's advice and kept all the pieces. Moreover, we also must know which pieces belong where. If we lack the basic natural history — the species lists for the communities, then we may have little chance of assembling the species into the desired persistent community.)

The presence of deliberately or accidentally introduced species should have much the same effect as the loss of native species. They create a completely new transition graph and the persistent states may only rarely contain all the native species.

If the diversity of communities is mainly a result of their different histories, there is some relief from the difficulties of the second alternative. When we restore communities we may really be hoping to create a diversity of communities. We will likely get just what we want, that is, many of the different persistent states coexisting side by side. Moreover, the persistence of the restored communities may be a sign of the success of the process.

Finally, the rugged nature of community landscapes, even ones produced from minimal assumptions, suggests that the diversity of communities we see in nature is a likely result of accidents of history. In our experience, ecologists (including one anonymous reviewer of this paper) often explain the diversity of communities as the results of subtle effects of the physical environment. This hypothesis may be the correct one, but our results show that it cannot enjoy logical supremacy. Yes, organisms differ in their adaptations to the environment, but communities differ in their history too. These differences in history appear easily capable of completely altering the composition of the persistent community. The answer to the question of why there are so many communities may be "historical accident" (Pimm 1991). The parallels to the process of evolution are obvious.

### **On building minimalist models**

The familiar two parameter (" $r$ " and " $K$ ") equation is almost as simple a model of population growth as one could imagine. Yet it has encouraged ecologists to think of evolutionary trade-offs between its parameters. When expressed in a finite difference form it has played a central role in the development of mathematical chaos. Ecologists recognise these and other advances while simultaneously adding great complexity to the model whenever they wish to describe any real population's dynamics.

The motivation behind this study is similar. We and our colleagues have built complex models of community assembly both in the computer and in microcosms (Post and Pimm 1983; Drake 1988, 1989, 1990, 1991; Pimm 1991; Drake, et. al., 1992). Until now we had little idea of which results were the results of the complexity and

which were results of the simplest processes of assembly. Our analyses should not be taken as evidence that we believe community assembly is as simple as the minimalist models, only that we find them a guide to more complex models.

Are they are reasonable guide? Experience teaches us that unreasonable simplifying assumptions belong, like accents, to the other person. We shall finish, therefore, with a consideration of what may be wrong with, and what we should change in, the models we have presented.

First, there is the assumption of sequential invasion. We thought initially that this was a reasonable assumption. Surely, we argued, no two species can invade or become extinct at exactly the same time. Now we are less certain. The presence or absence of species in the models is most sensible viewed as the presence and absence of species in sufficient numbers to have dynamical affects. Moreover, the movement from one state to another occurs over an interval, and not at an instant of time. In such an interval we can imagine more easily two or more species dropping to such low levels that they no longer play functional roles within the community. To relax this assumption we could explore models that allow diagonal moves. The nature of the diagonal determines the number of simultaneous invasions or extinctions. Across a square the diagonal models two events, across a cube, it models three events and so on.

Second, there is the nature of the details we have omitted. Any real community has species interactions organised in a food web. The set of known food webs has a long list of special features (Pimm, et. al., 1991). Not least of these is the complete absence of predators without even one prey species. Consider a random model of the assembly of five plant species, five herbivore species, and five predator species. A

vast number of pathways would dominate this model that involve predators invading before the required herbivores and plants and herbivores before the required plants.

The simplest plausible description of food web structure, Cohen's cascade model (Cohen, et. al., 1990) has several more rules. Given the number of species in the web, this model uses an empirical relationship to determine the chance that one species will feed on another. The model assumes that species can be arranged a priori into a cascade or hierarchy such that a given species can feed only on species below it in the hierarchy, and itself can be fed on only by species above it in the hierarchy. Even these simple rules greatly restrict the number of possible assembly pathways. We have yet to build models with these restrictions. When we do so, at least we will have something against which to compare them.

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Figure 1. The simplest transition graph.

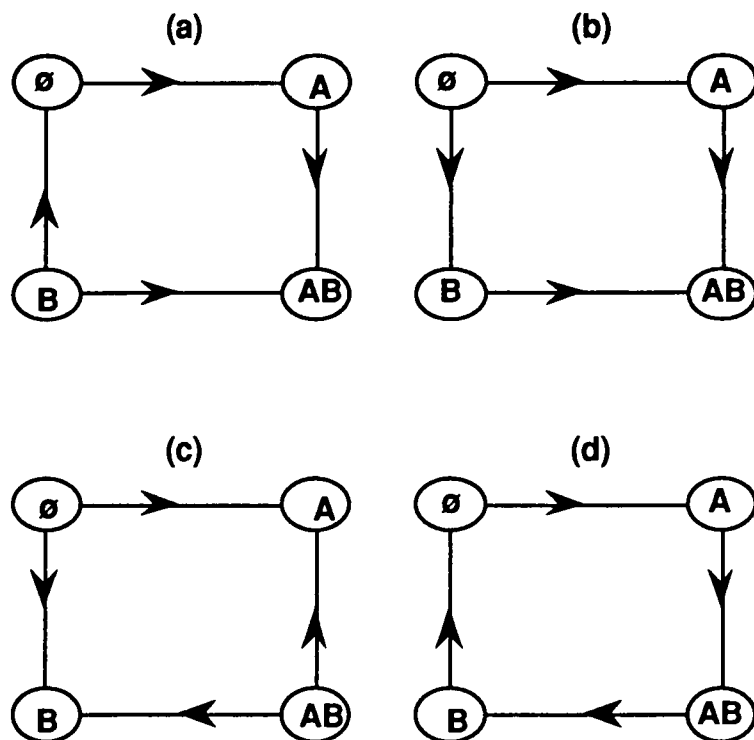


Figure 2. Examples of two-species transition graphs.

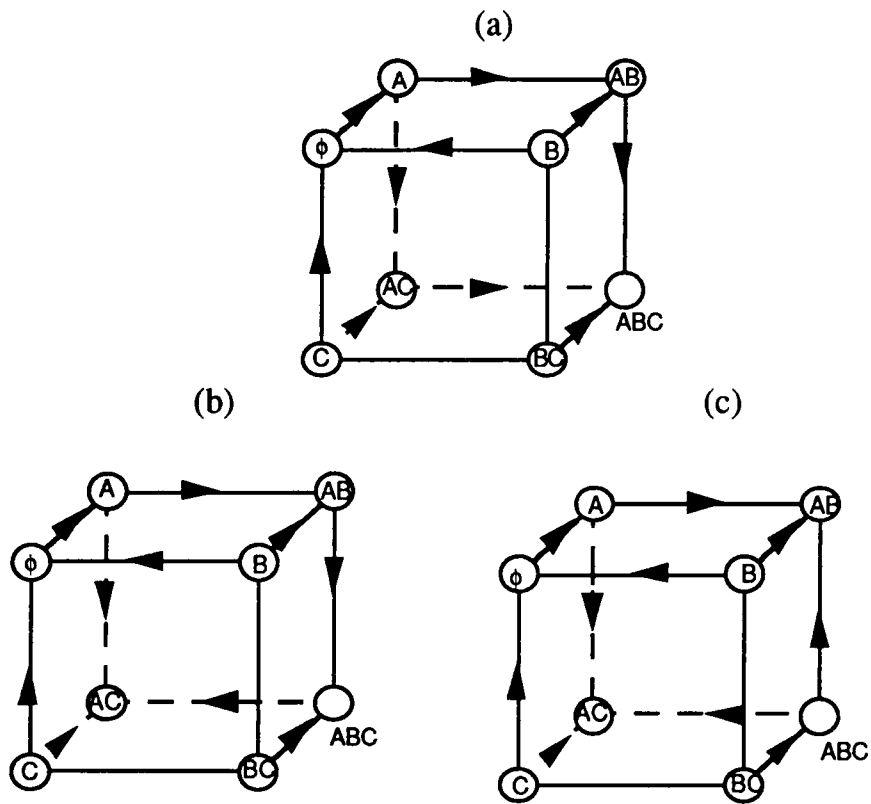


Figure 3. Examples of three-species transition graphs. (Some arrows are not shown, if their directions are irrelevant to the discussion.)

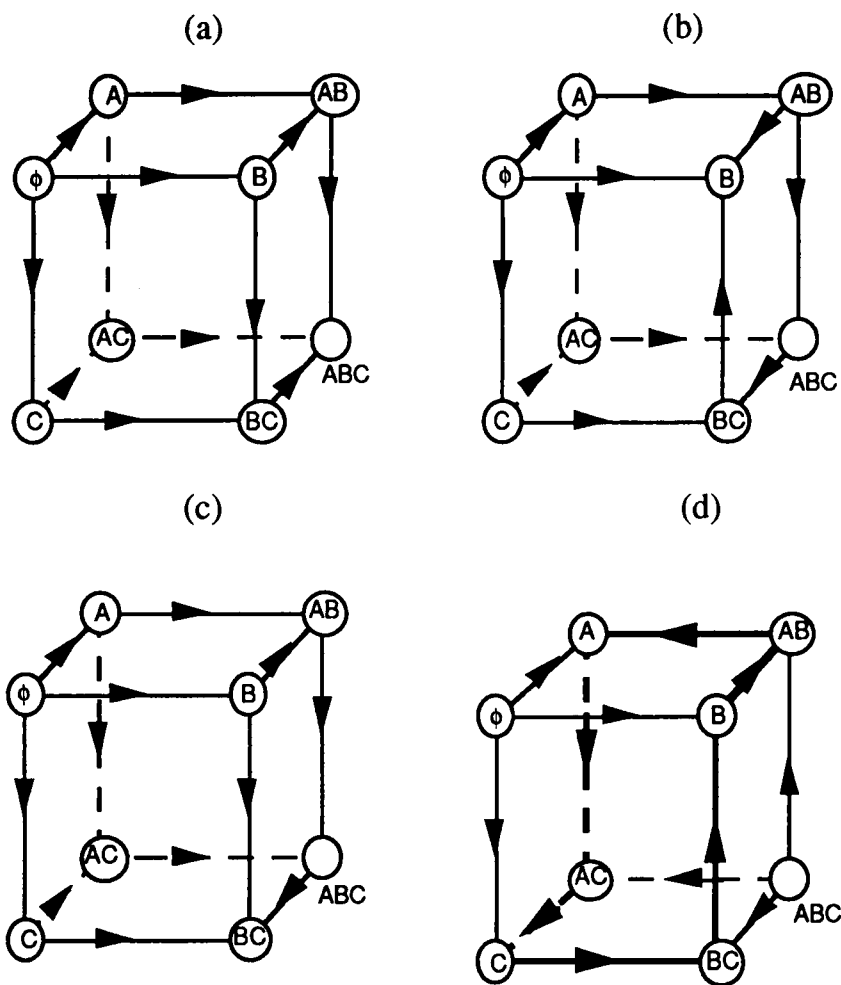


Figure 4. More examples of three-species transition graphs.

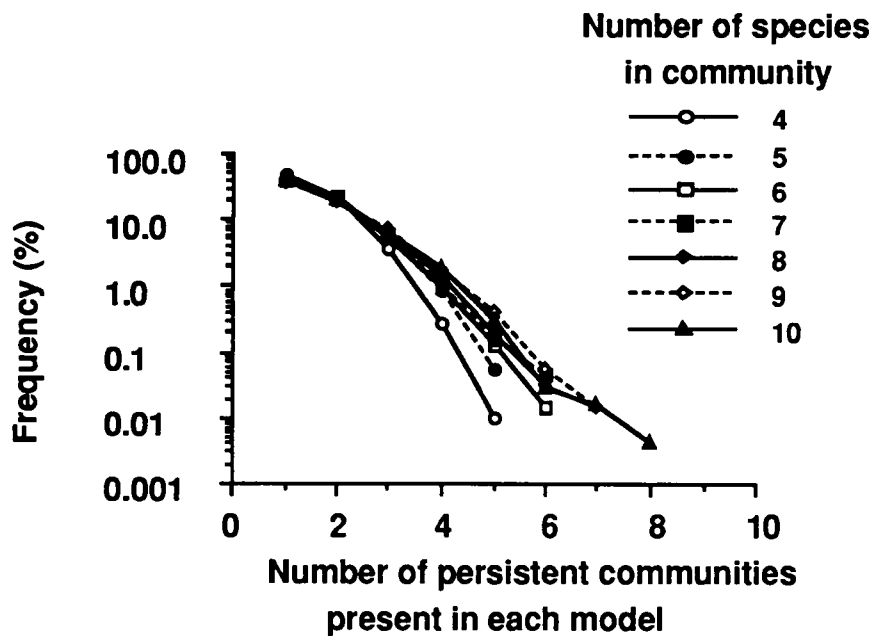


Figure 5. The frequencies of number of persistent communities present in each model. Usually there is only one persistent state in a model. As the number of persistent states coexisting in a model increases, so the frequency of that number declines. The scaling of this decline is approximately exponential (i.e. approximately linear on the logarithmic scale used here) and is relatively independent of the number of species in the model. The frequencies plotted here are based on a total sample of 100,000 models for each number of species.

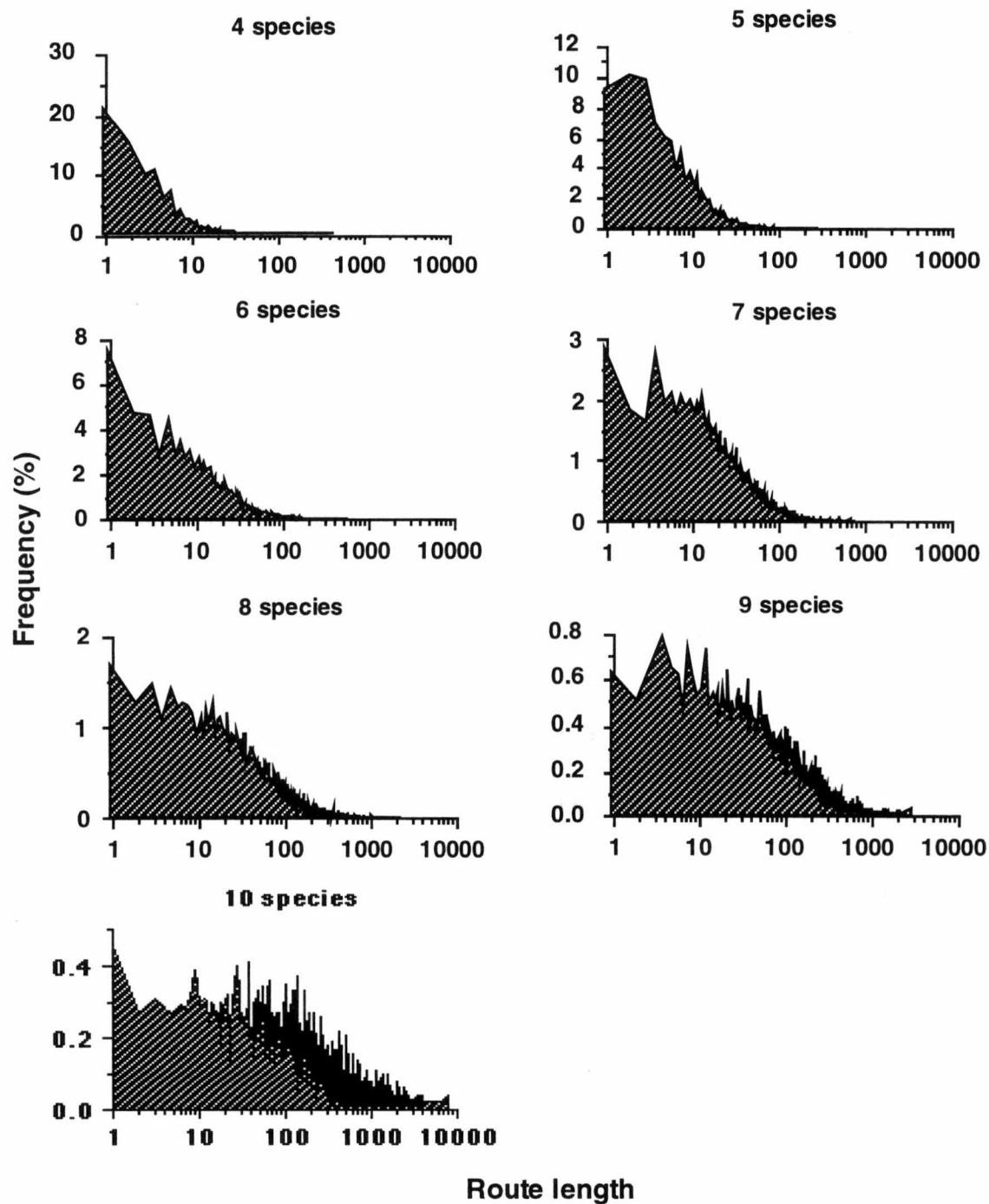


Figure 6. The frequency of route lengths. For four-species models, the persistent state(s) is usually reached by route lengths of less than ten steps long. With ten-species models, route lengths can often be several hundred steps long.

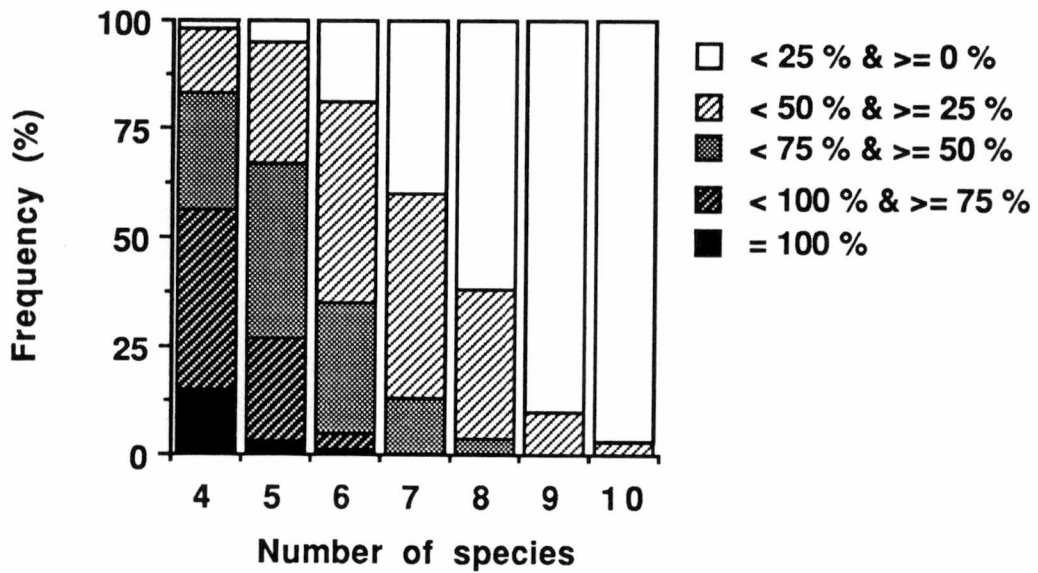


Figure 7. Percentages of models that do not pass through loops. In the four-species models, the different assemblies never pass through loops in about 15% of the models. In only a small percentage of the models do the paths always pass through loops. With eight or more species, in most models, most of the assemblies pass through loops on their way to persistent states.

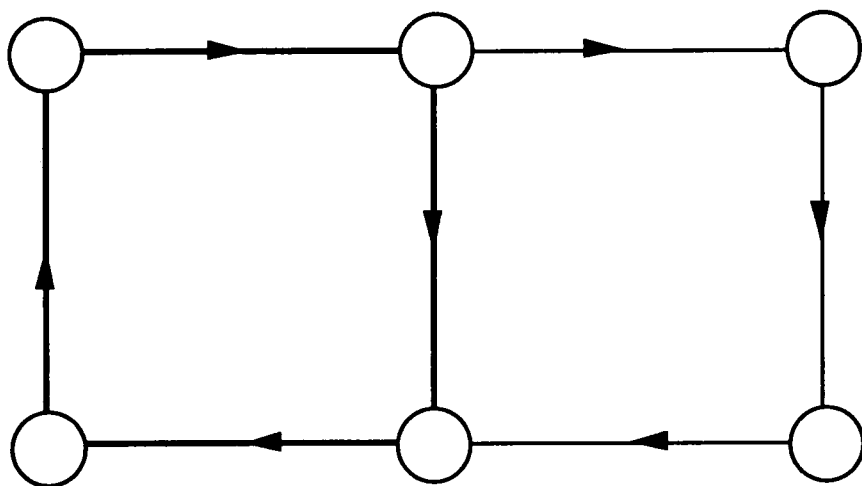


Figure 8. Hypercube with a simple loop and a complicated loop. A graph that contains both a simple loop, (around the four states at the left) and a more complicated loop (all the states) in which the four states are embedded.

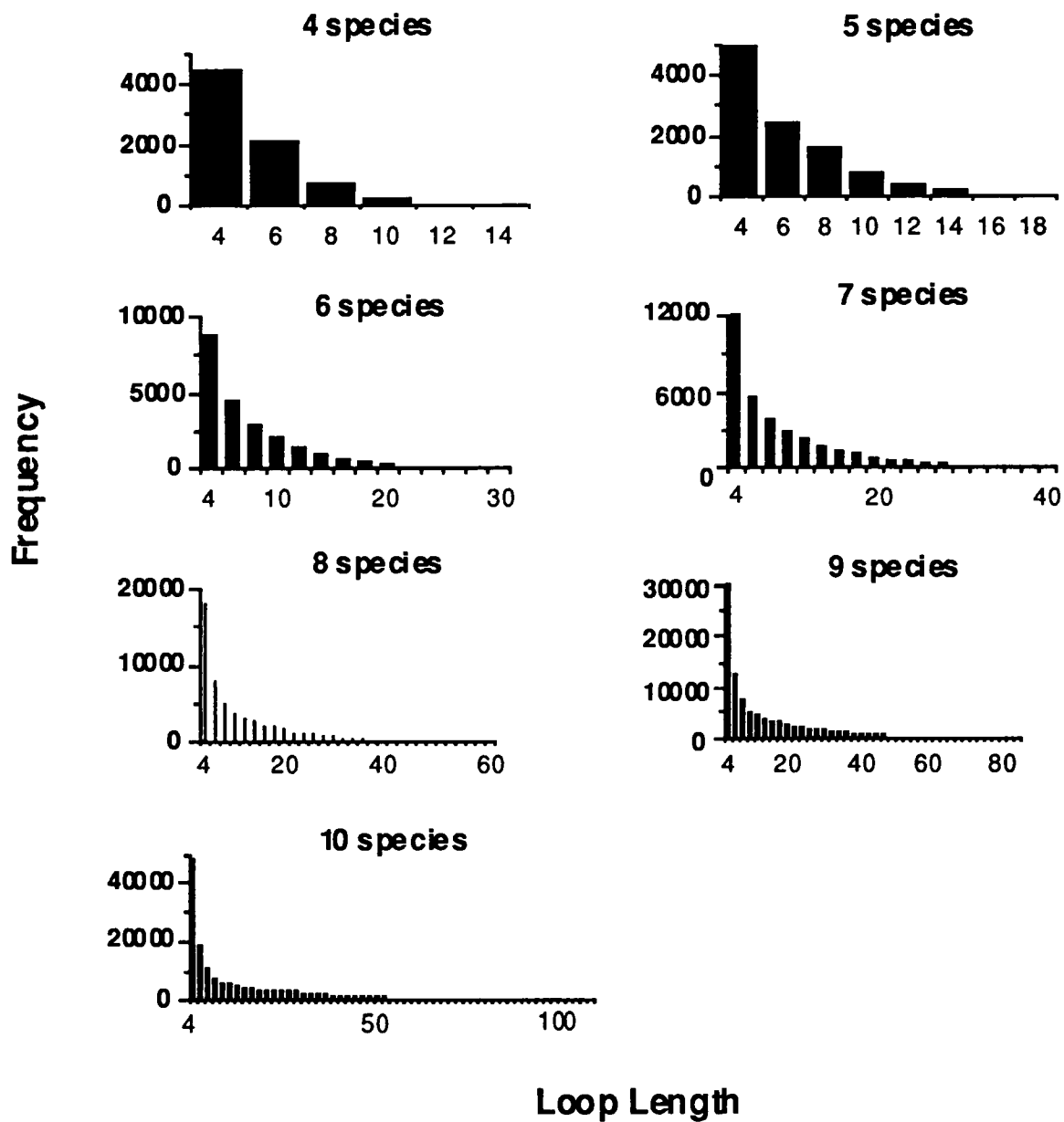


Figure 9. Distribution of route lengths for models with different numbers of species. A loop length of four — a cycle round the face of the hypercube is always the most common cycle. These frequencies are from 100 assemblies of each of 100 different models.

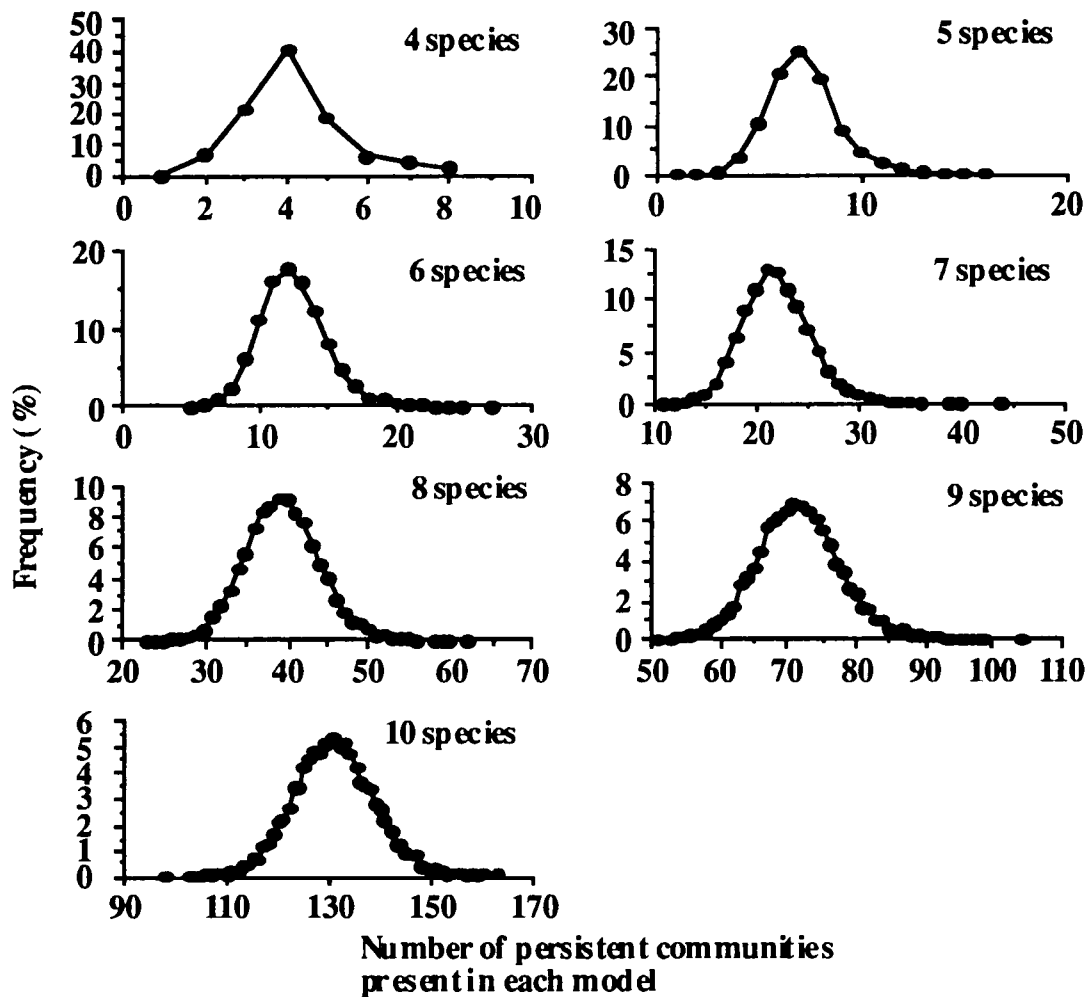


Figure 10. Number of persistent states in landscape transition graphs. Unlike random transition graphs (see Fig. 5), the modal number of persistent states is larger than unity. The number also increases rapidly with increasing numbers of species in the models.

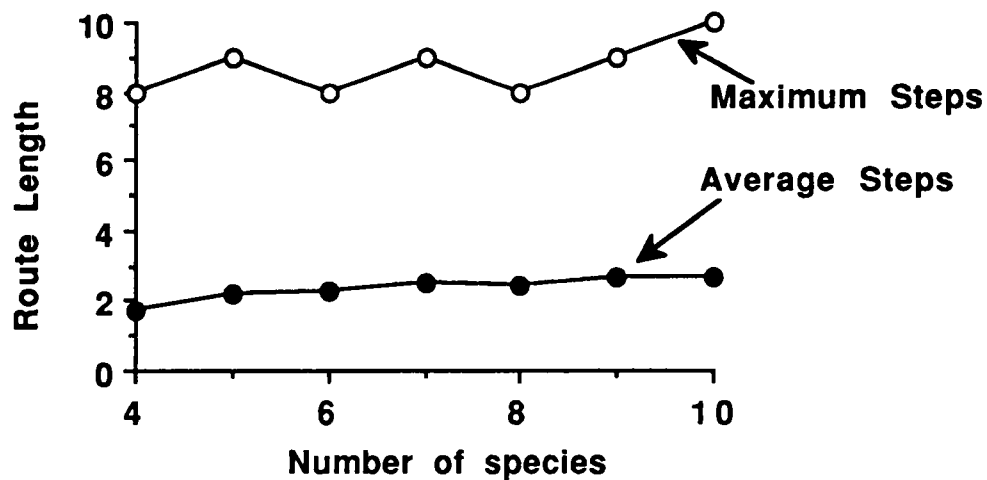


Figure 11. Route lengths and the number of species in the landscape community assembly models. Route lengths change little with increasing numbers of species, in contrast to the results from random community assembly models — see Fig. 6. (Fig. 6 shows the full distribution of route lengths, this figure only the means and maxima for each species.)

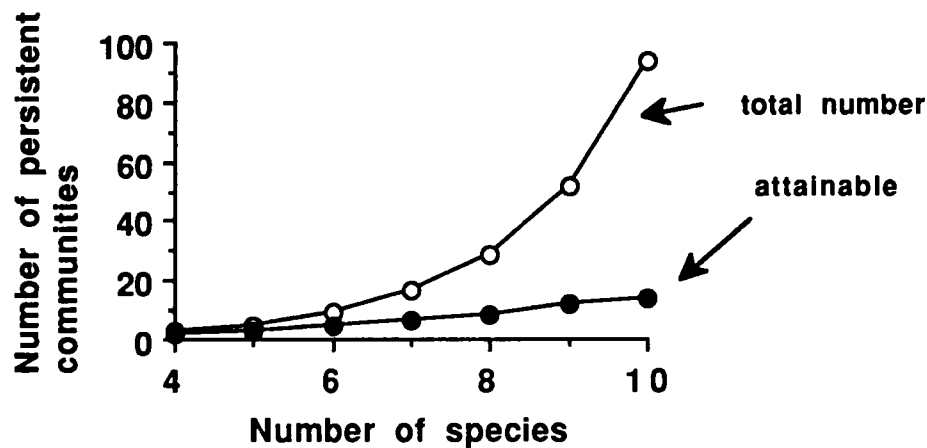


Figure 12. The total number of persistent states and the total number of reachable persistent states in models of landscape community assembly. The attainable number of states is a small and decreasing proportion of the total number. This is in contrast to the random community models, where unreachable states are very rare. (These data are from the one hundred sample graphs used to explore the dynamics in detail. Therefore, the maximum numbers of states are not those found in Fig. 10; these are from samples of 100,000 graphs. The numbers in this figure are approximately the modal number of persistent communities in that figure.)

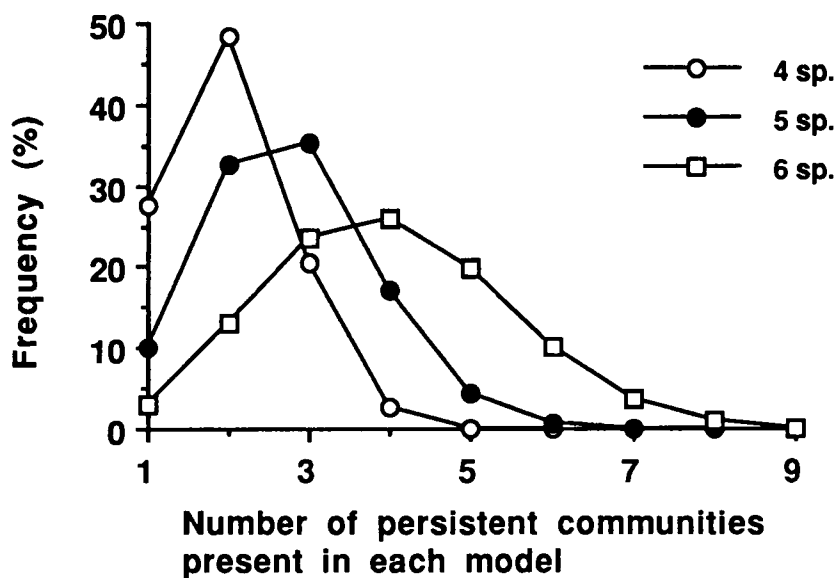


Figure 13. Distribution of number of persistent communities for the minimal community transition graphs with four, five, and six species. Compare with Fig. 5 and Fig. 10. Computational limits prevented the analysis of models with more than six species.

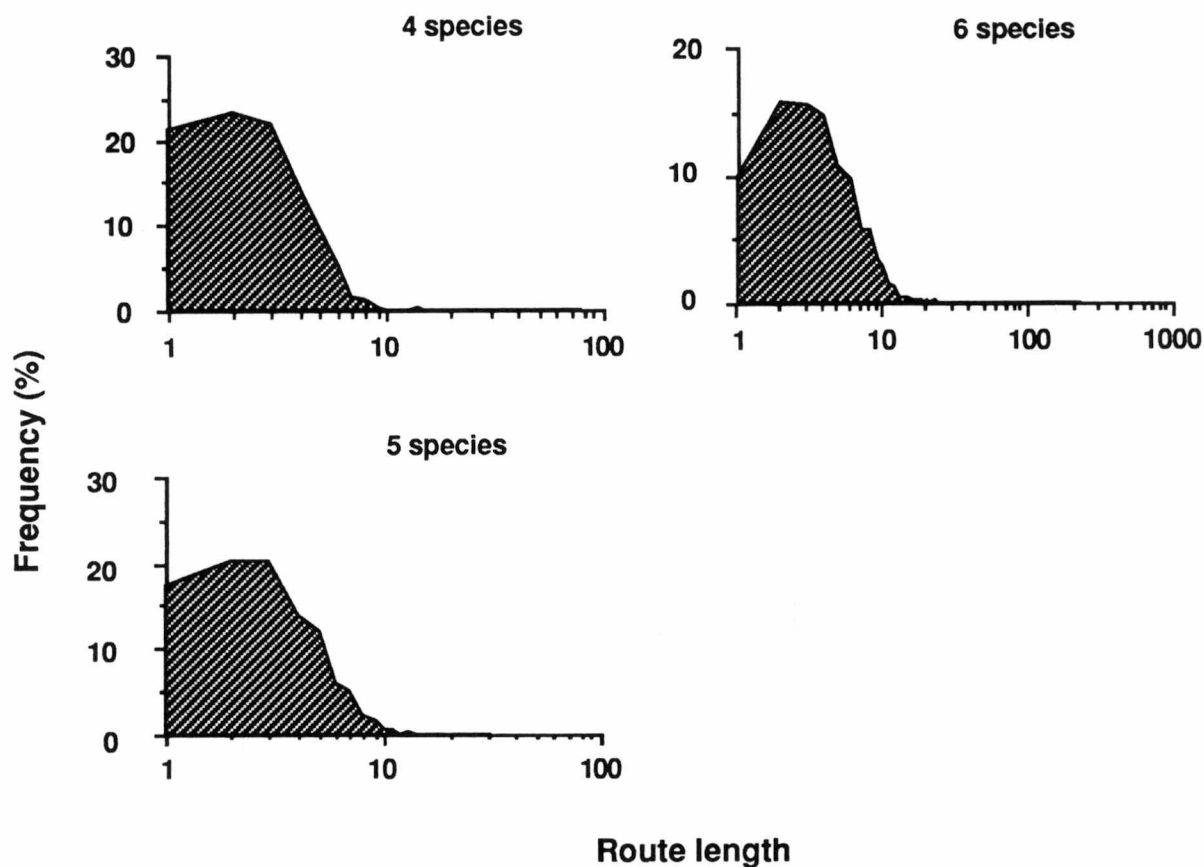


Figure 14. Distribution of route lengths for minimal community transition graphs. Compare this figure with Fig. 6 (which shows the full frequency distribution) and Fig. 11 (which shows only the mean and the maximum of this distribution).

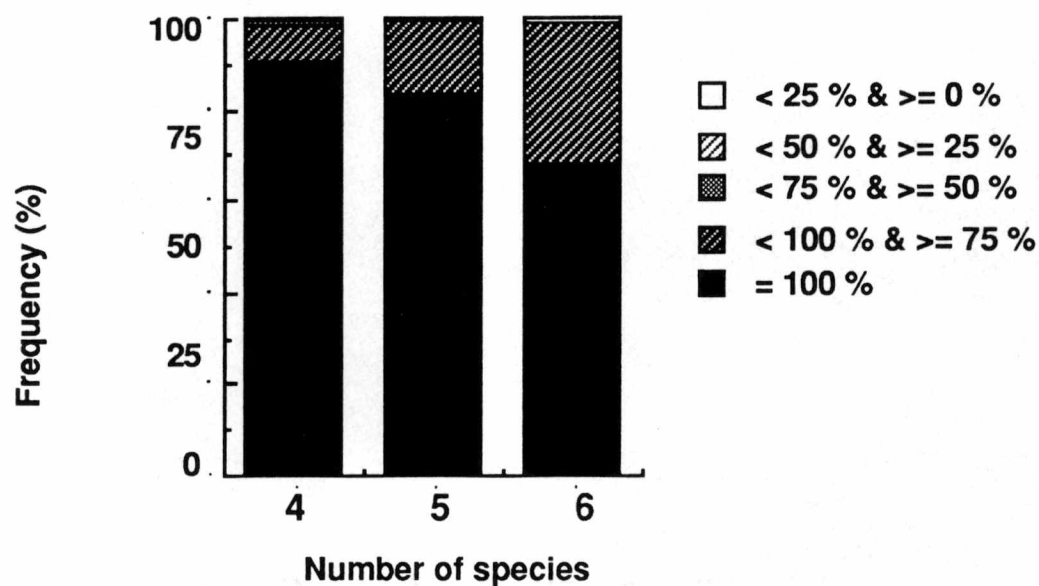


Figure 15. The percentage of models that passes through different number of loops. Compare with Fig. 7 for random transition graphs.

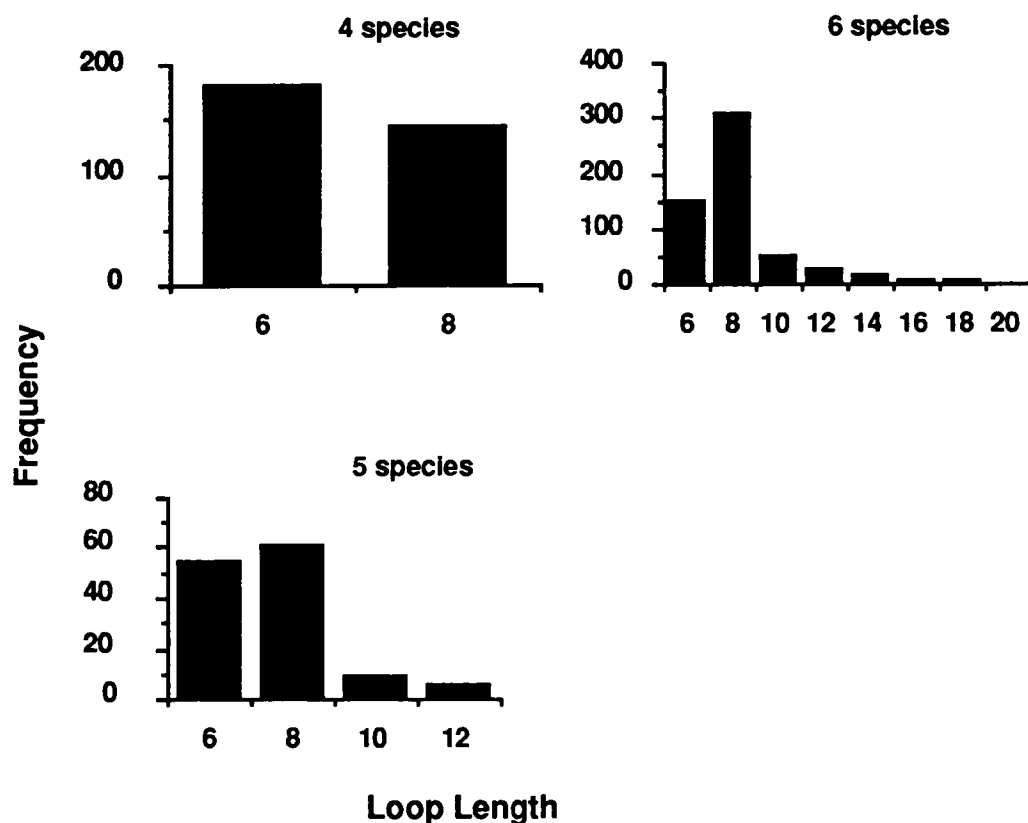


Figure 16. Distribution of loop lengths for the minimal community transition graphs with four, five and six species. These frequencies are from 100 assemblies of each of 100 different models. (Most models have no loops — as shown in Fig. 15). Compare this figure with Fig. 9.

**PART 3: THE ASSEMBLY OF ECOLOGICAL  
COMMUNITIES - A FOOD - WEB APPROACH.**

## Introduction

Community assembly is a state transition process showing how the composition of an ecological community changes by species invasion and extinction. What are the factors that determine the change of species composition in an ecological community? Is the structure of an ecological community determined by assembly rules (Haefner, 1978; Lawton, 1987; Drake, 1990), or by "random grammars" (Connor and Simberloff, 1979; Kauffman, 1993)? To answer these questions, two elements must be considered: (1) mechanisms that control structure, and (2) information about historical events during community assembly.

Community structure is determined by a variety of mechanisms (Pimm, 1982; Pimm et al, 1991). The relative importance of these is highly variable, both among different communities and at different times within the same community. In aquatic systems, predators play a crucial role in maintaining the established community structure (Paine, 1966), but in the early stage of a new habitat, such as an artificial reef, the community composition might be determined solely by which species arrive first. The principal mechanism in the formation of a community probably depends upon the ecosystem type and the scale at which the community is defined (Drake, 1990).

Historical events are another important factor affecting the current species composition of a community (Drake, 1990; Luh and Pimm, 1993). A species invasion or extinction in the past might be a key factor in the current composition. The importance of such critical events lies more in when they occurred than in their magnitude. Community assembly naturally reaches a critical state, at which a minor perturbation might start a chain effect that leads the community to an alternative composition (Bak, 1991; Drake, 1989).

Most models of community assembly are based on food-web structures. Population dynamics are put in the models to create the dynamics of the community, usually with Lotka-Volterra differential systems (Drake, 1990; Post and Pimm, 1983). One criticism of this approach is that the resulting community dynamics depend on the particular functions selected for the population dynamics, and so are not robust (for example, the Lotka-Volterra equations are extremely sensitive to initial conditions).

In this paper, we abandon such theoretical models and represent community assembly using a switching Boolean network. In this network, the nodes are community states with different combinations of species. Community assembly, which is a sequence of community states, can be represented as a trajectory around the network. The direction of each transition is regulated by simple probabilistic criteria rather than species interaction models. We construct networks using different levels of ecological constraint based upon common food-web characteristics, and simulate community assembly. Depending upon the amount of constraint, it is possible to identify recurring subsets of nodes (sub-domains) that share characteristics of species interaction and strongly influence the assembly process.

### **Community transition graphs**

Community assembly can be viewed as a movement on a directed Boolean hypercube, where the community only gains or loses one species in each transition (Figure 1). We call this directed Boolean hypercube the *community transition graph*. The vertices on the graph represent all possible communities. The transition pathways connecting the community states show the directions of community assembly.

A community transition graph with  $N$  species has  $2^N$  different community states (nodes), that may be labeled from 0 to  $2^N - 1$  in decimal notation. The *binary* notation of each label exactly shows the species composition of this community. Consider one community state in a ten-species assembly model, in which species one, two, four, and five are present, and species three, six, seven, eight, nine, and ten are absent. If 1 represents presence, and 0 represents absence, then the binary notation of this state is 0000011011, and the decimal notation is 27.

Two community states can be linked by a transition pathway only if their binary presentations differ by the presence or absence of one species. Therefore, in a ten-species model, each community has ten 'nearest neighbors' (Table 1).

Every assembly process on a community transition graph is a finite or infinite sequence of community states. The sequence may be finite if the community transition graph has at least one persistent community state that the community can reach. A persistent community is a state with all directed transition pathways only going towards it, and represents a stable equilibrium. The sequence is infinite if the community becomes trapped in a loop or cycle, and never reaches an equilibrium. The general definition of a loop is: an assembly pathway taken by a community which returns to any state that it has previously passed through. There are many types of loops. The simplest loop is a *persistent cycle*, a closed loop in which every community state has only one outgoing pathway. Once the assembly process enters a persistent cycle, it will continually repeat this sequence. The most complex loop involves the entire community transition graph. The *route length* is the number of community states from the beginning of the assembly process to a persistent state.

## Different community transition graphs

How many alternative community transition graphs are there? A community transition graph with  $N$  species has  $2^N$  community states and  $N * 2^N - 1$  transition pathways. Each pathway has two possible directions, so there are  $2(N * 2^N - 1)$  possible community transition graphs. It would certainly be impractical to examine all possible graphs if the directions of the transition pathways are determined purely by chance. By applying certain criteria, we can reduce the number of possible graphs. For example, if we state that communities have to have persistent compositions, then about one third of transition graphs do not meet this criterion (Luh and Pimm, 1993 ). If we disallow four-step loops, then we can remove 55% of the possible configurations from a four-species model (Luh and Pimm, 1993). In the following, we will discuss several criteria based upon ecological principles.

### 1. *Community transition graphs without any loops*

In this criterion, we view the community assembly process in a simple manner: communities must have persistent compositions, and the assembly process can never pass through a loop or cycle.

To implement these criteria, we borrow Kauffman's idea of evolution as the assembly of phenotypes from complex genetic systems (Kauffman, 1993). Kauffman also uses a Boolean hypercube, to represent a fitness landscape in the space of phenotypes. In his model, each phenotype has  $N$  traits, and each trait has two possible states (such as 'on' or 'off'). Phenotype fitness is determined by the way that traits contribute to this phenotype. During the phenotype 'assembly process', adaptation pushes the species' phenotype higher until it reaches a peak of fitness.

Kauffman's model includes a number of epistatic interactions,  $K$ , that influence phenotype fitness. There are two extreme cases. If  $K = 0$ , the contribution of a trait is independent of the others. This is an additive fitness model—the fitness landscape has a single global maximum and no local maxima (a topology similar to Mount Fuji in Japan). When an assembly process starts from any phenotype, the end point will be always the global maximum. The other extreme case is  $K = N - 1$ . Here, the contribution of a trait is epistatically affected by all other traits, and the landscape is thus totally random with many peaks and valleys (more like the Alps). As  $K$  increases from 0 to  $N - 1$  (i.e., the epistatic effect increases), the landscape goes from smooth to rugged.

In a similar manner, community assembly can be viewed as a fitness landscape in which the community always moves from a state with lower value to one of its higher neighbors. This constraint keeps the community transition from any kind of loop. We call this the *landscape transition graph* because each movement will push the community to a higher position until it reaches a local maximum.

In ecology, a random and very rugged landscape transition graph is produced by the simplest assumption that the presence or absence of one species will influence all other species. This assumption involves too many ecological factors—for certain circumstances, we are not sure whether the absent species affect the interactions among present species. This model, however, is easy to simulate. We can simply assign a random number to each community state as its height or fitness. Since every number is independent of the others, it will generate the most rugged landscape, and because each assembly movement pushes the community to a higher state, there is no loop.

## 2. *Predators' sink hypercube*

One of the important properties of any hypercube is that it is constructed recursively from lower dimensional cubes. Each  $N$ -dimensional hypercube is formed by two identical  $(N - 1)$ -dimensional hypercubes. One  $(N - 1)$ -dimensional hypercube has vertices *without* the  $i$ th species; the other  $(N - 1)$ -dimensional hypercube has vertices *with* the  $i$ th species. Repeating this process in the sub-dimensional hypercubes, a hypercube can be divided into several sub-hypercubes of lesser dimensions.

In a community transition graph, one simple sub-hypercube is that containing only predators. Because there are no prey at all, the predators are eliminated one by one—the community will always move to a state with one less predator until all the predators are removed. We call this sub-hypercube the *predators' sink hypercube*. The predators' sink hypercube is similar to the special case of Kauffman's model where  $K = 0$ , because there is only one configuration and one global maximum in the predators' sink hypercube.

## 3. *Predator is removed if there is no prey*

A community transition graph represents all possible community compositions for a given number of species. Depending upon the way the species interact ecologically (e.g., as described by a food web), many states in a community transition graph may be unstable. One example is a state in which a predator does not have any prey. We can thus eliminate any transition pathways that introduces the predator before its prey is present.

## How to include these ecological criteria in a community transition graph

### 1. *Rugged landscape transition graph*

The assumption of the rugged landscape transition graph is that the presence and absence of one species will affect every other. The landscape is thus random, each state being uncorrelated with every other state. There is clearly no optimal way to find the highest peak because of the many local peaks that divide the landscape transition graph into many independent areas. Assembly is very short, and it is easy to reach a persistent state, but the community can only explore a certain small area on the landscape.

In ecology, rugged landscape transition graphs represent some environmentally sensible communities. The fitness (or "height") of each community state is determined by species interactions, both with other species and with the physical and chemical environments. Within a short period of time the environmental factors may not change, and the community will reach a persistent state rapidly. If the environment *does* change, the heights of locations on the landscape change too. The persistent state the community reached before may not be persistent now, and the community will move to another persistent state (Figure 2).

### 2. *Predators' sink hypercube*

This transition graph is very sensitive to the number of predators because this determines the size of the predators' sink hypercube. For example, in a ten-species community transition graph, if there is only one prey species, the nine predators will form a nine-dimensional sink hypercube. Obviously, persistent states will not occur in this sub-hypercube and must be in the other nine dimensional sub-hypercube (the one

including the producer). Global extinction may occur frequently if the community in the sub-hypercube with the producer is easily able to move to the predators' sink hypercube.

### 3. *Predator is removed if there is no prey*

The previous criterion only focuses on the sub-hypercube formed by predators. This criterion extends the predators' sub-hypercube into another sub-hypercube formed by both predators and producers. We check the interactions among species in every community state. If there is a community state in which a predator does not have its prey, the predator cannot invade this community state. In other words, the direction of transition pathway connecting the two states is from the community with this predator to the community without this predator, and not vice versa.

### **Statistical properties of community assembly**

With these ecological criteria, we can ask several interesting questions about the topology of community transition graphs and the dynamic behavior of community assembly. For a given number of species: How many persistent communities exist? How many unattainable community states are there? How often do persistent cycles occur? How long will it take a community to reach a persistent state? If the assembly sequence is finite, is it simple (i.e., with few loops) or complex (i.e., with many loops)? Do different ecological criteria affect the configurations and dynamic behavior of transition graphs, producing phenomena such as the humpty dumpty effect (Pimm 19??)?

## **Method**

The first criterion (producing rugged landscape transition graphs) has been broadly discussed by several researchers (Kauffman, 1993; Luh and Pimm, 1993; Palmer, 1991). In this study, we only concentrate on the second and third criteria. Our simulations involve a three-stage process. We first create a food web containing ecological information, such as the ratio of predators to prey and the interactions between species. Second, we determine the directions of the community transition pathways according to the structure of the food web. Third, given a community transition graph, we simulate community assembly from an empty state to a persistent state.

### **Simulation of the food web**

Food webs are simulated using certain biologically reasonable rules provided by Pimm (Pimm, 1982; Pimm et al, 1991).

- (i) Food chains are short. The number of trophic levels in a food web is either 3 or 4.
- (ii) There is no loop in which a species feeds on another species with the same trophic level or higher.
- (iii) Omnivores are rare. When they occur, they usually feed on adjacent trophic levels.
- (iv) Webs are not compartmentalized.
- (v) There are more species of predators than species of prey.

## **Simulation of ecologically sensible transition graphs**

Given a food web, we first set the community state representing the entire food web (i.e., the maximum number of species) as a persistent state. This guarantees that the community transition graph is stable and has at least one persistent state. To be sure that the empty state is not also a persistent state, prey *always* invade the empty state.

We use two recipes to build the community transition graphs. In the first one, we apply the ecological criterion that the predators form a simple predators' sink hypercube. To construct this type of community transition graphs, we do not use all the information contained in the food web; only the ratio of predators to prey is necessary. Given the number of predators, we can specify all the directions in the predators' sink hypercube (Figure 3). For the rest of transition pathways, we assume that the events of invasion and extinction have equal probabilities.

In the second recipe, we use the extended criterion that predators cannot invade a community without their prey being present (Figure 4). This criterion includes recipe I, which is applied in the predators' space in the community transition graph.

After the directions of all the transition pathways are determined, we check the persistent states. If a persistent community contains two or more predators sharing same species of prey, then by invoking the competitive exclusion principle, we skip this configuration and generate another. This criterion is applied to both recipes.

## **Simulation of community assembly on community transition graphs**

Given a community transition graph, how does the community assemble? For each transition, a community state first 'looks around' at its immediate neighbors. Then the community estimates how many choices it can select for its next state. "No

choices" means that the current state is a persistent community. "One choice" means that there is only one outgoing transition pathway. When there is more than one choice, the community selects one of the outgoing pathways.

When the community has multiple selections for its next state, how does it decide which pathway to take? Two assembly methods are appropriate. In the first method, the community may choose any possible pathway with equal probability. We call this method *random assembly*, and apply it to the community transition graphs constructed by recipes I and II. In the second method, the criterion that a predator has to be removed when there is no prey has priority over other choices. We call this method *restricted assembly*. We do not apply this method to the community transition graph constructed by recipe I because there is no ecological constraint in the sub-hypercube with prey. Rather, restricted assembly is applied to community transition graphs constructed by recipe II (see Table 2 for a summary of construction recipes and assembly methods).

The following example illustrates the difference between the two assembly methods. Consider a community state composed of a species of top predator and a species of herbivore (Figure 5). The herbivore is the food of the top predator. Since there is no food for the herbivore, the herbivore may be removed or may gain its food in the next state. If we apply the first method, both choices have equal probability. If we apply the second, the community will move preferentially to the state without the herbivore.

The consequence of applying restricted assembly is that a community transition graph is compartmentalized. Figure 5 shows community state 123 to be unattainable, as there is no available transition pathway to that state. Consequently, community state

12 is also unattainable because the only pathway leading to state 12 is from state 123. This type of constraint in conjunction with the rule of restricted assembly makes most states unattainable. Such a community can reach a persistent state only through a few transition pathways. For example, there are two possible transition routes to the persistent state 24:  $0 \rightarrow 4 \rightarrow 24$  or  $0 \rightarrow 4 \rightarrow 34 \rightarrow 234 \rightarrow 24$ , and only one transition route to a persistent state describing the complete food web:  $0 \rightarrow 4 \rightarrow 34 \rightarrow 234 \rightarrow 1234$ .

### Analysis

Our program first generates a random food web with  $N$  species where  $N = 6, 7, 8, 9, 10$ . Then we construct two community transition graphs according to the two recipes. For each number of species, we repeat this simulation 10 000 times. For each simulation, we record: 1) the number of persistent states, 2) the number of unattainable states, 3) the number of directed pathways pre-determined by the recipes, and 4) the number of persistent cycles.

The next stage of the analysis explores the dynamics of the assembly process. For each number of species, we randomly choose one hundred transition graphs from each recipe. Then we simulate the community assembly process from the state with zero species to one of the persistent states or persistent cycles. In this analysis, we record: 1) how often the community cannot reach a persistent state, 2) the route length in each assembly process, and 3) the length of the loops.

## Results

### Configurations of community transition graphs

Community transition graphs with one and two persistent states are the most frequent result of both recipes (Figure 6). The frequency of graphs with more than two persistent states drops approximately exponentially. The community transition graphs with recipe I have more coexisting persistent states than those with recipe II. The probability that many persistent states will coexist in one community transition graph is very small. For instance, the ten-species model has 1024 possible community states. However, in our simulation, the maximum number of persistent states is eight in recipe I and is six in recipe II (and the relative frequency of ten-species community transition graphs with these numbers of persistent states is both 0.01% for both).

For each number of species, recipe I generates a few community transition graphs (1%–10%) in which all states are attainable (Figure 7). Recipe II generates at least one unattainable state in each simulation except those with ten species. Compare Figure 7 with Figure 6 for the number of coexisting persistent and unattainable states. The community transition graphs constructed by recipe I generate more persistent states but fewer unattainable states.

No persistent cycle is found through the whole simulation.

Figure 8 shows the percentages of transition pathways pre-determined by the two recipes. Recipe I can pre-determine fewer transition pathways than recipe II. Increasing the number of species does not change the percentages of pre-determined pathways.

## Dynamics

Given a community transition graph, the probability that the community cannot attain any persistent state is very small—in most cases the community is able to reach a persistent state eventually. We only find one transition graph in the six-species models, three in the seven-species models, and one in the eight-species models in which the community cannot reach a persistent state.

Figure 9 is the distribution of the route lengths for each number of species under different construction recipes and different assembly methods. The shortest route lengths are the most common. The most frequent route lengths are less than ten steps in recipe II transition graphs, no matter what assembly method is used. The frequency distribution for less than ten steps has a sharper decline in recipe II than in recipe I. However, the longest route lengths in recipe I are much shorter than those in recipe II. There are very small probabilities that the community assemblies will follow transition routes in recipe II, but by using restricted methods community assembly can follow longer transition routes.

Loops are very common when species assemble on community transition graphs (Figure 10). Most loops are four-step, the simplest cycle on the surface of the hypercube. The probability of long loops is very small. The number of loops and the length of the longest loop increase as the number of species increases. Communities will follow smaller numbers of loops in recipe I than in recipe II. However, recipe I has longer loop lengths than recipe II. Community assembly using the restricted method produces more loops than the random method.

There is a conflict in recipe II. The dominant route lengths are less than ten steps (see Figure 9). A short transition route means that the community reaches a

persistent state without following many loops. However, Figure 8 shows that the community follows many loops in recipe II transition graphs. Apparently, these loops do not come from the dominant short transition routes, but rather from long transition routes. When community assembly occurs on the recipe II transition graph, there are two possible assembly processes. In most cases the community will take short routes without loops or with very few simple loops. However, there is still a small probability that the community will take very long transition routes. These long transition routes are not composed of complex loops passing many different community compositions. They simply repeat many simple loops that causes the high frequencies of short loop lengths.

Why are there a few very long transition routes in the recipe II community transition graphs? Why are the configurations of transition graphs constructed by recipes I and II are so similar (see Figure 6 and 7), but showing entirely different dynamic behavior? To answer these questions, we should examine how the imposed ecological criteria affect the topologies of community transition graphs. Increasing the ecological constraints to construct the community transition graphs doesn't change the frequency distributions of persistent and unattainable states, but increases the percentage of pre-determined transition pathways. These pre-determined transition pathways divide the transition graph into several, relatively isolated areas. The community might never pass through some of these before it reaches a persistent state. Figure 11 shows the percentages of community states that are attainable in theory, but which were not attained in 100 assembly simulations. The more ecological constraints in the configurations and assembly, the more community states that the community cannot reach.

This compartmental effect, caused by ecological constraints, also affects whether or not the community assembly process can reach all the possible persistent states. In the simulation of community assembly with recipe I, the community reached all persistent states in 100 trials (Figure 12). As the ecological constraints increase (recipe II with two assembly methods), some community assembly transition graphs show that the community cannot reach all persistent states.

## **Discussion**

### **A comparison of the results**

In a previous study, one of us used three recipes to construct community transition graphs ('random', 'landscape', and 'minimal') and one assembly method ('random walk') (Luh and Pimm, 1993). If we place the static and the dynamic properties of these recipes on a spectrum, the random and the landscape transition graphs are located at the extremes and the minimal transition graphs are close to where the landscape transition graphs in this study would be (Luh and Pimm, 1993). Where in the spectrum should we place the assembly models with ecological criteria from this study? To answer this question, we first define the static and the dynamic properties of community transition graphs at each end of the spectrum. Then, we compare the two new assembly models with the previous ones.

The features of random and landscape transition graphs and their dynamics are as follows

- (i) Random transition graphs are ecology-free. They most commonly have one persistent state, and the frequencies of more than one persistent state drop

approximately exponentially. The landscape transition graph contains many ecological constraints. They have many more persistent states that increase with the number of species in the models. The percentages of persistent and unattainable states are approximately the same in both transition graphs.

- (ii) There are no pre-determined transition pathways in the random transition graphs. Conversely, in the landscape transition graphs, all transition pathways are pre-determined.
- (iii) In the random transition graphs, the short route lengths are the most common in models with small number of species. When the number of species is above six, the most common route lengths may be very long. In the landscape transition graphs, the transition routes are always very short. The route lengths are approximately equal to  $\log 2^N$ , where  $N$  is the number of species in the models (Kauffman, 1993).
- (vi) Cyclical changes in the composition of a transition route are very common in the random transition graphs. In the landscape transition graphs, the routes to a persistent state are free of loops.

From a static point of view, the distributions of persistent and unattainable states in the two new models of community assembly are similar to those of random transition graphs. However, there is no pre-determined transition pathway in the random transition graphs. The proportion of pre-determined transition pathways is dependent upon the amount of ecological constraints (compare recipe I and recipe II).

Dynamic properties depend upon the amount of ecological constraints. For community transition graphs with fewer ecological constraints (recipe I), their dynamic

behavior is similar to the random transition graphs—transition routes are long and involve some complex loops. As ecological constraints increase (recipe II with two assembly methods), their dynamic behavior tends towards the landscape transition graphs—the most common routes are short.

### **Ecological constraints increase complexity of community assembly.**

If a community is structure-free (i.e., the connections between species are random), then the assembly process is best described by models of random community assembly. During the process of assembly, the community might pass any type of species composition because the transition graph is a fully connected network. A particular persistent community is attainable from any starting point. A transition route may be very long because the community has more than one choice in each transition. During community restoration, a damaged community might eventually return to its original composition (Luh and Pimm, 1993).

The recipe I assembly models have similar properties to random assembly models. The predators' sink hypercube is very simple because all transition pathways are pre-determined. The transition pathways on the other sub-hypercube are specified at random. Since one sub-hypercube is random and the other one is 'frozen', the whole assembly model is exactly the same as the model of random community assembly.

Complexity of community transition graphs increases when more restricted constraints of configuration and assembly are applied. The community transition graphs become partitioned into *disconnected areas*. Ecologically, areas containing unattainable states represent the most unstable combinations of species. However,

communities may not reach some other states that are ecologically meaningful because most available transition pathways leading to them are blocked by unattainable states or prohibited by restricted assembly. We call this the 'Humpty-Dumpty' effect (Pimm, 1986)—it is impossible to put the community together from its pieces (single species or subsets of species). The Humpty-Dumpty effect is not significant when community assembly is random. However, as ecological constraints increase, the Humpty-Dumpty effect becomes very strong.

The results of our simulations allow us to answer the questions we posed earlier. Community assembly is controlled by various rules. Mechanisms driving the formation of a ecological community vary with the domains of sub-hypercubes partitioned from a community transition graph. In a predators' sink hypercube, predation is the force for driving the sequence of transition. In a sub-hypercube with only competitors, mutually inhibitory interaction (competitive exclusion) is important in determining the formation of a community (Pimm, 1991). 'Critical states' are another important factor in determining the sequence of community assembly. When assembly must pass only a few states to enter another sub-hypercube, these states are critical. Because of the small chance of reaching these critical states, community assembly may only proceed in a restricted area. If the community does pass a critical state, its eventual composition may be entirely different.

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Table 1. Binary and decimal descriptions of the ten 'nearest neighbors' of the state 27 in a ten-species assembly model.

| Binary notation | Decimal notation |
|-----------------|------------------|
| 0000011010      | 26               |
| 0000011001      | 25               |
| 0000011111      | 31               |
| 0000010011      | 19               |
| 0000001011      | 11               |
| 0000111011      | 59               |
| 0001011011      | 91               |
| 0010011011      | 155              |
| 0100011011      | 333              |
| 1000011011      | 539              |

Table 2. Summary of construction recipes and assembly methods.

|           | Configuration                                                                                          | Random assembly? | Restricted assembly?                                             |
|-----------|--------------------------------------------------------------------------------------------------------|------------------|------------------------------------------------------------------|
| Recipe I  | (1). Specify only predators' sub-hypercube.<br>(2) Specify the rest at random.                         | Yes.             | No.                                                              |
| Recipe II | (1). Specify all community states with the lack of predators' prey.<br>(2) Specify the rest at random. | Yes.             | Yes.<br>Predators' extinction has priority than prey's invasion. |

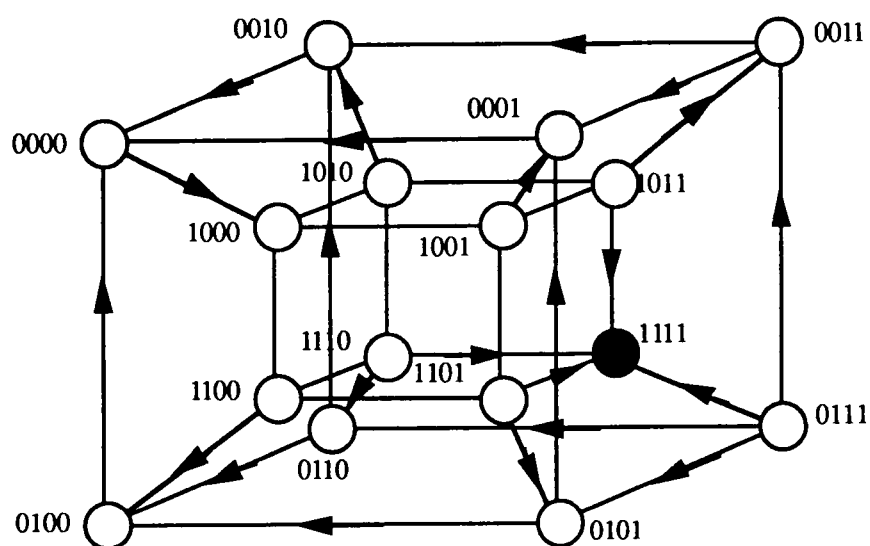


Figure 1. This is a four dimensional hypercube, where each vertex is a community state. '1' represents the presence of a species, and '0' represents absence. The arrows on the edges describe the possible directions for community transitions. The solid node is a persistent community. Community assembly will stop when it reaches a persistent state.

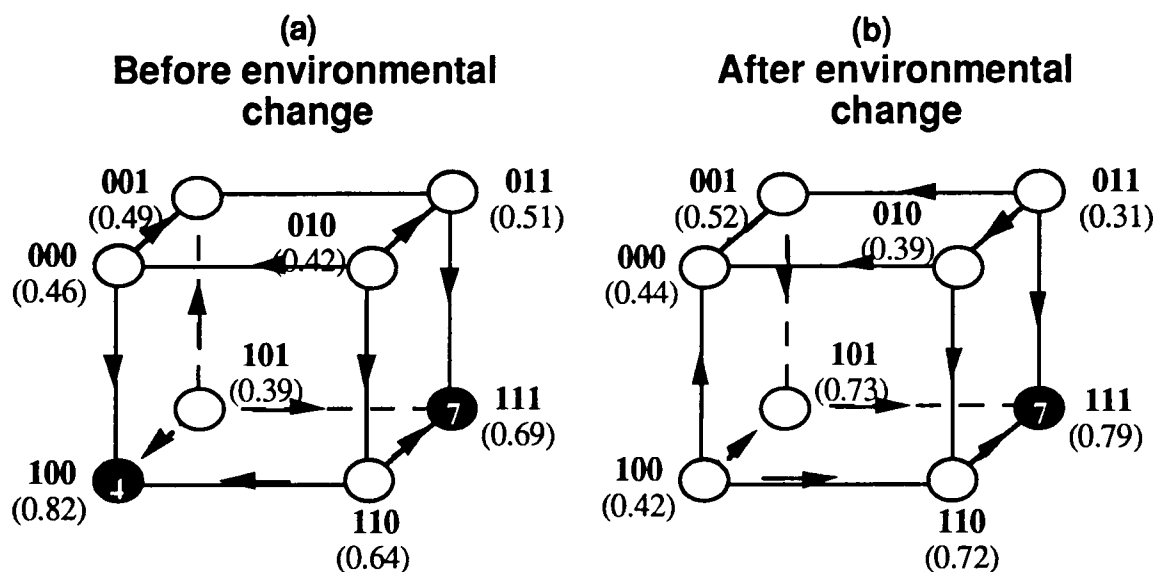


Figure 2. Landscape transition graphs. Each community state has its decimal and binary notations and its fitness value. (a) This is a landscape transition graph with two persistent communities, state four and state seven. If a community moves from the empty state zero to state four, the process of assembly stops. (b) After environmental change, state four is not a persistent state, and the community assembly process will continue.

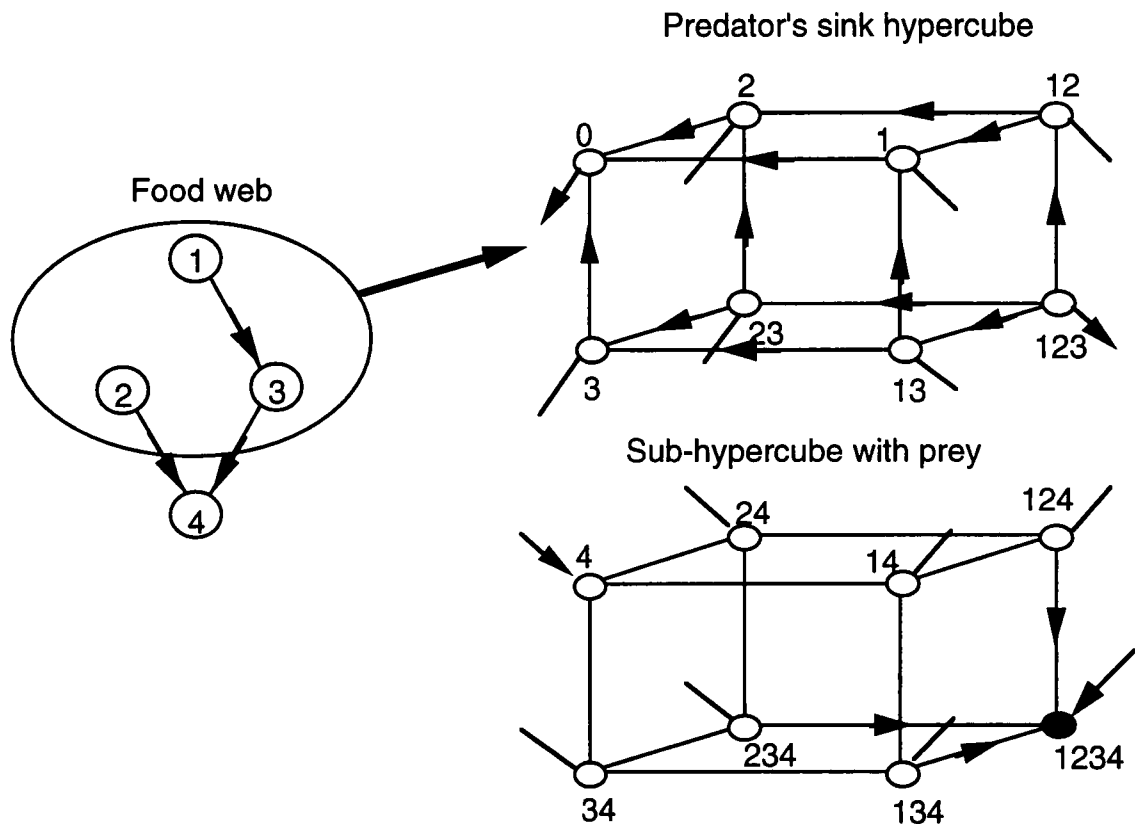


Figure 3. Community transition graph constructed by recipe I. This is a four-species food web, three predators and one prey. The community transition graph can be divided into two three dimensional sub-hypercubes -- one predators' sink hypercube and one sub-hypercube with prey. Each vertex in one sub-hypercube should be connected to the vertex at the same location in the other sub-hypercube. The transition pathways of predators' sink hypercube are pre-determined. The solid circle is a persistent state representing the food web, so all pathways connecting to this state are also pre-determined. Because there is only one producer, the transition pathway allows this producer invade to empty state.

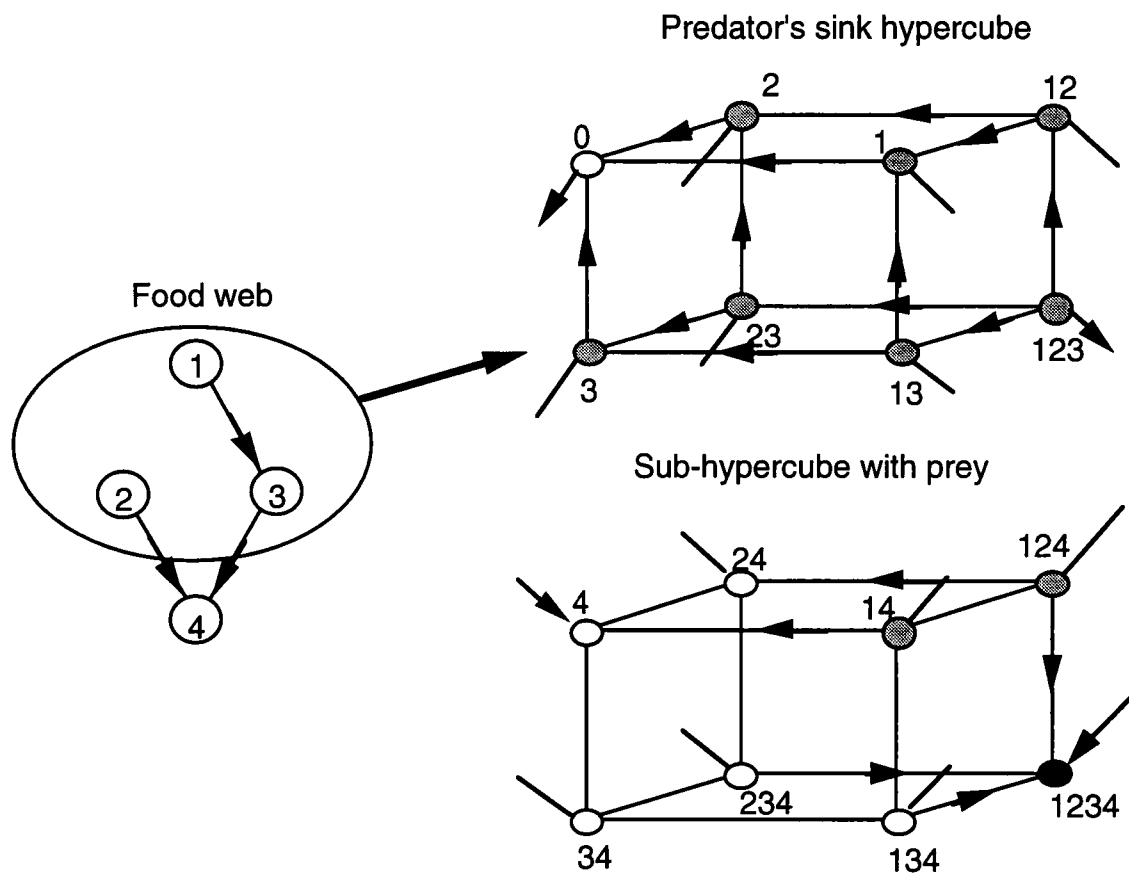


Figure 4. Community transition graph constructed by recipe II. We use the same food web as in figure 4. The gray circles are the communities that some predators do not have their prey. Most of them are in the predators' sink hypercube. Two are located in the other sub-hypercube. Two more transition pathways are pre-determined by comparing to figure 3.

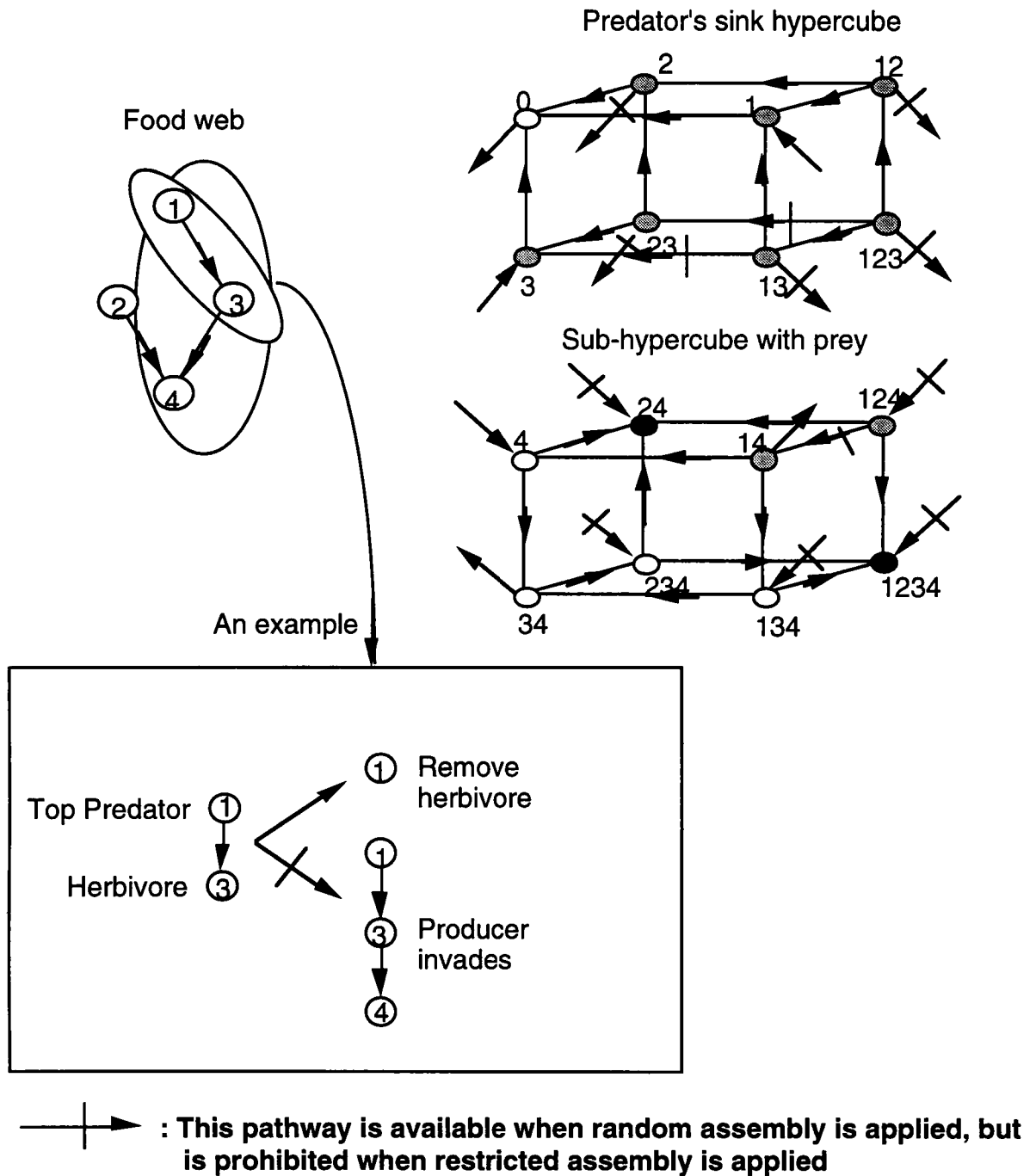


Figure 5. Restricted assembly. We use the same food web as in the figures 4 and 5. After we specify some transition pathways by the recipes, the rest are specified at random.

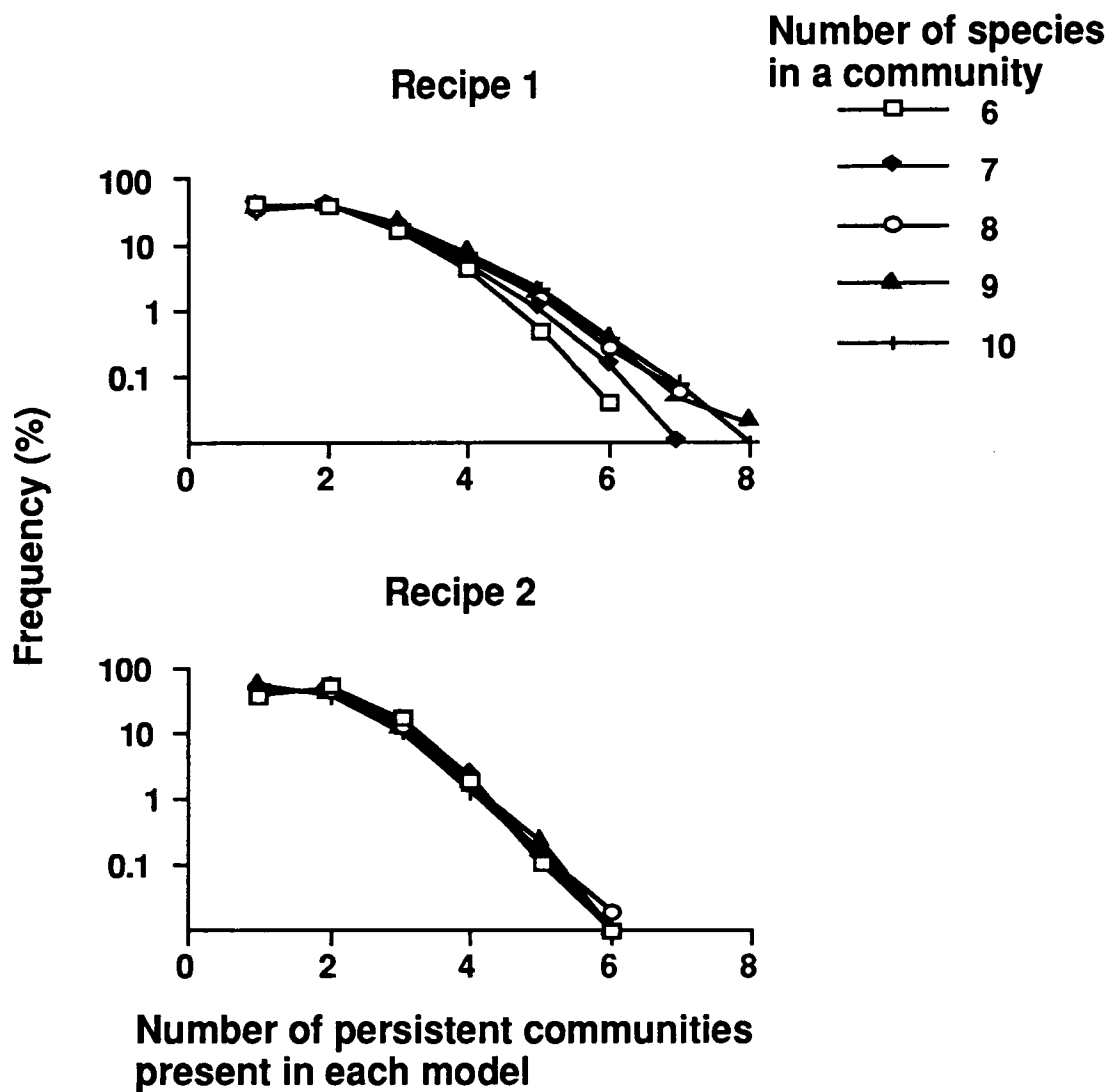


Figure 6. One or two persistent states are the most common in both recipes. The number of persistent states coexisting in a model is independent of the number of species in the model. The frequencies of more than two persistent states decline approximately exponentially.

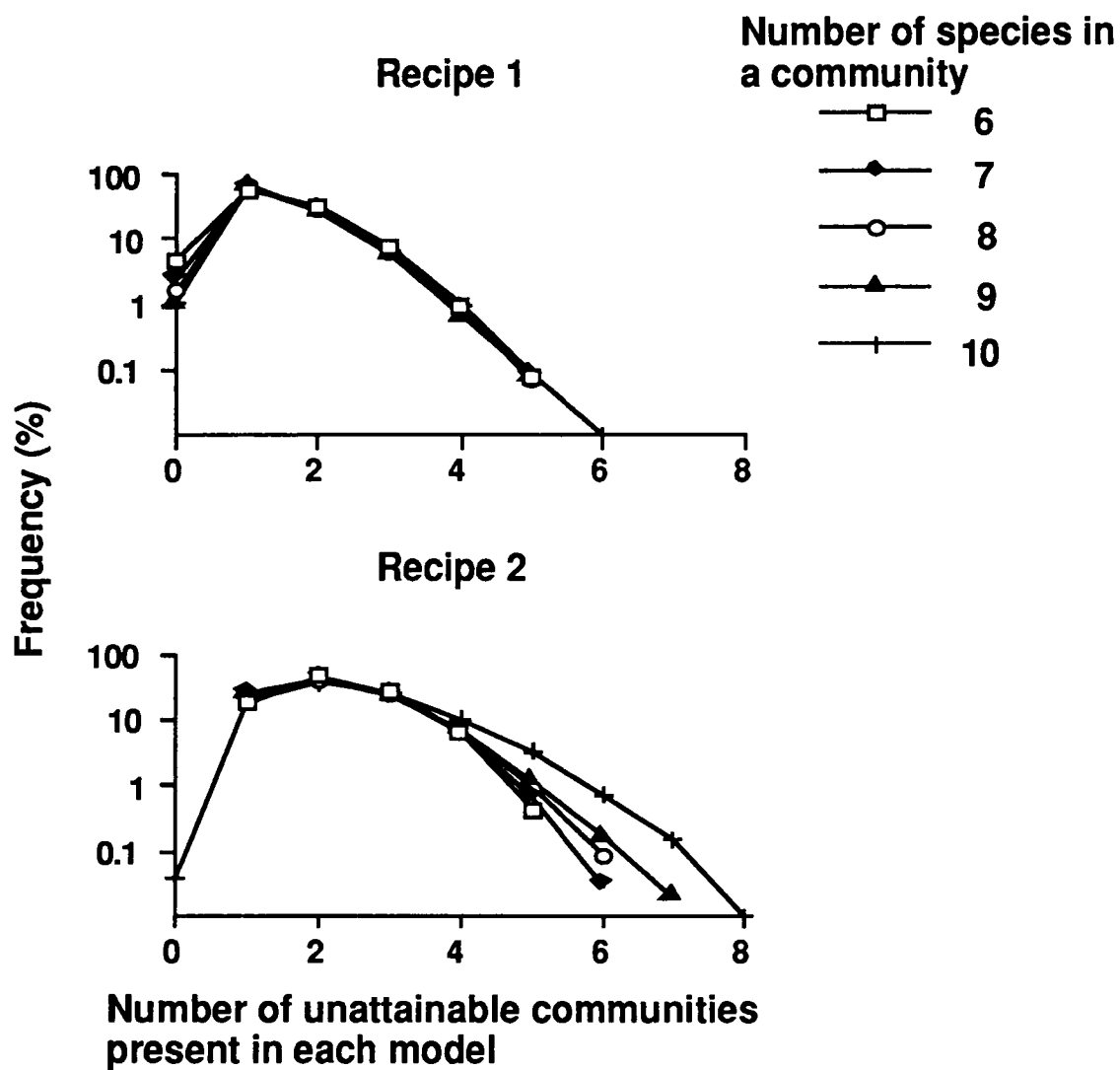


Figure 7. The frequencies of unattainable communities in the models.

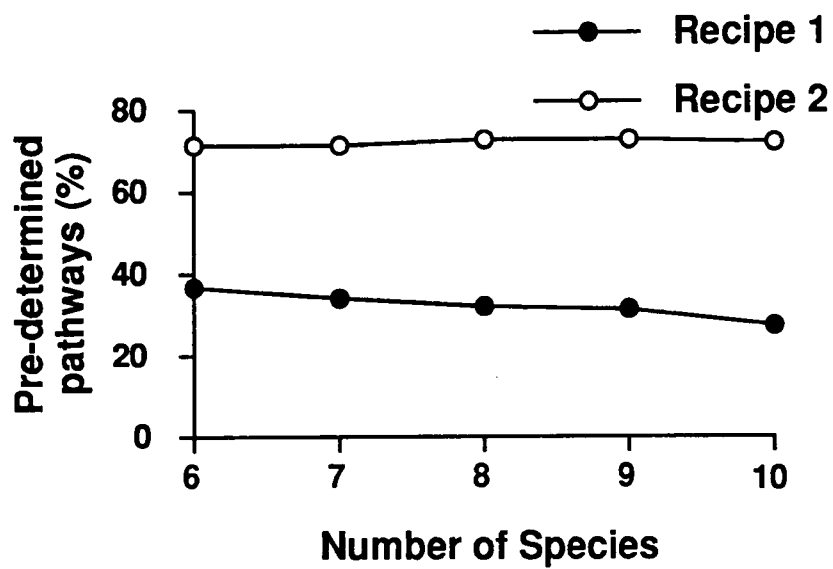


Figure 8. The average percentages of transition pathways are pre-determined by the recipes.

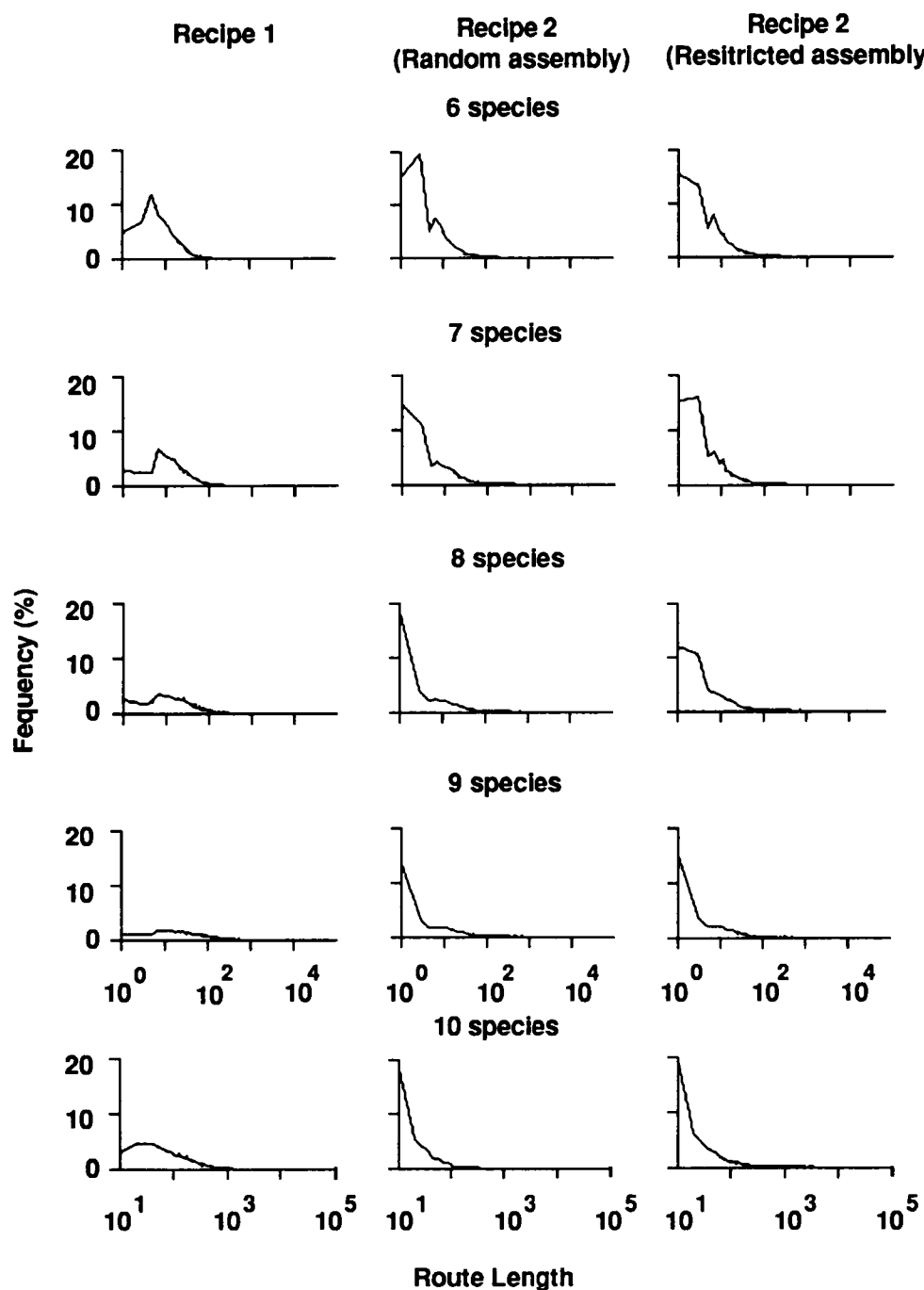


Figure 9. The frequency of route lengths. Two intervals are used here. Below ten-species models, the interval of route length is 2 steps. In ten-species modes, the interval is 10 steps. These frequencies are from 100 assemblies of each of 100 different transition graphs.

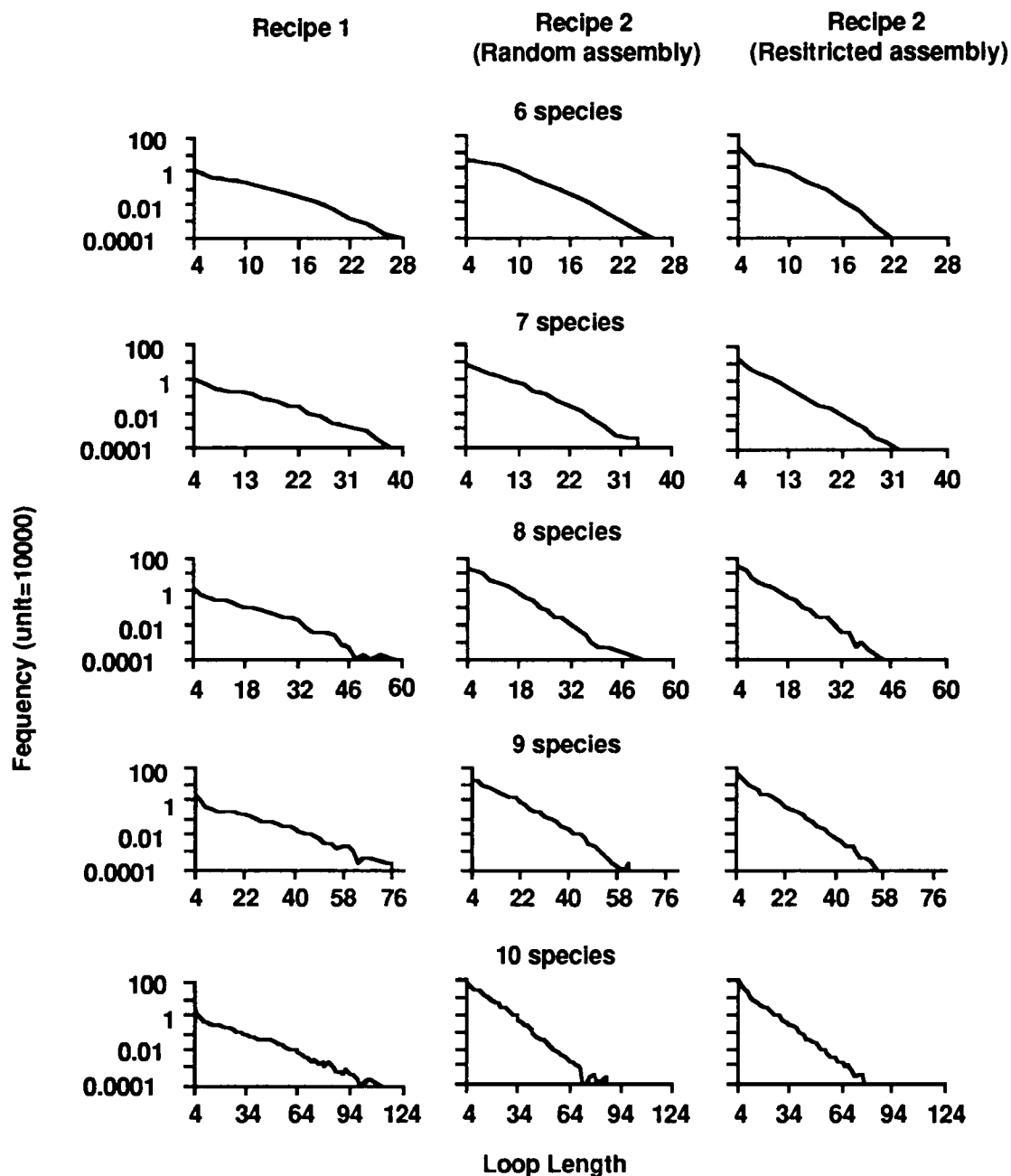


Figure 10. The frequency of loop lengths. These frequencies are from 100 assemblies of each of 100 different transition graphs.

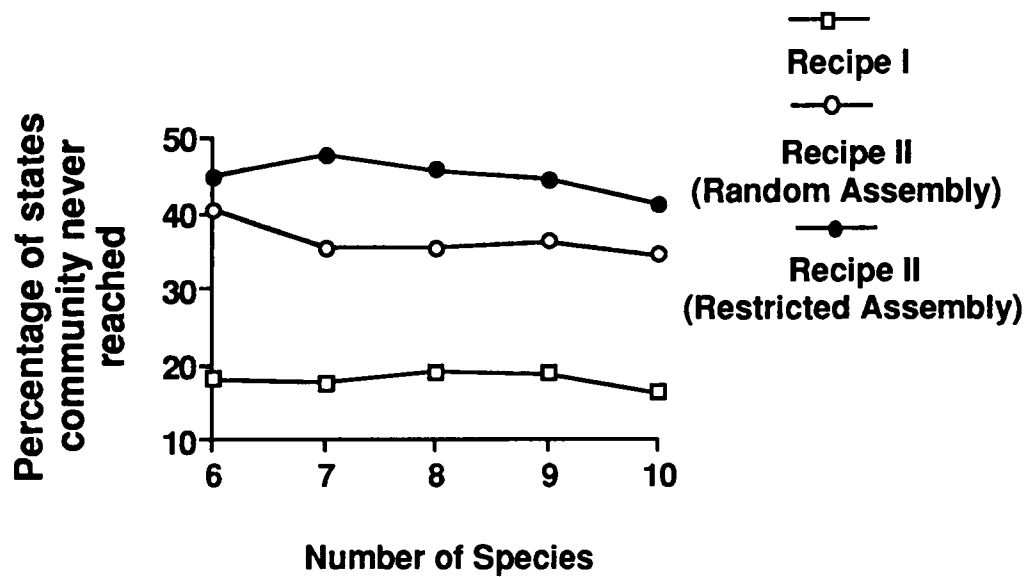


Figure 11. The percentages of community states that are attainable in theory, but which were not attained in 100 assembly simulations.

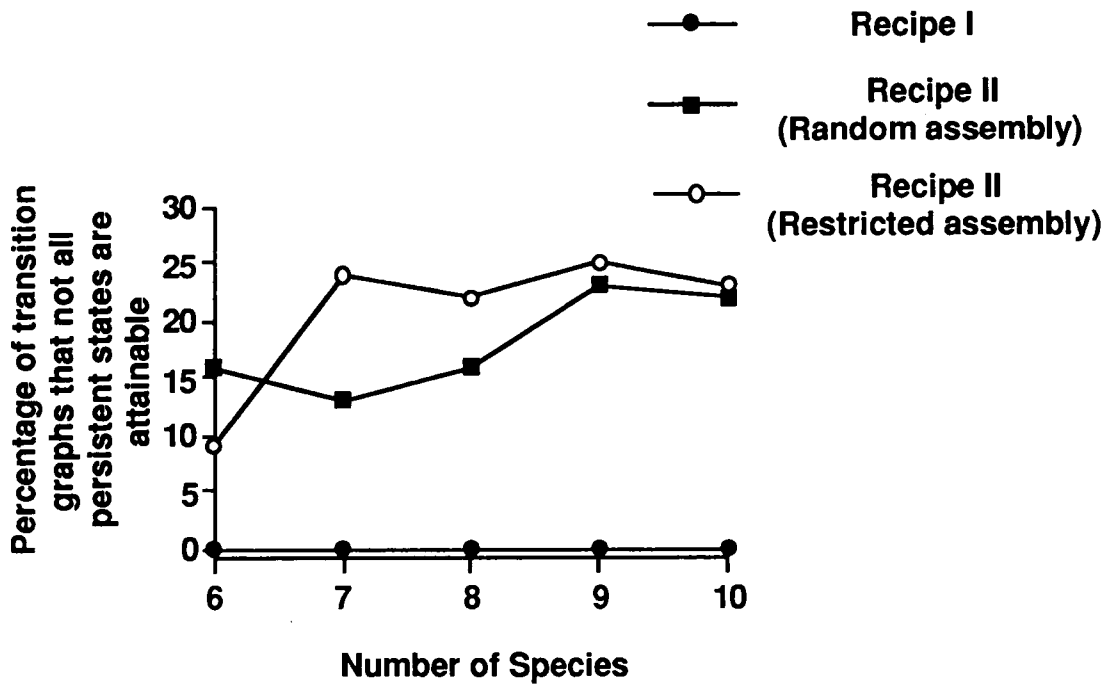


Figure 12. Percentage of transition graphs that the community can not reach all persistent states. These data are calculated from 100 graphs used to simulate community assembly.

**PART 4: PHYLOGENY, EVOLUTIONARY MODELS, AND  
COMPARATIVE METHODS: A SIMULATION STUDY**

## Introduction

Haldane (1938) wrote, "The analysis of interspecific differences is a prerequisite for any complete theory of evolution" (p. 79). The steady accumulation of comparative data and phylogenetic information along with greater understanding of the evolutionary process is testimony to this view. Nevertheless, with this knowledge comes an increasing awareness of what we do not know about comparative study. This is especially true in applications of the comparative method itself. Any comparative test of an ecological or evolutionary hypothesis requires an initial diagnosis of whether the data are statistically independent from phylogenetic relations (Felsenstein 1985; Harvey and Pagel 1991; Gittleman and Luh 1992). Although not guaranteed, phylogenetic relations are often found and therefore comparative methods are needed to account statistically for or partition out phylogenetic correlation prior to hypothesis testing. At least seven methods are currently available to carry out this task; detailed descriptions and applications of these methods are available elsewhere (for review, see Harvey and Pagel 1991; Gittleman and Luh 1992). The purpose of this paper is to investigate, by quantitative simulation, the extent to which the comparative methods themselves might influence comparative findings.

We chose two methods, independent contrasts and autoregression, for simulation tests. These methods are used not because of their superiority over others but because of inherent analytical differences, thus perhaps exposing the range of effects, and their common use in the literature. The basic ideas behind each method are as follows.

The independent contrasts method derives from a model by Felsenstein (1985, 1988) that suggests calculating contrasts between pairs of species at each bifurcation in

a phylogeny. Because these contrasts are at each node which link species that share an immediate common ancestry, essentially this is removing phylogenetic heritage and creating values that represent *independent* evolutionary events. If two traits are correlated (e.g. population density and body size), then a large calculated contrast with one trait at a given node should be associated with a large contrast in the other. As Felsenstein originally stated, a known phylogeny is central to using the independent contrasts method. Unfortunately, phylogenetic information is often lacking and therefore an estimation must be made. Two general approaches may be taken. First, when ancestral values are unknown but branch length information is available, the equation

$$X_k = \frac{\sum_{i=1}^m \left( \frac{1}{v_i} \right) X_i}{\sum_{i=1}^m \left( \frac{1}{v_i} \right)}$$

may be used to estimate ancestral nodes, where  $X_i$  are trait descendants,  $v_i$  are branch lengths, and  $m$  is the number of descendants (Pagel 1992). Second, when both branch lengths and ancestral values are unknown (i.e. the current state of affairs in many, if not most, comparative studies that must rely on species trait values and systematic information based on taxonomic rank), evolutionary change may be assumed to follow a punctuational model in which trait evolution only occurs at a node. Since the variance of change is unrelated to branch length, all branches are equal to each other (Harvey and Pagel 1991). In other words, the estimated ancestral node is the mean of its descendants. The independent contrasts method has been usefully applied to a wide variety of problems (e.g. locomotor morphology in lizards: Losos 1990; metabolic rate and life histories in birds: Trevelyan, et. al., 1990; sperm competition in birds: Moller

1991; see also Harvey and Pagel 1991; and a computer version is easily employed, see Purvis 1991). Fundamental features of the technique are that it (1) equally weights each (independent) evolutionary event; (2) explicitly uses phylogenetic (branch length) information for calculating expected contrast variances according to some model of evolution (e.g. gradual); and, (3) uses all of the variation in traits throughout a phylogeny rather than partitioning certain phylogenetic and nonphylogenetic components, as in autoregression (see below).

The autoregressive approach is based on a method developed by Cheverud, Dow and Leutenegger (1985) that considers trait variation in terms of a phylogenetic component and a specific component. The reasoning behind such trait division is based on similar models of quantitative genetics where phenotypic values are considered as additive genetic and environmental values. The statistical properties of Cheverud et.al's technique is derived from the autocorrelation literature for analyzing problems of spatial pattern. For comparative study, the method takes the form:

$$y = r Wy + e$$

with **W** an  $n \times n$  weighting matrix. The vector **y** of standardized trait values takes the linear combination  $r Wy$  as its phylogenetic component and the residual vector  $e$  at its specific component. The autocorrelation coefficient,  $r$ , measures the correlation between the phenotypic trait vector **y** and the purely phylogenetic value **Wy**. The residual  $e$  depicts the independent (adaptive) evolution of each species. Empirical examples of the autoregressive approach include studies of body size sexual dimorphism in primates (Cheverud, et. al., 1985; Ely and Kurland 1989), brain size and life history patterns in carnivores (Gittleman 1991; Gittleman 1992), and ornament dimorphism in birds (Bjorklund 1990). A macro- or microcomputer version of the

method is available from us. Basic features of this method are that it (1) calculates values for each taxonomic unit (typically species) under study; (2) retains flexibility to match systematic information (either taxonomic ranks or phylogenetic trees) with phenotypic similarity, particularly when applying a maximum likelihood procedure (Gittleman and Kot 1990) and (3) assumes an autoregressive statistical process whereby comparative data are correlated with phylogeny and this correlation tends to fall-off with phylogenetic distance (Gittleman & Luh, 1992). As stipulated in the spatial processes literature (Cliff and Ord 1981; Upton and Fingleton 1985), autoregressive methods assume some correlation in the data and are designed to remove it. If phylogenetic correlation is not apparent, then the autoregressive method is likely to make errors. Therefore, a prerequisite for using the autoregressive method for comparative problems is diagnosing phylogenetic correlation in the data (Gittleman and Kot 1990).

Both the independent contrasts and autoregressive methods involve particular kinds of data in comparative tests. These include quantitative (or continuous) traits, systematic information either in the form of taxonomic rank or phylogenetic trees, levels of correlation between traits and phylogeny, and rate of trait evolution through phylogenetic time. The certainty of these comparative characteristics vary from empirically-observed factors as with sample size or phylogenetic correlation of traits to venturing into the unknown with evolutionary rate. Understanding the impact of these factors on the effectiveness of our methods is critical. For example, evolutionary models are essential for testing comparative hypotheses (see Harvey and Pagel 1991; Harvey and Ourvis 1992), yet we rarely know anything about them for specific traits. The aim of the following simulations, therefore, is to investigate relative differences in

results from each comparative method as contingent on how the methods use different kinds of comparative information.

## Methods

Our simulation studies involve a three-stage process: (1) creating different phylogenetic topologies; (2) simulating trait evolution along each phylogeny; and (3) using the simulated phylogenies and associated traits to test the robustness of each comparative method. The general sequence of these simulations is similar to Martins & Garland (1991), however, various methodological details are different so as to reflect more realistic comparative problems (see also Gittleman and Luh 1992).

### Phylogenetic trees

The simulated phylogenetic topologies used in this study are generated by random joining (Maddison and Slatkin 1991). Given a number of species, each simulation begins with the lowest taxa (i.e. species) and randomly groups taxa to form larger taxa in the next higher levels (i.e. genera) until only one taxon is formed. A random joining tree only provides information about the hierarchical taxonomic rank among species, genera, families, etc. It does not show the evolutionary distance between nodes. To generate random *phylogenetic trees*, we simply use the above taxonomic ranks and assign a random number to each branch as its length. One restriction is necessary for generating phylogenies: branch lengths between higher nodes must be longer than the branch lengths between lower nodes. This assumption is, however, suitable for either comparative method. In autoregression, it is assumed that nodes nearer to one another are more closely related. In the independent contrasts,

based on a Brownian motion model, the expected variance along a branch is related to its length; thus a contrast between higher nodes will have a higher variance than a contrast between lower nodes.

From the simulations of phylogenetic trees we first construct three sets of phylogenies which comprise 10, 50 and 90 species respectively. For each sample size, we generate 50 different trees.

In contrast to Martins & Garland (1991), we simulated multifurcating rather than bifurcating phylogenies. Multifurcating (or polytomic) trees were used because they more closely reflect the type of phylogenetic information typically available in the systematic literature, both from taxonomic rankings or phylogenetic trees. This issue is fundamental in comparing comparative methods. The independent contrasts method calculates data values at each node in a tree rather than per species. As mentioned in the 'Introduction', Pagel (1992) (see also Purvis 1991 for implementation) presents a model for calculating contrasts from unresolved trees which essentially expands multiple branches from a node into two sub-groups. These contrasts, as determined from the number of nodes in a tree, are then used for hypothesis testing and for setting appropriate degrees of freedom. Thus, with multifurcations, the independent contrasts method will retain fewer analyzable values than the original (species) sample size. By comparison, autoregression calculates data values for each species, thus providing  $n - 2$  degrees of freedom. Obviously, such disparate procedures for statistical tests will influence results between the two comparative methods. Rather than preset degrees of freedom in our simulations, we chose to calculate them according to typical systematic conditions (i.e. unresolved multifurcating trees) observed in comparative studies.

Further simulation work is currently investigating the degrees of freedom issue by setting the number of nodes in bifurcating trees (Purvis, et. al., 1993).

### **Trait evolution and evolutionary models**

Evolutionary changes of two continuous (quantitative) traits can be viewed as two random variables drawn from a bivariate normal distribution. The pattern of evolutionary change is determined by parameters of the probability distribution. The mean of each variable indicates the net change of evolution in each trait. The correlation of the bivariate distribution shows the general relationship of two traits changing along a tree. All simulations of trait evolution assume that the two random trait changes are drawn from a bivariate normal distribution with means of zero (i.e. the evolutionary changes are neutral) and a correlation of zero (see Figure 1).

Evolutionary models determine the way that traits evolve along the phylogeny (Martins and Garland 1991; Gittleman and Luh 1992). In this study we used two evolutionary models - gradual and punctuational. If simulated trait evolution follows a gradual manner, random trait change occurs at each time step (i.e. an arbitrary time scale) along the branch (see Figure 2a). If simulated trait evolution follows a punctuational manner, random trait change only occurs at the splitting from a node (i.e. the speciation events) and branch lengths are not involved (see Figure 2b). One simulation was structured as if there were no evolutionary model. In this case (see Figure 2c), trait values are randomly placed on the tips with no evolutionary structure in relation to branches or nodes, as in the other evolutionary models. This case is also meant to represent the condition of no phylogenetic correlation of traits (i.e. no relation between trait variation and phylogenetic structure), a condition verified by descriptive

statistics (see below). It should be pointed out that in Martins & Garland's (1991) study, a simulated "star" phylogeny was used to reflect no phylogenetic correlation. Branch lengths were extended to increase independence among contemporary tip species. Variance of the traits, however, remained proportional to the branch lengths. Therefore, *some* phylogenetic correlation was likely.

All trait simulations began at the initial base node (i.e. the original ancestor). We assigned two random numbers as two trait values of that ancestor, then random evolutionary changes were continuously added to the previous trait value until trait values of species (i.e. tips on the phylogeny) were obtained. For the gradual model of evolutionary change, the number of changes along any branch is proportional to that branch length (see Figure 2a). Therefore, each offspring derived from one particular ancestor not only receives a copy of that ancestor's trait values but also the total evolutionary changes along the branch derived from the ancestor. For the punctuational model of evolutionary change (see Figure 2b), the number of evolutionary changes is the number of speciation events from one ancestor. Each branch has only one trait change. The trait value of offspring is the summation of ancestor's trait value and one trait change.

For each simulated phylogeny, 50 sets of two traits are generated.

### **Simulated comparisons**

Given the above protocols, simulations involve three comparative problems which reflect various conditions and availability of information (see Table 1). (1) No evolutionary model is involved in the simulation of trait evolution. That is, no evolution occurs along the phylogeny: two sets of trait values are simply placed on the

tips of phylogenies as representing the trait values of species. (2) Trait evolution follows a punctuational model of evolutionary change. (3) Trait evolution follows a gradual model of evolutionary change. For each condition, comparative methods use either of two kinds of systematic information to analyze the simulated data, taxonomic ranks or phylogenies with branch length information

### **Statistical analysis**

*Descriptive statistics in autoregressive method.* To investigate whether and the degree to which descriptive statistics (i.e. Moran's  $I$ ) are necessary for using the autoregressive method, we compare the effects of comparative tests from autoregression with and without applying Moran's  $I$  statistics. For testing the autoregressive method without using a Moran's  $I$ , we simply apply the method regardless of whether or not simulated traits are phylogenetically correlated. In other words, all phylogenetic information is involved in the comparative test. In contrast, with applying Moran's  $I$ , a series of  $I$ 's are calculated at different taxonomic levels and then plotted on a graph (a phylogenetic correlogram) to show where autocorrelation varies with taxonomic listing or phylogenetic distance. Four criteria are applied to the phylogenetic correlogram to detect the extent and location of phylogenetic correlation (see Gittleman and Kot 1990 for details of this statistical procedure).

- (1) At least one of the  $z$  values is greater than 1.96 (i.e., observed phylogenetic autocorrelation at  $p < 0.05$ ).
- (2) The correlation coefficient in the correlogram must be less than -0.5, indicating a negative (autoregressive) slope.

(3) Cutoff distance is set when  $z$  values drop to negative (i.e., data are not filtered through the method when uncorrelated).

(4) No  $z$  values which are below the cutoff distance are above 1.96.

In essence, these criteria permit a more effective application of the autoregressive method because it detects the level and location of phylogenetic correlation. Consequently, there is appropriate determination of what phylogenetic information to involve in a comparative test.

*Statistical comparisons of methods.* Two approaches are adopted for comparing comparative methods. First, to assess general patterns, frequency distributions are examined of bivariate correlation coefficients in each of the three evolutionary conditions. Second, to evaluate statistical power, observed differences in significance tests of correlation (rate of Type I error) are compared. Because of the different calculations of the degrees of freedom in both comparative methods, it is impossible to compare the robustness of two methods according to the frequency distributions. With independent contrasts, correlation is computed from contrasts at each node, so the degrees of freedom are set according to the number of nodes rather than total sample size. Conversely, with the autoregressive model, degrees of freedom are determined by the number of species. For each of different evolutionary models and different phylogenetic information, we count the number of correlation coefficients out of 2500 simulations which are significant at the 0.05 level (two-tailed  $t$ -test with different degrees of freedom).

## Results

We report results of simulations in two forms. (1) General frequency distributions for each evolutionary model, using taxonomic or phylogenetic information, after applying the independent contrasts or autoregressive methods; (2) Statistical (Type I) error rates for the same conditions.

The general frequency distributions of each comparative method are shown against the null distribution, i.e., a normal distribution around a mean of 0.0. In general, when traits are evolving with an *assumed* evolutionary model, then the variance of the frequency distribution will be wider as expected by the traits evolving on a phylogeny, either along branches (gradual model) or nodes (punctational model). In each figure we also present the distribution represented by analyzing the species tips so as to designate the degree to which phylogenetic correlation is removed.

Prior to examining simulation results, it is important to assess whether the general condition of phylogenetic correlation is fulfilled. Moran's *I* statistics revealed that, out of 2,500 simulations for each condition, the percentage of significant correlation is only found in 0.72-4.84 cases in comparison to the phylogenetically correlated assumption in which 22.2-85.68 cases were significant with phylogeny (Table 2). Thus, the assumption of phylogenetic correlation is satisfied.

*Independent contrasts.* In the first condition, with no evolutionary model (i.e., no phylogenetic correlation), the null distribution represented by species tips has a small variance, as expected given there is no phylogenetic correlation and an input (bivariate) correlation of 0.0 (Figure 3). With small sample size ( $n = 10$ ), the independent contrast does a relatively poor job with both taxonomic rank and phylogenetic tree information. With larger samples ( $n = 50$  or  $90$ ), contrasts appear to yield better results. Overall,

though, it is important to recognize that in this situation with no phylogenetic correlation, the contrasts method does not seem to perform as well as species tips correlation. Assuming a punctuational model (Figure 4) we first observe more variance in the overall distribution owing to phylogenetic correlation, as we expected (i.e., the traits are evolving in relation to the nodes on a given tree); also, note the greater variance in small samples owing to the relatively unstable situation of correlations with few data points. Thus, we are comparing how well the contrasts method removes this correlation and reveals the *real* (null) distribution (i.e., a mean of 0.0). In each case, except possibly with the small sample size of 10 species, the contrast method produces acceptable results. The independent contrasts method also appears to yield more acceptable error rates with taxonomic rank rather than phylogenetic tree information. Assuming a gradual model (Figure 5), the frequency distributions again have a wide variance when phylogenetic correlation exists. The contrasts method also performs well, removing phylogenetic correlation and revealing the null distribution. However, in contrast to the punctuational condition, systematic information with phylogenetic trees appears to yield better results.

In Table 3 we present Type I error rates for each of the above frequency distributions. Results are given in relation to an alpha equal to 0.05, the error rate of the null distribution and standard of comparison. However, because our primary purpose in these simulations is to examine *relative* error rates in relation to different conditions and given sample sizes are extremely high, we are also interested in rates approximating the 0.05 level. For comparison, we also present the error rates for analyzing species tips.

A number of results are consistent with the patterns of frequency distributions. First, small sample sizes (<10 species) produce unacceptable error rates under all conditions. Second, when there is no phylogenetic correlation the independent contrasts only work (relatively) well with taxonomic ranks. Third, and perhaps most interestingly, the error rates between gradual and punctuational models emphasize the fact that independent contrasts are model-dependent, that is in terms of an evolutionary model. And, that the form of systematic information is tied to this model-dependence: In the punctuational model, when trait evolution relates to nodal change rather than branch lengths, taxonomic rank information elicits more acceptable error rates; conversely, under a gradual model where trait evolution relates to branch lengths, phylogenetic tree information elicits more acceptable error rates.

*Autoregression.* As stated, descriptive statistics (i.e., Moran's  $I$ ) are necessary *prior to* appropriately and effectively using the autoregressive method. Thus in the following simulation results we first show effects of comparative tests from autoregression without examining the data, as in the previous independent contrasts simulations. We then present results, after applying criteria from diagnostic statistics, which show relative effects of evolutionary models and different kinds of comparative information.

With general frequency distributions, the autoregressive method in the condition of no evolutionary model (or phylogenetic correlation) simply mimics the null distribution (Figure 6), with little effect from either sample size or kind of systematic information (i.e., taxonomic vs. phylogenetic). To an extent, these patterns are misleading because, as we will show in our statistical comparisons, the autoregressive method may generate some phylogenetic correlation from the null distribution. Under the punctuational model, the autoregressive method performs equally well with

systematic information based on either taxonomic ranks or phylogenetic trees (Figure 7). More importantly, though, the autoregressive technique performs better after the Moran's *I* criteria are applied: there is a greater frequency distribution around the mean of 0.0 after executing the diagnostic statistics. With the gradual model (Figure 8), as in the figures for the independent contrasts, the frequency distribution is wider due to increasing correlation between the traits as they evolve along the branches. The autoregressive method in the gradual condition performs about the same as with the punctuational model: different systematic information reveals similar patterns and application of the Moran's *I* is necessary for better results.

In Table 3 we present Type I error rates for each of the above frequency distributions. Results are given in relation to an alpha equal to 0.05, the error rate of the null distribution and standard of comparison; autoregressive performance is given with and without applying Moran's *I* criteria. For comparison, we also present the error rate of analyzing species tips. When the Moran's *I* criteria are *not* applied to the simulated data, the autoregressive method *only* provides acceptable error rates under the condition of no evolutionary model; in this case, systematic data either in the form of phylogenetic trees or taxonomic rank produce the same patterns. This is simply because there is little or no phylogenetic correlation at the tips (see above). But, even though error rates are acceptable, the autoregressive method generates higher error rates than in the original data unless the Moran's *I* is used.

Second, when the Moran's *I* criteria are applied and consequently non-phylogenetically correlated data sets are excluded from analysis, the autoregressive method generally removes correlation under any condition. It seems to perform best with smaller sample sizes ( $n = 10$  or  $50$ ) and under the condition of punctuational

evolution. The larger samples ( $N > 50$ ), especially with the gradual model, produce some degree of error.

## Discussion

### Comparing independent contrasts and autoregression: selecting a method

A comparative researcher is faced with making decisions about which comparative method to use based on the kind of information available. Comparing the *relative* results of these simulations with each method emphasizes this point. Thus we discuss the relative merits of each method in terms of information conditions:

(1) Sample size- When sample sizes are small ( $n < 10$ ), the autoregressive method will almost always yield better results, because of the method of calculating contrasts at each evolutionary event. If one must deal with small samples then autoregression is more appropriate. In general, though, comparative studies with such small samples are (probably) less likely anyway. With larger samples ( $n = 50$  or  $90$ ), selection of an appropriate method then depends on access of systematic data and/or evolutionary model.

(2) Taxonomic rank versus Phylogenetic tree information- Despite efforts to provide more accurate and detailed phylogenetic information, most comparative studies are still left with taxonomic rankings devoid of branch lengths. Given the current state of the art, both autoregression and independent contrasts yield acceptable rates within a punctuational framework. With the gradual model, autoregression may be more suitable with taxonomic data probably because of the maximum likelihood estimator.

With phylogenetic information containing branch lengths, the independent contrasts method performs best under a gradual model, and indeed outperforms the

autoregressive method. The reason for this may be that with real branch length information the autoregressive method overcompensates the phylogenetic component and therefore makes errors in estimating the true bivariate relationship. With branch length information but with a punctuational model of evolutionary change, an unrealistic scenerio, the autoregressive method is able to adjust to this situation.

(3) Evolutionary model- Deciding on an assumed evolutionary rate is guesswork in most comparative studies, thus it is difficult to draw conclusions of this factor based on access of real data. Nevertheless, assuming evolutionary rate is known, the independent contrasts is more appropriate with taxonomic rank information under a punctuational model and more appropriate with phylogenetic tree information under a gradual model. The autoregressive method is essentially model-independent in an evolutionary sense.

General results and conclusions of this study are summarized in a flow chart (Figure 9) to aid in selecting an appropriate comparative method given different conditions of comparative tests. None of these guidelines are uncontroversial. Ironically, one of the most difficult decisions is what to do when there is no phylogenetic correlation. Our simulations suggest that it is probably (statistically) acceptable to simply analyze species tips; under similar conditions (Table 6), Martins & Garland (1991) concur. Even so, there might be reasons for still applying a comparative method. For example, if there are *a priori* assumptions for phylogenetic correlation with a particular trait or if phylogenetic information is extremely questionable such that a comparative method should be employed alongside species analysis to assess statistical error. Furthermore, suggestions based on our simulations do not consider effects of topology on selecting appropriate comparative methods.

Even more essential is the unknown of evolutionary model. Few traits are understood well enough to specify a mode of evolutionary rate. Nevertheless, as our simulations and others clearly show, the assumption of evolutionary models is essential for carrying out correct comparative analysis. Perhaps we are now at least understanding the real difficulty in satisfying Haldane's claim for comparative study being a prerequisite to a complete theory of evolution.

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Table 1. Condition for simulating comparative methods.

| Condition                   | Model                    | Systematic Information |
|-----------------------------|--------------------------|------------------------|
| No phylogenetic correlation | None (random)            | Taxonomy/Phylogeny     |
| Phylogenetic correlation    | Gradual or Punctuational | Taxonomy               |
| Phylogenetic correlation    | Gradual or Punctuational | Phylogeny              |

Table 2. Percentage of cases in which significant phylogenetic correlation was detected using the Moran's I statistics.

| Evolutionary<br>Models | Sample<br>Size | Trait A | Trait B |
|------------------------|----------------|---------|---------|
| No model               | n=10           | 4.84    | 1.48    |
|                        | n=50           | 3.20    | 0.72    |
|                        | n=90           | 3.32    | 0.84    |
| Punctuational          | n=10           | 31.52   | 22.20   |
|                        | n=50           | 80.56   | 81.36   |
|                        | n=90           | 84.28   | 83.84   |
| Gradual                | n=10           | 47.52   | 38.80   |
|                        | n=50           | 81.40   | 81.60   |
|                        | n=90           | 84.16   | 85.68   |

Table 3. Statistical results of comparing independent contrasts and autoregressive methods. Comparative results are reported as relative rates of Type I error ( $\alpha = 0.05$ ). Comparing error rates are given for species tips analysis and second for the comparative method. For autoregression, values are given without and then with using Moran's I.

| Evolutionary Models | Comparative Methods  | Sample Size (d.f.) | Systematic Phylogeny | Information Taxonomy |
|---------------------|----------------------|--------------------|----------------------|----------------------|
| No model            | Independent Contrast | n=10(2-7)          | .064/.131            | .064/.075            |
|                     |                      | n=50(11-34)        | .048/.112            | .048/.057            |
|                     |                      | n=90(21-56)        | .035/.111            | .042/.0608           |
|                     | Autoregressive       | n=10(8)            | .064/.090/.037       | .064/.090/.037       |
|                     |                      | n=50(48)           | .048/.051/.048       | .048/.050/.048       |
|                     |                      | n=90(88)           | .035/.036/.036       | .042/.044/.044       |
|                     | Independent Contrast | n=10(2-7)          | .138/.093            | .138/.077            |
|                     |                      | n=50(11-34)        | .292/.080            | .292/.049            |
|                     |                      | n=90(21-56)        | .349/.089            | .349/.065            |
| Punctuational       | Autoregressive       | n=10(8)            | .138/.091/.042       | .138/.090/.042       |
|                     |                      | n=50(48)           | .292/.085/.048       | .292/.091/.048       |
|                     |                      | n=90(88)           | .349/.084/.061       | .351/.099/.060       |
|                     | Independent Contrast | n=10(2-7)          | .227/.065            | .227/.111            |
|                     |                      | n=50(11-34)        | .384/.050            | .384/.100            |
|                     |                      | n=90(21-56)        | .417/.069            | .417/.100            |
|                     | Autoregressive       | n=10(8)            | .227/.114/.047       | .227/.120/.047       |
|                     |                      | n=50(48)           | .384/.121/.073       | .384/.125/.073       |
|                     |                      | n=90(88)           | .417/.095/.074       | .430/.121/.073       |
| Gradual             | Independent Contrast | n=10(2-7)          | .227/.065            | .227/.111            |
|                     |                      | n=50(11-34)        | .384/.050            | .384/.100            |
|                     |                      | n=90(21-56)        | .417/.069            | .417/.100            |
|                     | Autoregressive       | n=10(8)            | .227/.114/.047       | .227/.120/.047       |
|                     |                      | n=50(48)           | .384/.121/.073       | .384/.125/.073       |
|                     |                      | n=90(88)           | .417/.095/.074       | .430/.121/.073       |

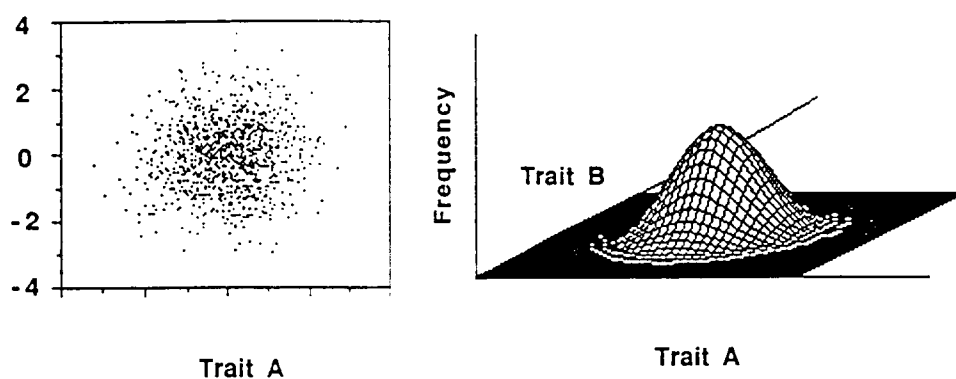


Figure 1. Illustration of simulated random traits A and B (left). Frequency of bivariate correlations are normally distributed with a mean of 0.0 (right).

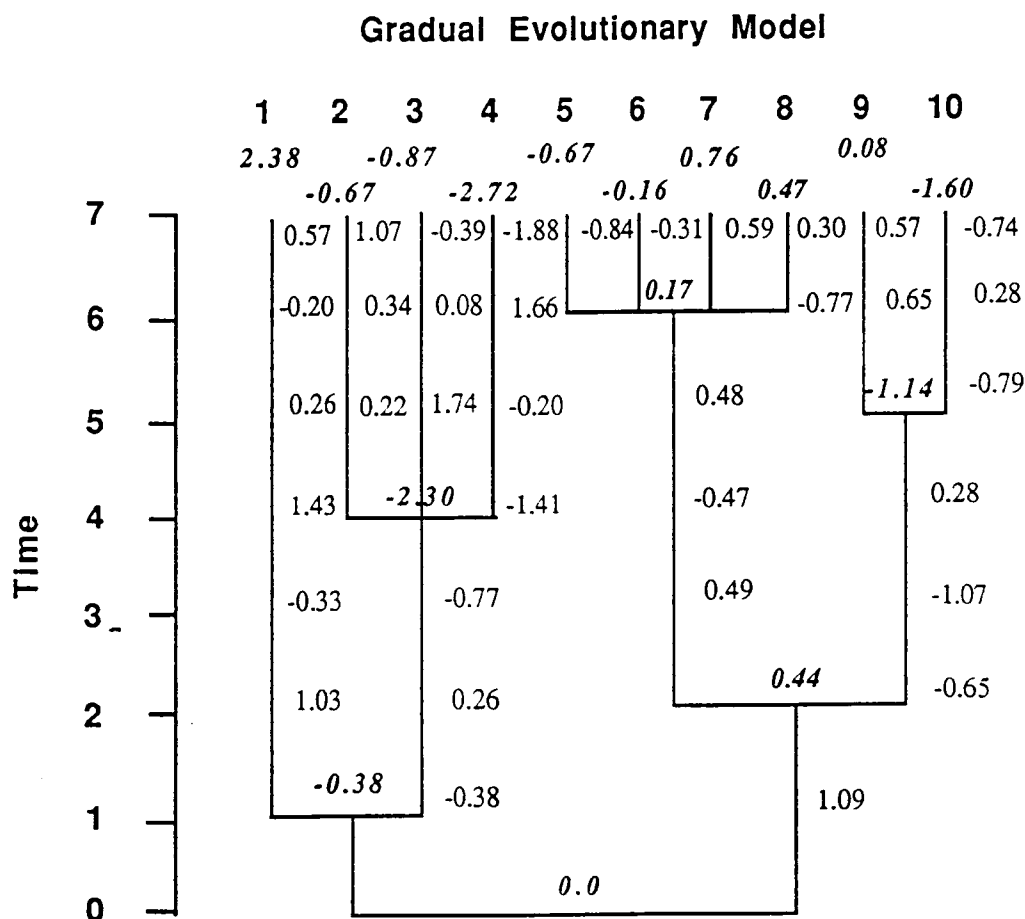


Figure 2. Three simulated evolutionary conditions for examining comparative methods. (a) Gradual evolutionary model where traits evolve in proportion to branch lengths; (b) Punctuational evolutionary model where traits evolve in relation to speciation events occurring at nodes; (c) No evolutionary model (also designates no phylogenetic correlation) where trait values are placed on species tips and not allowed to evolve along a phylogeny.

Figure 1 is a dendrogram illustrating the hierarchical clustering of 10 variables. The variables are numbered 1 to 10 at the top. The dendrogram structure shows the following fusion points (values in parentheses): (1, 2) at -0.58, (3, 4) at -1.54, (5, 6) at 0.67, (7, 8) at 2.16, (9, 10) at 1.74, ((1, 2), 3) at -0.08, ((5, 6), 7) at 1.26, ((9, 10), 8) at 1.87, ((1, 2, 3), 4) at -3.03, ((5, 6, 7), 8) at 1.57, ((9, 10), 6) at 1.37, ((1, 2, 3, 4), 5) at -0.77, ((5, 6, 7, 8), 9) at 0.48, ((1, 2, 3, 4), 5) at -0.38, ((5, 6, 7, 8), 9) at 1.09, and finally all variables at 0.0.

119

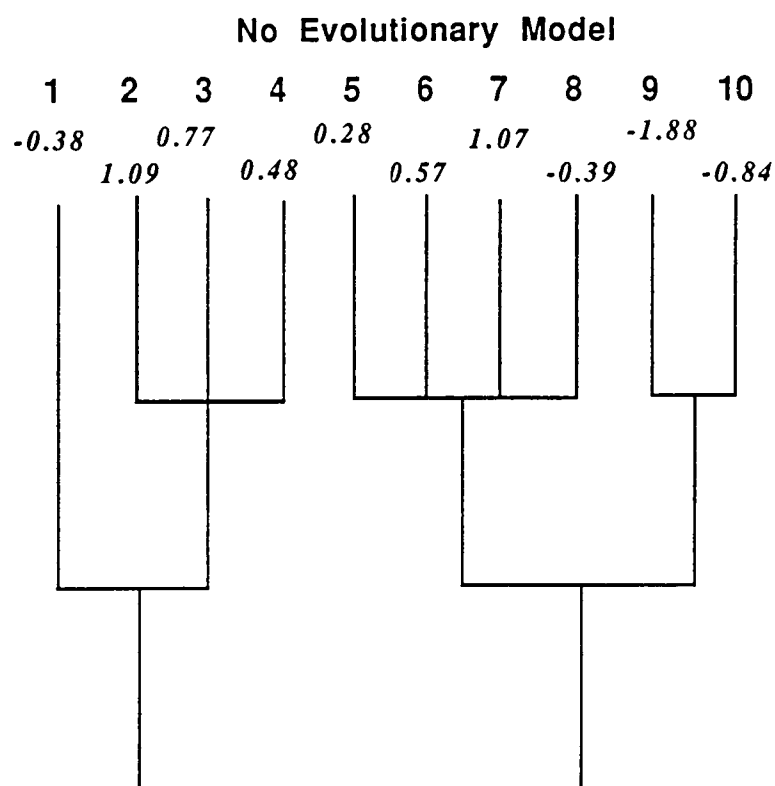


Figure 2c.

## INDEPENDENT CONTRASTS METHOD

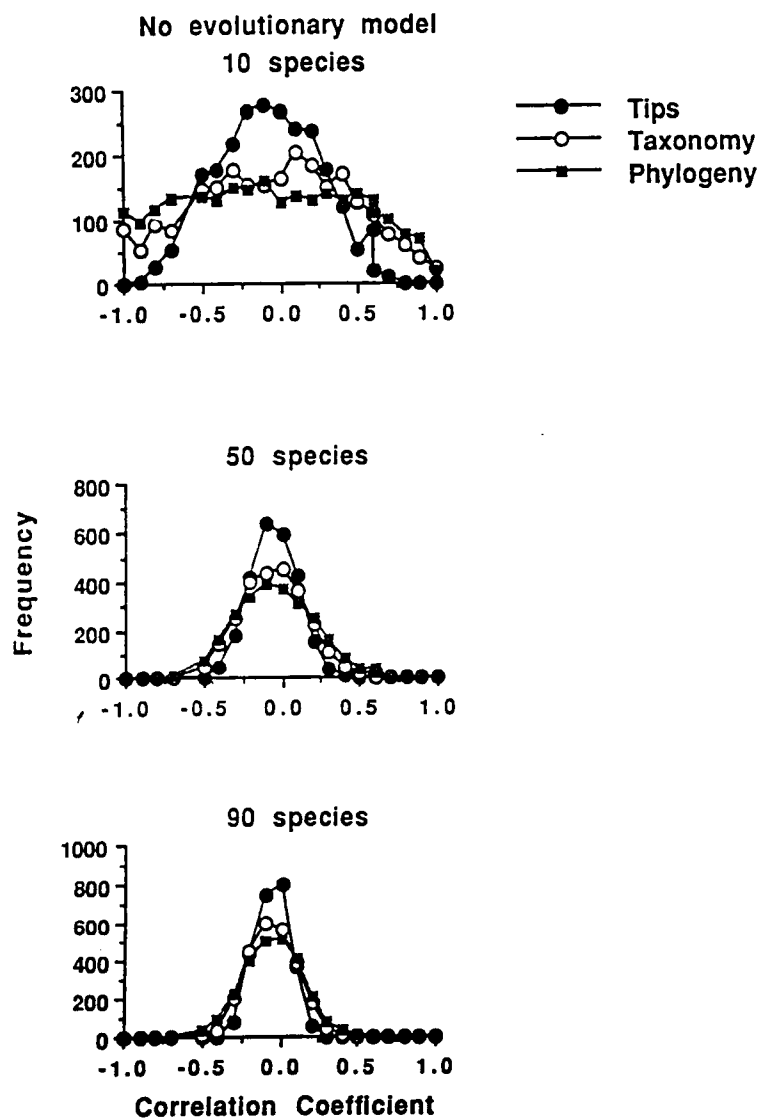


Figure 3. The independent contrasts with no evolutionary model. Assuming no evolutionary model of trait change, results of frequency distributions of bivariate correlations using the independent contrasts method on different sample sizes and systematic information. The null distribution of species tips is also shown.

## INDEPENDENT CONTRASTS METHOD

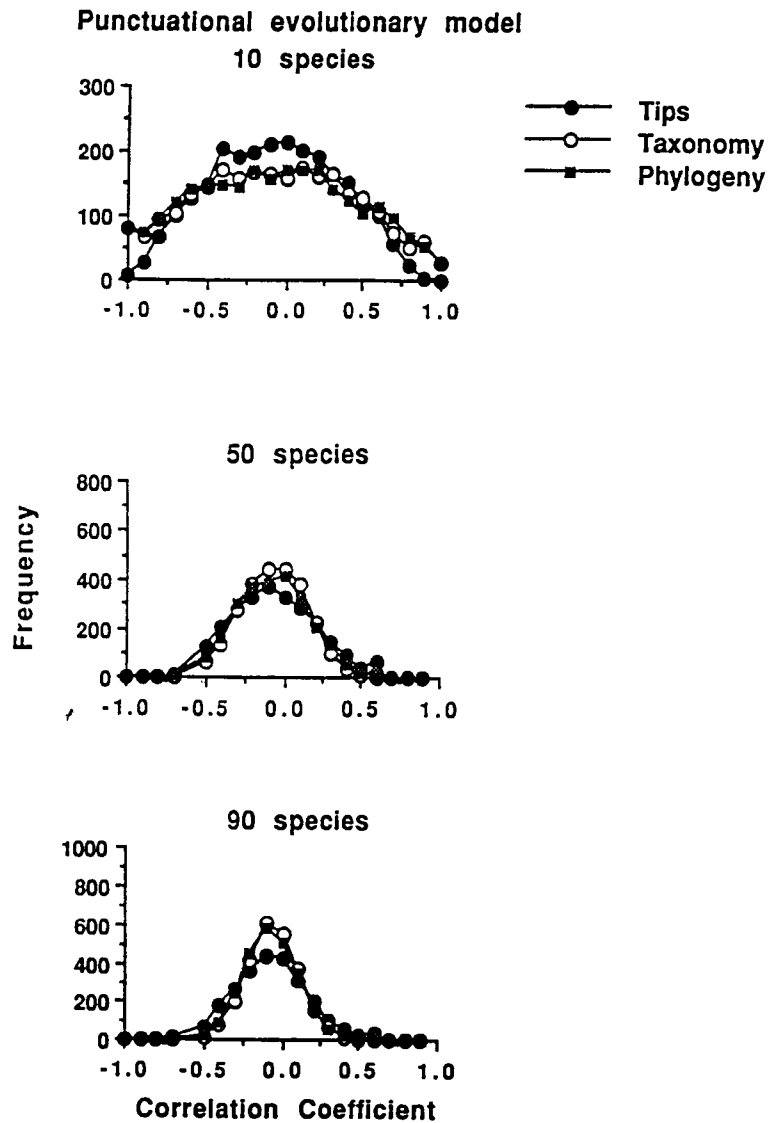


Figure 4. The independent contrasts with punctuational evolutionary model. Assuming a punctuational evolutionary model, results of frequency distributions of bivariate correlations using the independent contrasts method on different sample sizes and systematic information. Comparable values are shown for analyzing species tips data.

## INDEPENDENT CONTRASTS METHOD

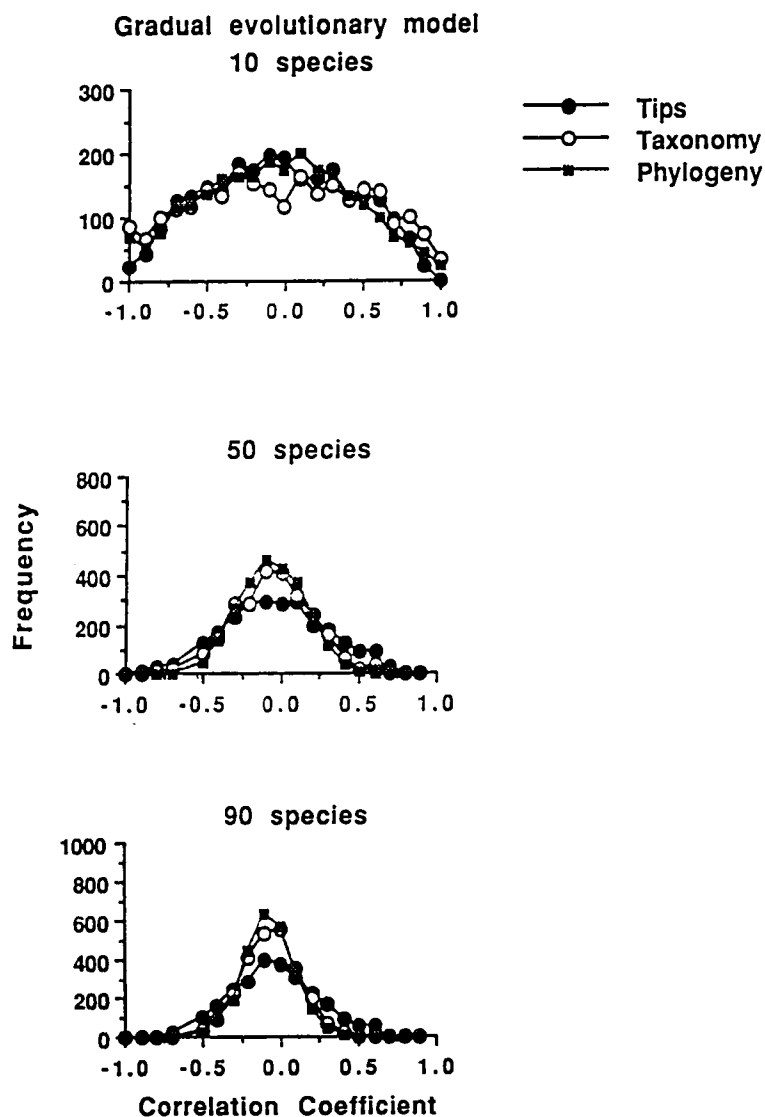


Figure 5. The independent contrasts with gradual evolutionary model. Assuming a gradual evolutionary model, results of frequency distributions of bivariate correlations using the independent contrasts method on different sample sizes and systematic information. Comparable values are shown for analyzing species tips data.

## AUTOREGRESSIVE METHOD

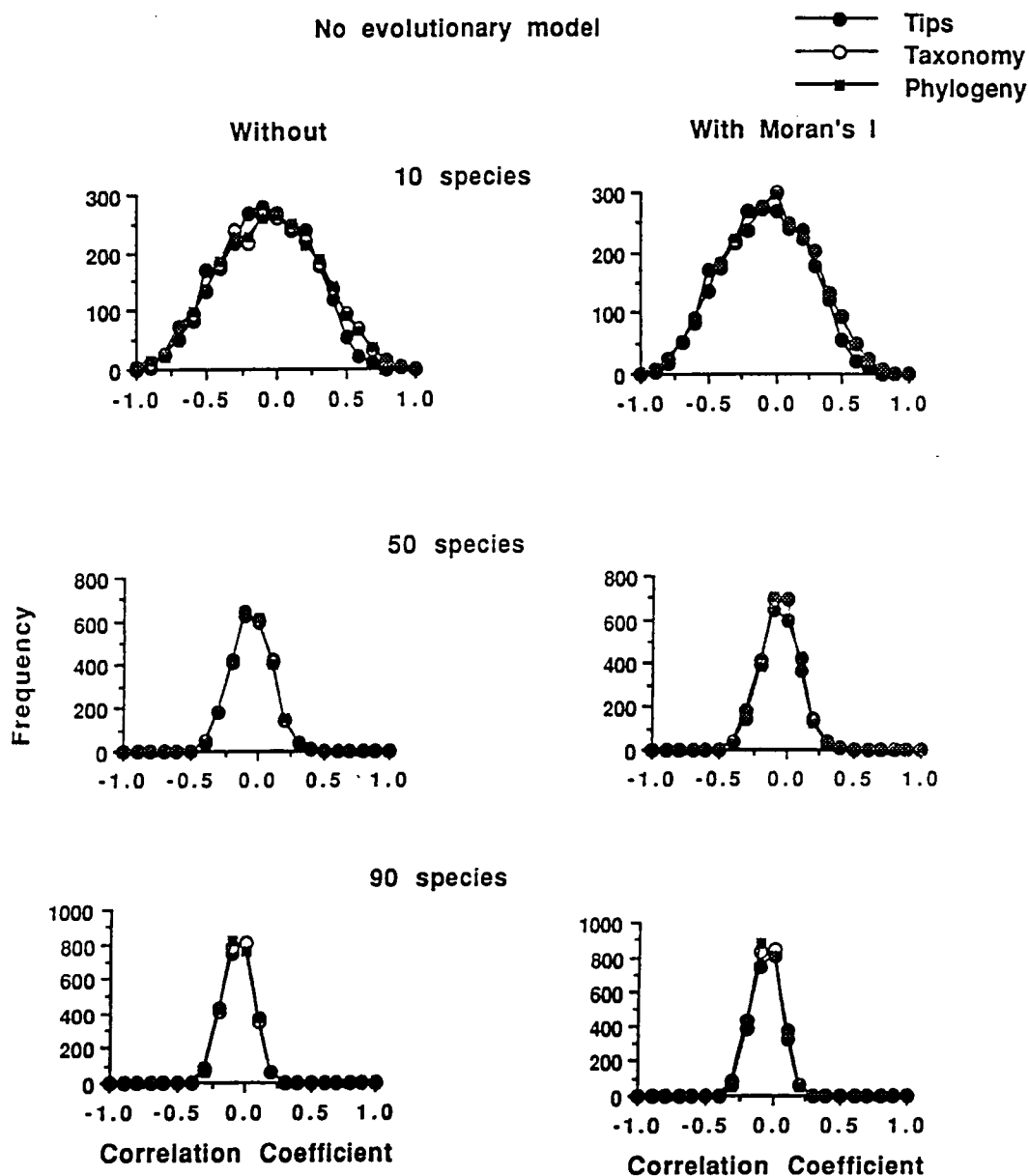


Figure 6. The autoregressive methods with no evolutionary model. Assuming no evolutionary model of trait change (i.e., no phylogenetic correlation), results of frequency distributions of bivariate correlations using the autoregressive method on different sample sizes and systematic information. Results are given with (right) and without (left) applying the Moran's I statistics and cut-off criteria (see text). The null distribution of species tips is also shown.

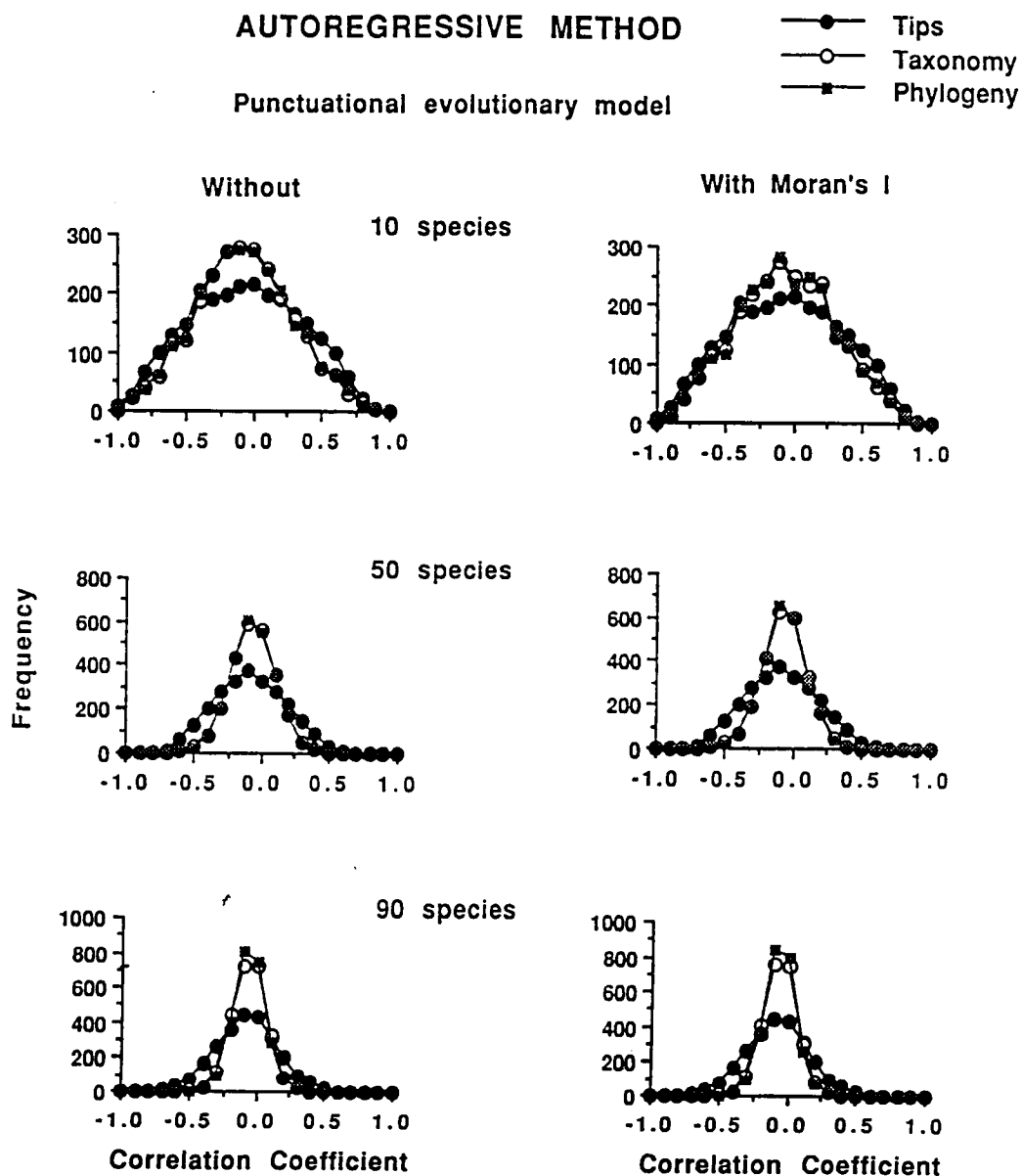


Figure 7. The autoregressive methods with punctuational evolutionary model. Assuming a punctuational evolutionary model, results of frequency distributions of bivariate correlations using the autoregressive method on different sample sizes and systematic information. Results are given with (right) and without (left) applying the Moran's I statistics and cut-off criteria (see text). Comparable values are shown for analyzing species tips data.

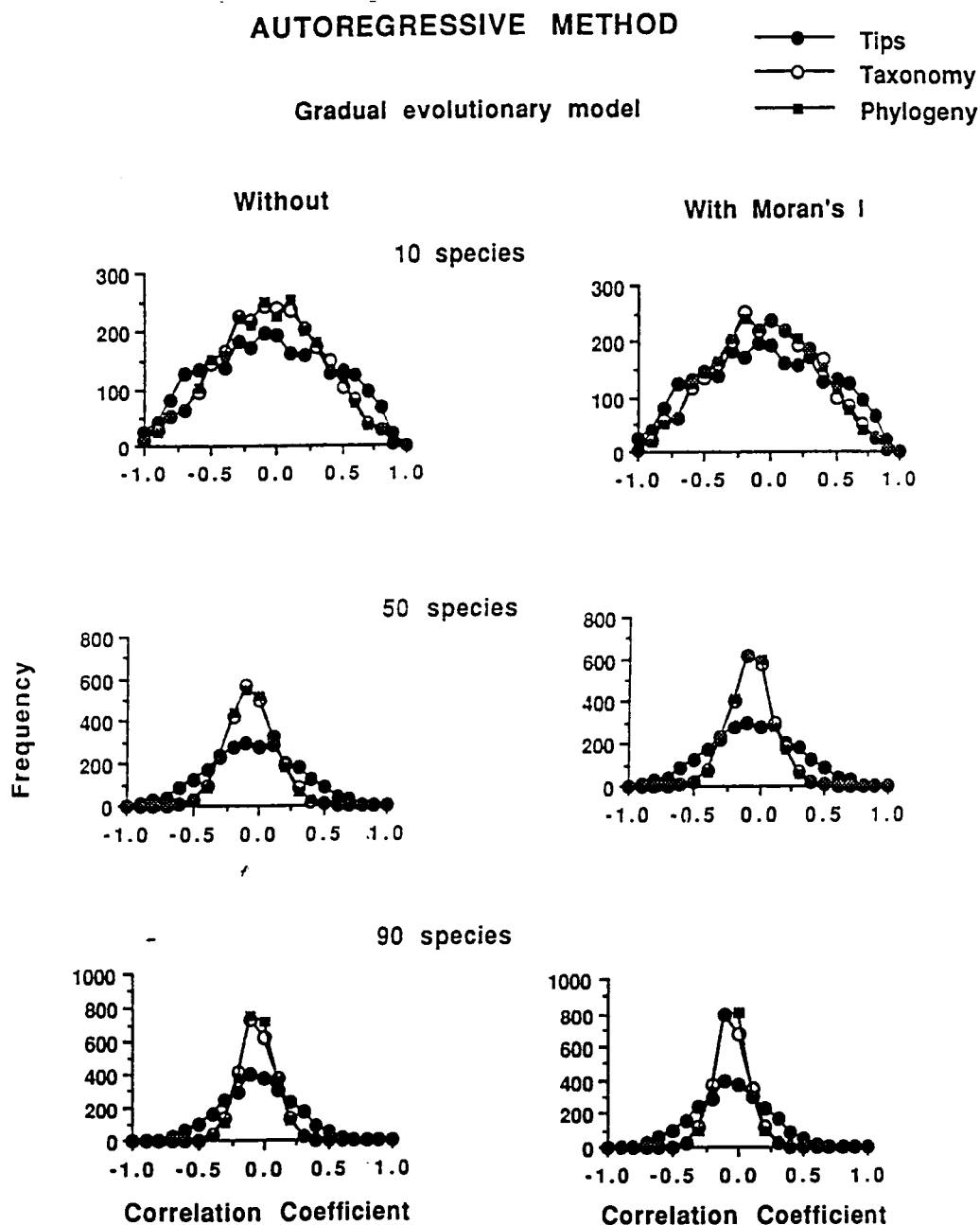


Figure 8. The autoregressive methods with gradual evolutionary model. Assuming a gradual evolutionary model, results of frequency distributions of bivariate correlations using the autoregressive method on different sample sizes and systematic information. Results are given with (right) and without (left) applying the Moran's I statistics and cut-off criteria (see text). Comparable values are shown for analyzing species tips data.

## GUIDELINES FOR SELECTING A COMPARATIVE METHOD

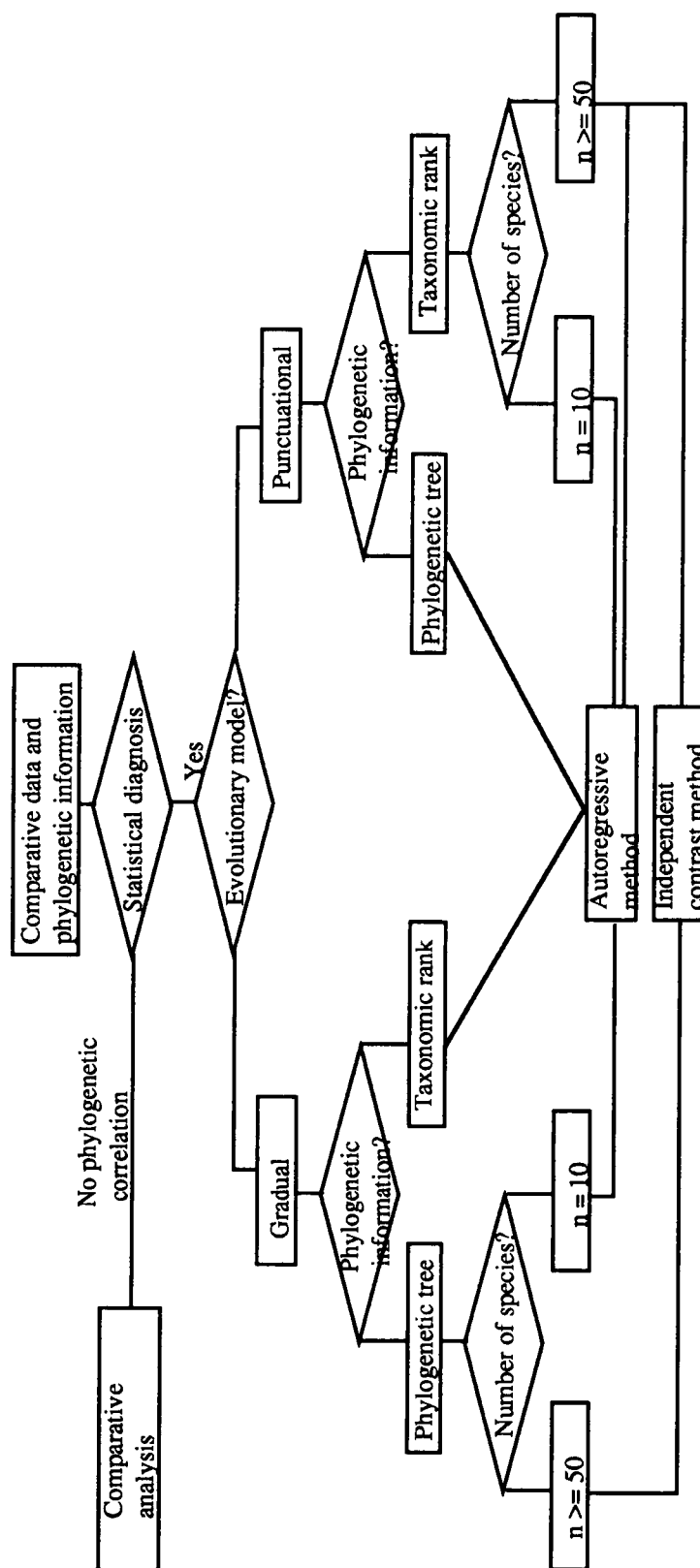


Figure 9. Flow diagram representing various comparative conditions and associated decisions for selecting an appropriate comparative method with either the independent contrast or autoregressive method.

**PART 5: TRUTH OR CONSEQUENCES - EFFECTS OF  
PHYLOGENETIC ACCURACY ON TWO  
COMPARATIVE METHODS**

## **Introduction**

Comparative biology has been revolutionised over the past few years. The touchstone for the revolution was the insight that species cannot generally be treated as statistically independent points for analysis: close relatives will tend to be too similar (Clutton-Brock and Harvey 1977). Many statistical methods have been developed to overcome phylogenetic non-independence, all of them much more realistic and reasonable than previous approaches (see Harvey and Pagel 1991, for a review). Biologists are now faced with the difficult decision of which method to use. This paper is concerned with two of the new methods: Pagel's (1992) method of independent comparisons (IC), and the phylogenetic autocorrelation (PA) method of Gittleman and Kot (1990). The validity of each has been questioned (Harvey and Pagel 1991; Grafen 1992). Here we consider some of the assumptions of each method and the criticisms they have attracted. The next section presents simulations which test each method's validity and power under a range of conditions, particularly in relation to phylogenetic information because this is an unstudied aspect of other simulations (see Gittleman and Luh 1992, 1993). Finally, we discuss the implications of our results for biologists embarking on a comparative study.

### **Some assumptions of the methods**

We do not intend to describe the methods in detail: such descriptions can be found in the original papers (Gittleman and Kot 1990; Pagel 1992). Rather, our aim is to discuss and compare some key assumptions of the methods, which suggest questions of performance that need addressing.

The extent to which we expect species to resemble one another depends in part on their true phylogenetic relatedness. To remove the non-independence among data points, both methods therefore require an estimate of the phylogeny of the taxa under study. To distinguish it from the (unknown) true phylogeny, we follow Grafen (1989) in calling this estimate the 'working phylogeny'. Although the true phylogeny is probably predominantly bifurcating, working phylogenies will often contain polytomies (nodes with more than two daughter branches). Polytomies in the working phylogeny do not generally mean that all daughter taxa at a node are equally closely related to one another. Rather, they reflect our ignorance about relationships among the daughter taxa (Grafen 1989). PA in fact assumes that polytomies in the working phylogeny represent multi-way speciation events. As Grafen (1989, 1992) and Harvey and Pagel (1991) point out, any method making this assumption will not remove all phylogenetic non-independence from the data if there are polytomies and so will be invalid: the simulations reported below will show to what extent polytomies invalidate PA. The first independent comparisons method (Felsenstein 1985) shares this limitation, but some subsequent developments (Grafen 1989; Pagel and Harvey 1989; Harvey and Pagel 1991; Pagel 1992) take polytomies into account by making the conservative assumption that each node can contribute only one piece of information to the test. Pagel's (1992) method is therefore more likely to be valid in the face of incompletely resolved working phylogenies.

However, Grafen (1992) has criticised the way Pagel's method handles polytomies. IC assumes that the variables in the data set contain information about the true phylogeny underlying the first bifurcation within a polytomy. Daughter branches are split into two groups: one group containing those with a greater than average value

of the key trait, the other containing the remainder. Grafen (1992) contends that it is both unnecessary and misleading to erect such phylogenetic hypotheses, and that incorrect guesses about phylogeny will cause the comparisons to lose statistical independence. Pagel and Harvey (1992) argue that the comparisons will be independent if the guesses are correct, and that it is no more correct to assume that the data contain no information about the phylogenetic structure within a polytomy (as Grafen 1989 method does): "The fact is that any method confronted with a multiple node has to make some guesses or commit itself in some way to a hypothesis about phylogeny" (Pagel and Harvey 1992:429). We use simulations to find out whether Grafen's criticisms are borne out by practical faults.

A further difference between the methods is their view of trait variation. PA splits variation into two components (Gittleman and Luh 1992): an inherited component related to phylogeny, and a specific component which might be adaptive. Only the specific component is tested for correlation with another trait. The component due to phylogeny is removed and discarded. IC, on the other hand, views all variation as potentially due to adaptation: today's inheritance was yesterday's adaptation. Consequently it seems likely that IC might have greater statistical power, as all of the variation present in the dataset can contribute to the test.

Any comparative method must embody an assumption about how evolution has proceeded (Harvey and Pagel 1991; Gittleman and Luh 1993). Methods with more realistic and more reasonable assumptions will perform better. IC explicitly assumes a Brownian motion model of character change: the amount of net change expected along a segment of the working phylogeny is proportional to the square root of the length of the segment. Biologists using the method can opt for a punctuational view of evolution by

setting all the segments to the same length, or can take a gradualist viewpoint by reflecting ages of taxa in the segment lengths. In either case, the assumption is that the influence of phylogeny is felt throughout the data set.

PA is not wedded to a specific model of character change (Gittleman and Luh 1992). It estimates from the data a maximum likelihood parameter indicating how phenotypic similarity seems to be scaling with phylogenetic similarity across the phylogeny as a whole. The single maximum likelihood parameter provides a dimension of flexibility that is not present in IC (but see Grafen 1989), where phylogenetic similarity is taken to be the same as expected phenotypic resemblance. Although a single parameter cannot capture all the details of how phylogenetic non-independence is varying throughout the dataset, it nonetheless gives PA extra flexibility. The critical element, however, in PA is that there is indeed a significant relationship between the phylogeny and the observed trait variation.

Flexibility is likely to be an important attribute, because any mathematically tractable models of character change are almost certainly wrong. It is therefore important that our methods perform well not only in 'perfect' conditions but also in realistic ones, which may well not meet their internal assumptions (Pagel and Harvey 1992). PA's performance ought not to be strongly affected under different models of character change, whereas IC is likely to be more susceptible: the comparisons will not be strictly independent and will be heteroscedastic if the model is in error. There are infinitely many ways that a model can be wrong, so all that can be done is to consider what are thought to be the most important; previous simulation studies assessed effects of evolutionary models on the PA and IC comparative methods (Martins and Garland 1991; Gittleman and Luh 1993). Here we have considered the effects of specifying

incorrectly the length of branch segments in the phylogeny. For IC, the branch lengths should be in units of expected evolutionary change (Felsenstein 1985) and, although ages of nodes or genetic distances will often be good approximations, the 'correct' branch lengths are never known. For PA, only the relative relationship among nodes are needed. To what extent does our lack of knowledge undermine each of the methods?

To summarise, this section has highlighted four questions which we now address by simulation. They are:

- To what extent do polytomies in the working phylogeny invalidate PA?
- Is IC valid when its assumptions are met ('narrow-sense' validity: Pagel and Harvey 1992)?
- How powerful are the two methods?
- How robust are they when faced with incorrect branch length information?

## **Methods**

The basic procedure used in the simulations was: 1) generate, according to a specified evolutionary model, many correlated and uncorrelated pairs of variables for a number of 'species' whose phylogeny was known in every detail; then 2) use IC and PA to analyse these data with a range of working phylogenies, some better (closer to the true phylogeny) than others.

### **Generating the truth**

The phylogeny used for data generation (the 'true phylogeny') is shown in Figure 1. It was produced using a stick-breaking model equivalent to a pure-birth

process or a birth-death process in which the birth and death probabilities per unit time do not vary among lineages, and in which simultaneous speciation events are precluded (S. Nee and R. M. May, pers. comm.). Because the model we have used is not an assumption of either method, the phylogeny shown in Figure 1 should provide a fair test.

Values of pairs of characters,  $\underline{Y}$  and  $\underline{X}$ , were generated for the 32 species by a BASIC program. At each branch segment, the square root of the true branch length was multiplied by each of two standard normal random numbers ( $\mu = 0$ ,  $\sigma = 1$ ). The products were the changes in  $\underline{X}$  and a third character,  $\underline{Z}$ , along the segment being considered. The change in  $\underline{Y}$  along a branch was calculated as

$$D\underline{Y} = g \cdot D\underline{X} + (1 - g) \cdot D\underline{Z}$$

where  $g$  is the input correlation (Martins and Garland 1991). The value  $g$  took was zero in the tests of Type I error rate and 0.3 in the tests of power. The value of  $\underline{X}$  and  $\underline{Y}$  at a tip (species) was calculated by summing the changes along all the branches linking the tip to the root of the tree. We generated 1000 pairs of  $\underline{X}$  and  $\underline{Y}$  variables with  $g = 0$  and a further 1000 with  $g = 0.3$ .

### **Generating what comparative biologists see**

Nine working phylogenies were derived from the true phylogeny for use in the simulations. These are shown in Figure 2. They are split into 3 groups; completely resolved (31 nodes), fairly resolved (25 nodes) and poorly resolved (10 nodes). Only the completely resolved group show all sister-taxon relationships that are truly present.

The incompletely resolved working phylogenies were derived from the complete phylogeny by collapsing randomly-selected branches to zero length. All of the working phylogenies are compatible with the true phylogeny, in that all taxa defined by nodes are truly monophyletic. For each degree of resolution, different branch length assumptions were tested as follows:

1) Correct branch lengths (left hand side of Figure 2). The length of the branch between two nodes is the difference between the times of the two speciation events. When the working phylogeny contains polytomies, the speciation events considered are the oldest ones within the group defined by the polytomy.

2) All branch lengths initially set equal (middle column of Figure 2). Such branch lengths imply that change is punctuational, occurring only at speciation events. Since the assumption is entirely incorrect here, these simulations ought to give an indicator of roughly how badly the method performs in the worst case.

3) Branches set from the tree topology (right hand side of Figure 2). The height of a node is assumed to be directly proportional to the number of species ultimately derived from it. The length of the branch linking two nodes is thus the difference between their heights. This algorithm was suggested by Grafen (1989) as a useful default method for assigning branch lengths in the absence of other information.

### **Comparative tests**

The association between each Y and X pair was assessed by IC, PA and non-phylogenetic cross-species regression.

Independent Comparisons. Andy Purvis has implemented this method as a computer package for the Apple Macintosh. This package was used for the analyses.

Comparisons were computed for each of the nine working phylogenies shown in Figure 2, according to Pagel (1992). The significance of the regression through the origin of  $\underline{Y}$  contrasts on  $\underline{X}$  contrasts was assessed. There was one fewer degree of freedom than nodes in the working phylogeny.

Phylogenetic autocorrelation. H.-K. Luh. have implemented this method as a computer package which is available from the authors; details of the method are presented in Gittleman and Kot (1990) and Gittleman and Luh (1992, 1993). The autoregressive model was applied using each working phylogeny in turn to factor out the inherited component of trait values. The correlation across species between the specific components was then calculated and its significance assessed. There were always 30 degrees of freedom – two fewer than the number of species in the dataset.

The primary difficulty in applying the autocorrelation method to phylogenies, in contrast to taxonomies (see Gittleman and Kot 1990), is in determining an appropriate weighting matrix to locate precise branching patterns. In the present simulations, a weighting matrix is calculated by first establishing a distance set for each phylogeny. The distance set is formed by arranging frequency distributions for the branch lengths in each phylogeny and then selecting the length with the highest frequency; this *maximizes* the chance of finding trait change at a given distance in a phylogeny (i.e., 'phylogenetic correlation'; see Gittleman and Luh 1992). With this methodology, weighting matrices are then defined by applying a Moran's  $\underline{I}$  (Moran 1950) statistic as follows:

$$\underline{W}_{ij} = 1 \text{ if the distance of species } i \text{ and } j \text{ belongs to distance set } \underline{C},$$

= 0, otherwise.

and the weighting matrices of the autoregressive model

$\underline{W}_{ij}$  =  $\underline{C}$  if the distance of species  $i$  and  $j$  belongs to distance set  $\underline{C}$ ,  
= 0, otherwise.

Additionally, the Moran's  $I$  estimates how much non-independence due to phylogeny is perceived in the data set.

Cross-species regression. Species values were treated as independent. The significances of all regressions of  $\underline{Y}$  on  $\underline{X}$  were recorded. Tests were based on 30 degrees of freedom (i.e., the number of species minus two).

## Results

The results of the simulations are in Tables 1 and 2. Table 1 summarises the tests of validity: values are the proportion of 1000 trials where the association between  $\underline{Y}$  and  $\underline{X}$  was significant at the level indicated in the first column: for a valid test, these should not differ significantly from the nominal p-values in the first column. Table 2 gives the results of the tests of power. Figures here are the number of 1000 trials where the relationship was significant at the level indicated in the first column, minus the number of Type I errors expected from the values given in Table 1. Table 3 gives, for each working phylogeny, the mean estimate of Moran's  $I$  associated with PA and the mean

estimate (with standard error) of  $g$  produced by IC in the test of power, i.e., when the true value of  $g = 0.3$ .

There are various trends in the results that are worth noting. Table 1 shows that PA becomes more invalid as the number of polytomies in the working phylogeny increases. PA has higher error rates than IC when the true phylogeny is available, but its rates are not affected much by incorrect branch length information. That said, it is worth noting that PA's highest Type I error rates are always found with equal branch lengths. IC shows a different pattern: it is always valid when the branch length information is correct (binomial test: all  $p > 0.05$ ), irrespective of the number of polytomies present, but loses some validity when branch length information is wrong. The topology branch lengths affect IC much worse than do the equal branch lengths. The cross-species analyses are always far more invalid than either IC or PA.

Table 2 shows that IC loses a great deal of power as the number of polytomies increase. PA is less strongly affected but shows the same pattern. At poor resolution (10 nodes), PA is considerably the more powerful. When the working phylogeny is fully (31 nodes) or fairly (25 nodes) resolved, IC is generally more powerful than PA, unless the branch lengths were generated from the topology. Whereas IC is least powerful with topology branch lengths, PA loses power most with equal branch lengths.

Table 3 shows that the degree of phylogenetic correlation perceived in the data (as judged by Moran's  $I$ ) declines as the number of polytomies increase, and is highest when branch length information is accurate.

## Discussion

The results of our simulations allow us to answer the four questions we posed earlier. Polytomies in the working phylogeny invalidate PA to a considerable extent, as has been suggested (Grafen, 1989; Harvey and Pagel, 1991): Type I error rates for the method were greatly elevated when the working phylogeny contained only ten nodes, being about a third of the way between the valid rate and the rate attained by (non-phylogenetic) cross-species tests (Table 1). The invalidity stems from the treatment of polytomies as statements of fact rather than statements of ignorance. IC conservatively claims only one degree of freedom for each node irrespective of how many ways it splits, whereas the degrees of freedom for PA depends only upon the number of species, not the number of nodes. The other factor causing high Type I error rates in PA with poorly resolved trees is the relationship between the working phylogeny and the trait variation, as diagnosed with the Moran's  $I$ . As Table 3 shows, the amount of *perceived* phylogenetic correlation (Moran's  $I$ ) declines with the resolution of a working phylogeny: the *true* amount is fixed, but PA's ability to detect and remove it depends on the degree of resolution. If the low values of Moran's  $I$  are caused by the low resolution of a working phylogeny (i.e., some phylogenetic correlation) not by incorrect phylogenetic information (i.e., no phylogenetic correlation), then a less stringent significance level of the Moran's  $I$  test might permit removal of phylogenetic effects. On the other hand, PA can perform well when extreme polytomies reflect a true phylogeny not simply a poor resolution (Gittleman and Luh, 1993), when IC is conservative (Purvis and Garland 1993). The usefulness and validity of PA as a method might be enhanced if it were developed to take a more conservative line with

extreme polytomies; adjusting the significance level of the Moran's  $I$  might better adapt PA to working phylogenies which contain more than a few polytomies.

Table 1 also shows that IC is valid, even with unresolved working phylogenies, when the model of character change it assumes is correct. Grafen's (1992) suggestion that the method used for resolving polytomies would invalidate IC is not supported by these simulations. Grafen (1992) makes other criticisms relating specifically to multivariate analyses which we have not addressed here (but see Pagel and Harvey, 1992, for a theoretical defense). Further simulations are planned to investigate these points. It is worth noting that IC gave unbiased estimates of the input correlation,  $g$ , in every set of simulations, with more accurate and more precise phylogenetic information producing more precise estimates (unpublished results).

The effects on the two methods of mis-specifying branch lengths fit in well with the earlier discussion of assumptions. PA uses information from the data to make its model of expected phylogenetic correlation more flexible. The result that PA performs about equally well with true and topological branch length information confirms that it does not require exact branch lengths (see Gittleman and Luh, 1993). It requires information about relatedness, which is largely contained in the topology branch lengths. Conversely, PA performs least well when all branches are assigned the same length: these do not give accurate information about relatedness so the method is misled.

IC is more tightly committed to a model of character change – that of Brownian motion. Its invalidity when the model is wrong is the flip side to its validity when the model is right. These test data were generated with a gradualist Brownian motion model. Had the data instead been generated according to a punctuational model, IC

would have produced valid Type I error rates when equal branches were used, whereas the branch lengths based on node ages would have led to inflated error rates (see also Gittleman and Luh, 1993). Perhaps more surprising is the poor performance of the topology lengths, which never better the equal branch lengths and are usually worse. Given that the algorithm was designed to reflect the notion that more evolution occurs along longer branches (Grafen, 1989), and that the notion is correct for these data, it is remarkable that making the completely wrong assumption of punctuational character change gives a more valid test. The topology method branch lengths ought be used only with caution, and care must be taken to check that the traits analysed fit the Brownian motion model acceptably well (see Garland, et. al., 1991; Purvis, 1992). If they do not, a transformation of the data, the contrasts or the branch lengths may be in order (Garland, et. al., 1991).

Unsurprisingly, power is related inversely to the number of nodes in the working phylogeny: it pays to have a working phylogeny that is as well-resolved as is possible. IC's poor power with poorly resolved phylogenies is the flip side to its validity in these cases: it is valid because it conservatively claims only one degree of freedom at each node. PA always claims 30 degrees of freedom in these simulations (the number of species minus two), so it has greater power but at the cost of some invalidity. It is also unsurprising that PA is again generally less affected than IC by branch length information (except at  $\alpha = 0.001$ ).

With real data sets, we never know the true model of evolution. This means comparative biologists face what seems at first sight like a dire truth: statistical methods are bound to be invalid or untestable. In fact, as discussed by Pagel and Harvey (1992), this should not be surprising and it need not be dire. They define 'narrow-

sense validity' as having correct Type I error rates when all assumptions are met, and 'broad-sense validity' as being robust against violations of assumptions. As they point out, no method has unlimited broad-sense validity, and we are unlikely to happen upon real data that fit our models exactly. What is important is that comparative biologists act upon this fact. IC allows tests of its underlying assumptions: it is possible to identify traits that may need to be transformed, or branch lengths that may need to be changed (see Garland, et. al., 1992; Purvis 1992). These tests are easy to apply and can reveal hitherto unsuspected patterns in the data (Pagel and Harvey, 1992). PA does not test the validity of an evolutionary model because it is relatively model-independent (with the exception of its way of dealing with polytomies - see above). On the other hand, PA is quite vulnerable to incorrect phylogenetic information and/or trait change that does not parallel the phylogeny: PA in the strictest sense is designed to remove our initial concern, that "close relatives will tend to be too similar". A diagnostic statistic (i.e., the Moran's  $I$ ) tests this assumption.

Neither of these methods, then, should be viewed as a black box to 'solve' the problems posed by comparative data. However, both allow diagnosis of some of them, and our simulations show that both can usefully test for correlated evolution between continuous characters even if their models for character change are gravely in error. They also show that remaining problems with the methods are very minor compared to the problems inherent in treating species values as independent points.

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Table 1. Results of the tests of validity. The input correlation,  $g$ , = 0. Numbers are the proportion of trials in which the relationship between Y and X was significant at the level given in the first column, according to independent contrasts (IC), phylogenetic autocorrelation (PA) and across species (last column) methods.

| P     |    | Fully (31 nodes) |       |       | Fairly (25 nodes) |       |       | Poorly (10 nodes) |       |       | Across species |
|-------|----|------------------|-------|-------|-------------------|-------|-------|-------------------|-------|-------|----------------|
|       |    | Real             | Equal | Top.  | Real              | Equal | Top.  | Real              | Equal | Top.  |                |
| 0.1   | IC | 0.104            | 0.194 | 0.221 | 0.115             | 0.175 | 0.243 | 0.123             | 0.124 | 0.204 |                |
|       | PA | 0.158            | 0.181 | 0.163 | 0.171             | 0.191 | 0.167 | 0.204             | 0.222 | 0.210 | 0.400          |
| 0.05  | IC | 0.054            | 0.124 | 0.139 | 0.061             | 0.124 | 0.174 | 0.060             | 0.068 | 0.136 |                |
|       | PA | 0.081            | 0.107 | 0.086 | 0.083             | 0.107 | 0.087 | 0.118             | 0.138 | 0.125 | 0.314          |
| 0.01  | IC | 0.011            | 0.045 | 0.054 | 0.012             | 0.046 | 0.067 | 0.007             | 0.013 | 0.045 |                |
|       | PA | 0.031            | 0.042 | 0.043 | 0.039             | 0.050 | 0.048 | 0.059             | 0.070 | 0.065 | 0.166          |
| 0.001 | IC | 0.002            | 0.011 | 0.016 | 0.002             | 0.005 | 0.018 | 0.002             | 0.003 | 0.003 |                |
|       | PA | 0.005            | 0.009 | 0.009 | 0.006             | 0.010 | 0.005 | 0.015             | 0.017 | 0.019 | 0.081          |

Table 2. Results of the tests of power. Numbers are the frequency in 1000 trials that the nominal p-value (first column) was exceeded, corrected for Type I error rate by subtracting the corresponding values from Table 1. Abbreviations are as in Table 1.

| P     |    | Fully (31 nodes) |       |      | Fairly (25 nodes) |       |      | Poorly (10 nodes) |       |      | Across species |
|-------|----|------------------|-------|------|-------------------|-------|------|-------------------|-------|------|----------------|
|       |    | Real             | Equal | Top. | Real              | Equal | Top. | Real              | Equal | Top. |                |
| 0.1   | IC | 624              | 499   | 468  | 539               | 472   | 366  | 233               | 244   | 195  |                |
|       | PA | 371              | 299   | 381  | 343               | 269   | 376  | 253               | 232   | 268  | 252            |
| 0.05  | IC | 554              | 472   | 450  | 472               | 427   | 354  | 167               | 188   | 160  |                |
|       | PA | 387              | 244   | 326  | 346               | 233   | 328  | 228               | 174   | 203  | 272            |
| 0.01  | IC | 359              | 331   | 345  | 247               | 268   | 285  | 78                | 82    | 101  |                |
|       | PA | 225              | 168   | 171  | 181               | 177   | 147  | 117               | 110   | 106  | 294            |
| 0.001 | IC | 126              | 156   | 190  | 86                | 118   | 137  | 15                | 31    | 39   |                |
|       | PA | 187              | 39    | 36   | 164               | 38    | 34   | 65                | 102   | 88   | 228            |

Table 3. The amount of phylogenetic autocorrelation. A measure (Moran's  $I$ ) of how much phylogenetic autocorrelation is perceived to be present in the data, for each working phylogeny. Note that the true amount is actually the same.

|                   | Fully | Fairly | Poorly |
|-------------------|-------|--------|--------|
| Correct branches  | 0.333 | 0.287  | 0.161  |
| Equal branches    | 0.221 | 0.135  | 0.054  |
| Topology branches | 0.308 | 0.242  | 0.130  |

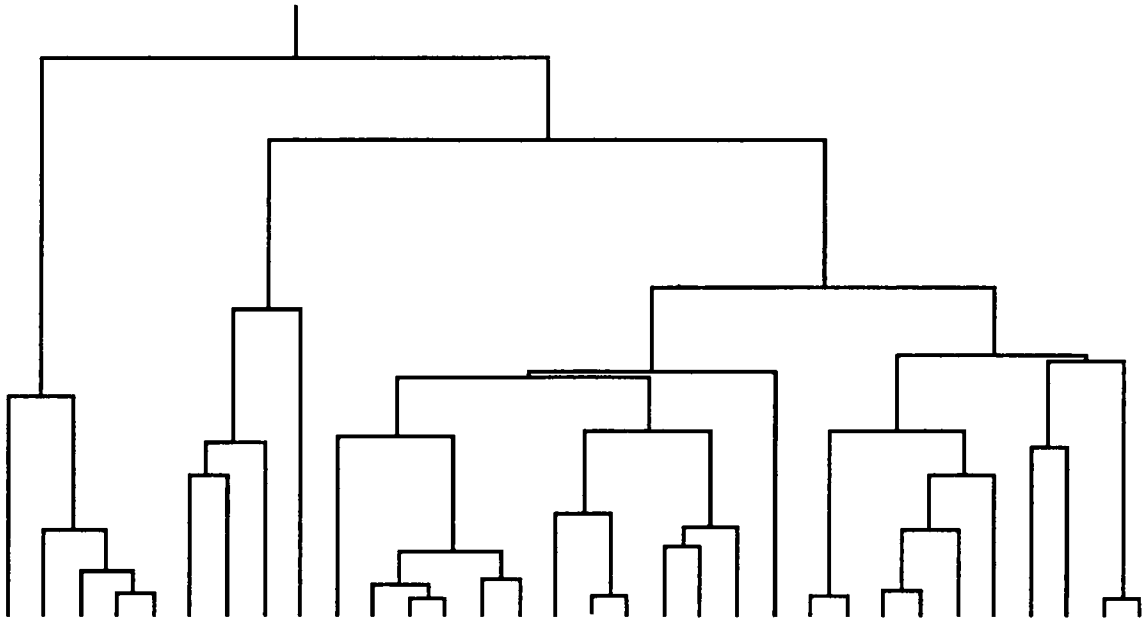


Figure 1. The true phylogeny used in data generation. See text for explanation.

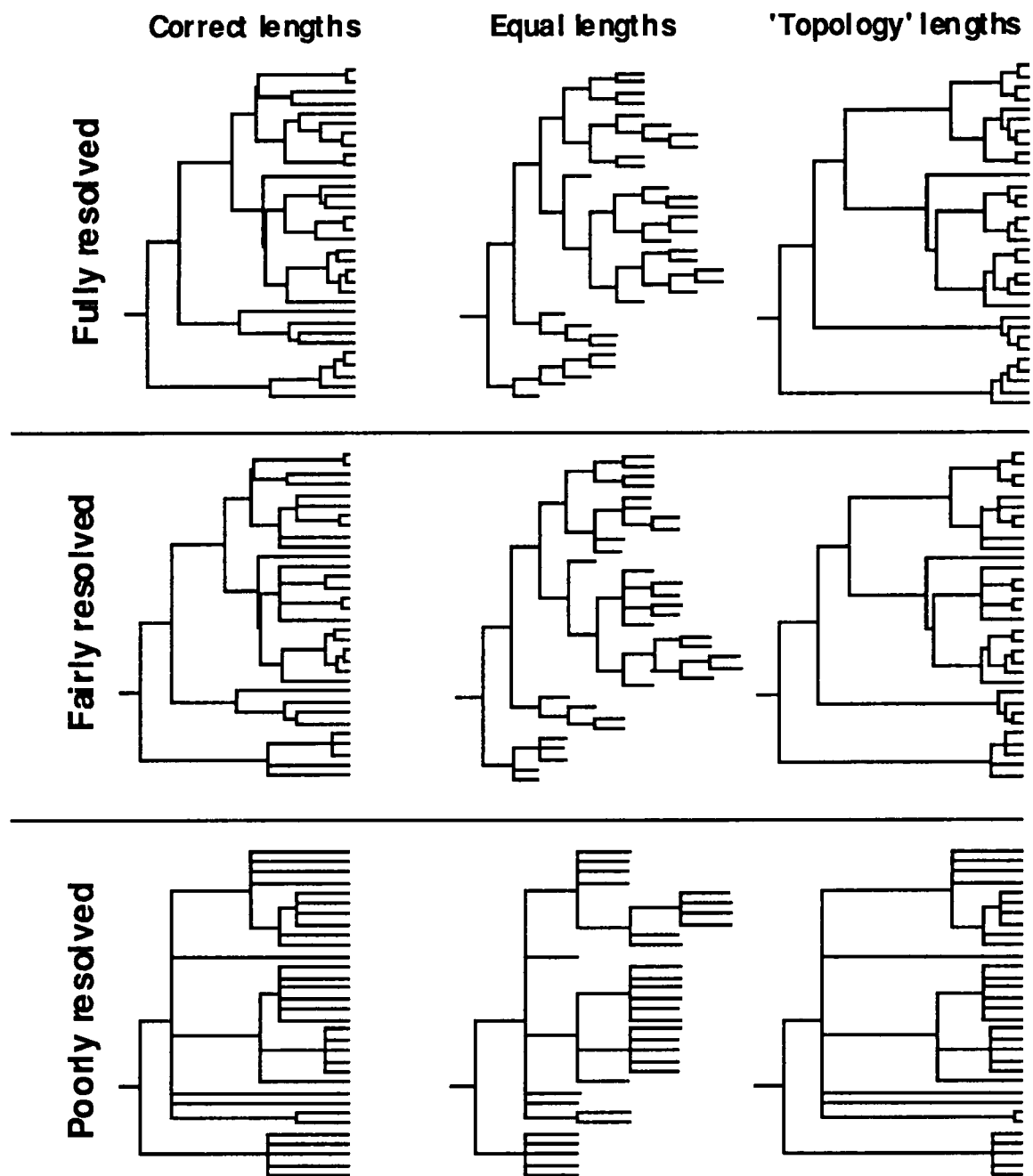


Figure 2. The nine working phylogenies used in the simulations. See text for explanation.

## **Vita**

Hang-Kwang Luh was born in Taipei on July 7 1961. He graduated from the Department of Fisheries at the National Taiwan College of Marine Science and Technology in 1983. Then, he entered the Institute of Marine Biology at the Sun Yat-sen University and received his MS degree in 1985. After finishing his compulsory military service in 1987, he entered the Institute of Zoology, Academia Sinica, as a research assistant.

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