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I am submitting herewith a dissertation written by Julie Lynn Lockwood entitled "Assembling ecological communities: investigations into theory and applications". 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.

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ASSEMBLING ECOLOGICAL COMMUNITIES: INVESTIGATIONS INTO THEORY AND APPLICATIONS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Julie L. Lockwood

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DEDICATION

This dissertation is dedicated to my family and friends as they are the foundation for any accomplishment.

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I want to thank Stuart Pimm, Michael Moulton, Richard Brooke, Bob Powell, Karla Balent, and Philip Nott for their insight, education and tolerance while collaborating on the material included here. My gratitude is also extended to my fellow graduate students, Gareth Russell, John Curnutt, Tom Brooks, and Audrey Mayer for reading drafts, providing encouragement and lending occasional brilliance. Mike McKinney, Jim Drake and John Gittleman provided much needed editorial, professional, and personal advice as well. I find at the end of this adventure how dependent I have become on the foundation of friendship built here in Knoxville. You know who you are and if you don't know, just look around the table one Friday night at the BrewPub.

In particular, I want to thank Rebel Wesley and Tabby Fenn – thankfully external to the BrewPub/Knoxville crowd. I can't express how much your love and friendship has contributed to the completion of this dissertation (and to the quality of my life). Finally, I must thank my family. They never failed to provide the extra push to get through the hard times, the extra money to fix the truck, the extra love to see me through rough days, and the extra hand to move my furniture. I feel compelled to name them all (as they currently exist): Dianne, Bob, Robert, David, Kathy, Susan, Jordan, Dylan, and Brennan Lockwood.

ABSTRACT

Ecological communities do not simply spring into existence. Rather, they are built through the addition and subtraction of species through time. This process, sometimes called community assembly, is an intrinsically complex event. This dissertation explores three aspects of this process. The first is the importance of interspecific competition in determining community membership. Through the use of introduced passeriforms on oceanic islands we uncovered two patterns consistent with the competition hypothesis: morphological overdispersion and a priority effect. Each pattern was found among the introduced passeriforms on the island of Saint Helena. In addition, we reviewed the evidence for similar pattern among the passeriforms on the islands of Oahu, Bermuda and Tahiti. We found good evidence to believe competition can play a deciding role in community membership among each island assemblage. The second aspect of assembly explored here was the influence of invasion rate on community structure and dynamics. Communities which are confronted with potential colonizing species sequentially reach stable, persistent endpoints. Those that are faced with groups of invaders churn through species regularly and quickly and never reach a persistent composition. Thus, invasion rate has profound influences on the resultant dynamics of the assembly process. Finally, we explored the implications of assembly theory to ecological restoration. Two aspects of restoration – achieving persistence and the appropriate species composition – can be directly translated into the lexicon of assembly theory. Using these two common points, we built a criteria for success. According to this criteria, only a very few restorations are considered completely restored. Most restoration are successfully returning a few ecosystem functions and sub–sets of the desired species composition. This discrepancy in results are placed within the context of assembly theory and alternative approaches to the art of restoration are discussed.

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Part 1

General Overview and Background

Overview

A community is an assemblage of interacting species and the various inter-relationships that bind them. Community assembly is then the addition and subtraction of these species through time. Inter-relationships change or develop through the assembly process, seemingly blinking in and out of existence. This view of nature is an inherently complex one, taking on new facets from various vantage points. With this in mind, I have approached the subject of community assembly from three distinct points of view. Each approach has its benefits and weaknesses. Individually they provide interesting parts to the whole picture. Together, however they outline the complex development of community organization.

I endeavor beyond this goal to identify moments within, and the results of, the assembly process that lend themselves to manipulation. It is only within this context that we will be capable of creating, or re-creating, the complexity we observe in nature. Such an understanding is necessary in order to successfully restore, sustain, and conserve species.

In part 2, I begin with a single species approach. Here, I ask the question: how can we determine if a particular species will successfully enter a community? A single species approach is applicable to problems of exotic species invasion and removal, recovery of endangered species, or single species management.

This approach leads me to question in part 3 the role of history in determining current community membership. To answer this question, I turn in part 4 to computer algorithms that mimic natural assembly processes. These models provide insights into what complexities we may expect given very basic ecological realities. Finally, in part 5 I try to translate these theoretical results into the more applied lexicon of restoration ecology.

Dissertation Evolution

I published or submitted for review the following material in various journals or edited volumes. Below I detail the evolution of each of these manuscripts, where they are currently in print or in review, and my contribution to each.

Part 2 is a conglomeration of two manuscripts. Richard Brooke and Michael Moulton co-authored each. Before detailing my contribution to each, perhaps a history of my interaction with my collaborators is in order. The story of Saint Helena came to me through Mike Moulton whom himself came to know the story through Richard Brooke. Richard was a well-respected South African ornithologist who died this past summer in Zimbabwe after a long illness. Richard had compiled a list of all avian species released on Saint Helena and used this information to test some of what he called "Pimm's predictions". He sent his manuscript to *Oecologia*, under his exclusive

authorship, in 1993. The manuscript was rejected. Richard, having become ill, contacted Mike Moulton concerning a possible collaborative re-write. Mike handed the idea off to me and I began to take some of the original data (i.e., only the Saint Helena passeriform species from the entire avian list compiled by Richard) and conduct new, more appropriate analyses. I was in contact with Richard and Mike throughout this process, and both contributed direction and detail to the evolving manuscript.

A particularly fateful decision made by the three of us was to separate our analyses into two independent manuscripts. The first would involve tests of the 'intrinsic hypothesis' and the Priority Effect. The second would deal exclusively with the pattern of morphological overdispersion.

The resultant manuscripts were a far cry from the one that I initially received from Richard. Mike and Richard had left the analyses, and the writing, of both manuscripts to me and I had molded them they way I felt most appropriate. When the work was completed, the question of authorship inevitably arose. Mike and I agreed to have Richard as first author, and myself as second, on the manuscript we submitted to *Oecologia*. Richard was clearly very ill and he had, after all, written an initial manuscript from which I had begun work. So, although I had conducted all the analyses and written the paper, we felt it only right that Richard be the first author on at least one

of the resultant manuscripts. The first to be submitted, which we would send back to *Oecologia* , would be the one.

The second manuscript, which we submitted to *Ostrich*, was first authored by myself with Richard listed second and Mike third. Separating authorship in this manner seemed democratic enough for all involved and reflected the long evolution of our collaboration.

The first manuscript, dealing exclusively with the priority effect and tests of the 'intrinsic hypotheses' of Simberloff, was printed in *Oecologia* in 1995 (Brooke, Lockwood and Moulton - 103: 337-342). The second (morphological analyses) is in press at the *Ostrich*, a South African ornithological journal (Lockwood, Brooke and Moulton). The decision to combine the two manuscripts into one Part, stems from my unwillingness to re-state the same things over and over (i.e., the species list is the same as are the underlying theoretical motivations). I wrote both manuscripts, thus it seemed reasonable to re-combine them in my dissertation however I felt most appropriate.

Parts 3 and 5 are chapters in an edited volume entitled: *Assembly rules: Perspectives, advances and retreats (edited by Evan Weiher and Paul Keddy), Cambridge University Press.* Mike Moulton and Karla Balent co-authored the chapter on introduction success (Part 3). This represented a long awaited

chance to synthesize my work with introduced bird communities on oceanic islands – much of which is the result of past collaborations with Mike Moulton. Past manuscripts had dealt with particular patterns found within individual island avian communities. The collective result was a hodgepodge, with some analyses having been conducted within some communities and some within others, but very few communities in which we had tested for all. Thus, I went back to each island data set and tested for any pattern that I had not previously published. In addition, we included a section on the effect of native range size on introduction success. The result was a manuscript in which half of the analyses were new and the rest a summary of my (or Mike Moulton's) past work.

Karla Balent helped with data collection (specifically counting intersections to estimate range size) and she and Mike helped with written revisions. I am first author (Lockwood, Moulton and Balent) as I was responsible for all new analyses, most of the work summarized, the writing, and much of the theoretical direction.

Stuart Pimm co-authored the review of restoration ecology (Part 5). Stuart introduced this work to me as a first project while at Tennessee. The evolution of this paper was laborious and difficult as it is not quite a review (it incorporates new ideas and has novel results) but is not quite a 'typical'

research paper (open to subjective biases). We submitted the result, which finally came to together in our collective mind last November, as a book chapter in the assembly volume as well (Lockwood and Pimm). The data collection, analyses, writing, and the manuscripts theoretical bent are all a product of my own will and determination.

Part 4 is my most recent work and I submitted it for review in *Oikos* just this past week (Lockwood, Powell, Nott and Pimm). M. Philip Nott, Robert D. Powell, and Stuart Pimm co-authored this manuscript. The original intellectual push for this research was from Stuart Pimm. He put forth the idea of fixed intervals of integrating of Lotka-Volterra equations as a substitute for 'time' in this type of model. From there I took over, enlisting the help of Bob Powell and Phil Nott from time to time with programming in the C language. All simulations, data analyses, and writing were my responsibility.

Hopefully, I have given enough detail to clarify my role in each section. To summarize, I am the intellectual mother of nearly all of the work that follows. From time to time, I have incorporated data sets that others have collected, or that I have collected in the past. On the one occasion when the resultant manuscript was first authored by someone besides myself, the motivation was exceptional and not related to my intellectual investment

(more a reflection of my emotional investment). With the exception of summaries of my past work with Mike Moulton (Part 3), all the information contained within is novel. Further, this is true whether or not the data sets were used previously for other purposes or in other manuscripts (I am speaking particularly of Part 5).

Parts 2 and 3 Preface

The first two Parts stem from a long controversy over the role of interspecific competition in determining community membership. This is a well documented argument and I will not repeat specifics here except to say that a paper by Colwell and Winkler (1984) describing biases in null hypothesis formulation is strictly adhered to here. My purpose is to point to the origins of the work and give some indication as to why we conduct our analyses the way we do. These arguments carried over into the work conducted by Mike Moulton and Stuart Pimm on the introduced avifauna of the Hawaiian archipelago (Moulton and Pimm 1983, 1986, 1987). Daniel Simberloff and William Boecklen (Simberloff and Boecklen 1991) criticized this work on a number of grounds. Parts 2 and 3 are a direct result of this criticism. We thus modified several of Moulton and Pimm's original methods to avoid specific pitfalls (Moulton and Pimm 1986, 1987).

First, each island in an archipelago are considered separately or better yet, we consider isolated islands. Second, non–passeriforms are treated separately as

an independent group. Moreover, careful attention should be paid to their release methods and current means of survival. Several quail and dove species were released on several independent occasions and many continue to live in a semi-feral state (Long 1981). With these considerations in mind, there were too few non-passeriforms introduced on Tahiti, Bermuda and Saint Helena, to provide a legitimate tests of the hypotheses. They were thus excluded here. Third, we are more stringent in deciding which species should be included in any particular analysis. For instance, we exclude any species in which 5 or fewer individuals were released. In addition, we treat species in which little information is provided with caution, conducting the tests with and without those species.

The final imprint of this exchange is the incorporation of tests of the "all or none" hypothesis of Simberloff and Boecklen (1991). According to this hypothesis, some species exhibit specific traits that allow them to be successful invaders anywhere they are introduced. It was argued by Simberloff and Boecklen (1991) that this mechanism just as easily explains the patterns of success among the birds on the Hawaiian Archipelago. Clearly, there are species attributes that allow them to do well in a particular environments. Indeed there is a growing literature devoted exclusively to determining these variables (see Karieva 1996). However, our focus is broad. Both the 'all or none' and the competition hypothesis seek to explain patterns of success at the community level and indeed compare across communities.

If the effects of species-specific attributes predominate at the community level we should see evidence for an 'all or none' pattern. In contrast, if interspecific competition predominates at the community level, we should see patterns such as morphological overdispersion and a priority effect. When appropriate I cite examples within the invasion success literature.

In Part 2 we conduct tests for morphological overdispersion, a priority effect, and the 'all or none' patterns among the introduced passeriforms of Saint Helena. In Part 3, we review and update tests on Tahiti, Bermuda and Oahu. In doing so, we can explore the implications of these tests in a broader context and show where our tests show negative results.

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Part 2

Patterns of success and morphological dispersion in passeriform bird introductions on Saint Helena

Abstract

Ecologists have long attempted to predict the success of species that are introduced into foreign environments. Some have emphasized qualities intrinsic to the species themselves, whereas others have argued that extrinsic forces, such as competition, may be more important. We test some of the predictions made by both the extrinsic and intrinsic hypotheses using passeriform bird introduced onto the island of Saint Helena. We found direct evidence that extrinsic forces are more important predictors of successful invasion. Species introduced when fewer other species were present were more likely to be successful. Moreover, the group of finches introduced on Saint Helena are morphologically overdispersed. In a direct test of the alternative hypothesis that intrinsic forces play a more prominent role in success or failure, we found a tendency for species which successfully established on Saint Helena to be also successful when introduced elsewhere. However, the vast majority of species unsuccessful at establishing on Saint Helena had probabilities of success greater outside Saint Helena of 50% or greater making this result somewhat equivocal. Finally, we found no evidence to support the hypothesis that species that are successful early are those that are intrinsically superior invaders. These results are consistent with similar analyses of the introduced avian communities on Oahu, Tahiti, and Bermuda.

Introduction

Many ecological studies have attempted to deduce explanatory principles for predicting which species of plants and animals are likely to succeed and which to fail when released into foreign environments (Elton 1958, Drake et al. 1989). Some authors have emphasized the importance of properties intrinsic to the particular species being released (Simberloff and Boecklen 1991, Simberloff 1992), whereas other have argued that extrinsic forces such as competition may be more important (Moulton and Pimm 1983, 1986a, 1986b, 1987; Moulton 1985, 1993; Lockwood and Moulton 1994; Lockwood et al. 1993). Here, we test some of these predictions in the light of a hitherto unexplored case history: the introduced passeriform birds on the island of Saint Helena in the South Atlantic.

The island of Saint Helena at 15° 58'S, 05° 43'W is volcanic and rises nearly 6000 m from the mid-Atlantic ridge. The island has an area of 122 km^2 and a maximum height of 830 m above sea level. Introductions of terrestrial birds began shortly after the first Europeans arrived around 1550 (Teale 1981). The early European settlers exterminated nearly all the indigenous terrestrial birds and converted most of the original native forest to plantations of exotic trees, agricultural land and rough grazing land (Teale 1981, Haydock 1954). The Saint Helena case history offers three attractive features for testing these predictions. First, the island is quite small, making species composition more

easily ascertained. Second, a relatively large number of passeriform species have been released there (at least 31). Third, the first introductions of passeriforms took place in 1776, so the time span over which introductions have occurred exceeds 200 years.

Two patterns that are consistent with the competition hypothesis are morphological overdispersion and priority effect. Morphological overdispersion refers to a pattern where the successfully introduced set of species are morphologically more different than expected by chance alone (Moulton and Pimm 1987). Avian morphological characters are used as a surrogate for various ecological requirements. Thus, morphological overdispersion is consistent with the Hutchinsonian idea of niche packing and competitive assortment (Hutchinson 1959). Only species which are sufficiently different in their ecological requirements may co-exist. If a species attempting colonization is too similar to an established community member (an extrinsic factor), it must either displace this competitor or fail to successfully colonize the community. If intrinsic properties govern the colonizers fate, the presence of an ecologically similar species will have very little influence — no pattern in morphology will be generated.

Similarly, if extrinsic forces such as competition influence introduction success, we may expect that species introduced when fewer other species are present will have greater chances for success (Elton 1958, Moulton and Pimm

1983, Moulton 1993). Early colonizers enjoy a competitive advantage over late arrivals, or a priority effect (Alford and Wilbur 1985).

Alternatively, if intrinsic properties govern species' chances to succeed, then species successfully introduced into one environment should be intrinsically more likely to succeed anywhere else they are introduced. This would be true regardless of when they are introduced or which other species are present (Simberloff and Boecklen 1991, Simberloff 1992).

We begin by conducting a test for morphological overdispersion among the passerines introduced on Saint Helena. We then test the hypothesis that avian introductions are more likely to succeed when fewer other introduced species are present (Elton 1958, Pimm 1989, Simberloff and Boecklen 1991, Moulton 1993). To test the alternative, we look to see if the species successfully introduced on Saint Helena are likely to be successful at other locales simply because they are intrinsically "good" invaders (Simberloff and Boecklen 1991, Simberloff 1991). Finally, we test a similar hypothesis that earlier introductions are intrinsically more likely to succeed.

The Species

The earliest introductions on Saint Helena involved non-passeriforms, whereas the first introductions of passeriform species occurred in 1776 (Haydock 1954). To be consistent with other recent work we consider only the introduced passeriforms (Lockwood and Moulton 1994, Lockwood et al. 1993,

Moulton 1993, Moulton and Pimm 1987, 1986a). Faaborg (1977) argued that non-passerines exhibit physiological differences from passerines, and Ricklefs and Travis (1980) also argued that these two groups should be treated separately. Moreover, no native passeriforms survive on Saint Helena (Baker 1868).

We compiled a list of the species introduced to Saint Helena, and the fates of those species, based on information in Long (1981), Lever (1987) and various other sources (Brooke 1808; Phillips 1805; Barnes 1817; Layard 1867, 1871; Baker 1868; Melliss 1870, 1871; Janisch 1908; Huckle 1924; Moreau 1931; Winterbottom 1936; Benson 1950; Haydock 1954; van Bruggen 1958; Watson 1966; Basilewsky 1970; Loveridge 1977; Teale 1981; den Hartog 1984). We excluded from our analyses species which likely did not have propagule sizes that contained a sufficient number of individuals to lead to self-perpetuating populations (i.e., species in which five or fewer individuals were released).

A total of 31 passeriform species have been introduced to Saint Helena, however only five remain today. Thus, the success rate for land-dwelling bird introductions on Saint Helena is quite low (16%). Of the 31 species introduced, 23 are finches. Of the five successful passeriform species, four are finches. The term finch includes seed-eating species from the families Estrildidae, Fringillidae and Passeridae. Thus, 74% of the passeriforms

introduced on Saint Helena are from only three families. There are a total of 9 families introduced.

The pattern of introductions through time was highly episodic. There were eight passeriform species introduced in 1820, two in 1850 and 1870, and 14 in 1929. Among the 12 species introduced in, or prior to, 1850, five were successful. The successful passeriforms were the Yellow Canary (*Serinus flaviventris*), Java Sparrow (*Padda oryzivora*), Common Myna (*Acridotheres tristis*), Common Waxbill (*Estrilda astrild*), and Madagascar Weaver (*Foudia madagascariensis*). None of the 19 species introduced after 1850 were successful. For a complete list of species introduced and their fates see appendix A.

The Morphological Analyses

Two aspects of the history of Saint Helena introductions make it favorable for a morphological analysis. The first involves timing. Introductions of passeriforms began in 1776 and did not cease until 1929 when the agricultural secretary, H. Bruins-Lich, introduced 14 species (none of which survived). This is an unusually long period of documented species introductions (153 years).

More important is the amount of time that has passed since the last colonization attempts. In past analyses of this nature, the last introduction event occurred within the recent past (i.e., within 10 to 20 years). Thus, an

inherent uncertainty existed about the success or failure of these latter introductions. It is difficult to determine if species present only in small numbers, or with restricted ranges, should be considered successful or the "walking dead" (Simberloff 1992). In the case of the introduced land-birds of Saint Helena, there is no uncertainty in success or failure. The last successful passeriform introduction took place more than 140 years ago. The last unsuccessful passeriform introduction occurred in 1929 (66 years ago).

A second reason Saint Helena provides a good opportunity for studying the effects competition is the complete absence of a native passeriform avifauna. On many islands (e.g., Bermuda), ranges of the few native species overlap completely with those of the introduced species. Thus, native-exotic interactions must be addressed and native species included in the analyses (see Lockwood and Moulton 1994). Since the earliest accounts of the birds of Saint Helena published in the 1800's, there is no indication of the presence of any native passeriforms (Brooke 1808; Phillips 1805; Barnes 1817; Layard 1886, 1871; Baker 1868; Melliss 1870, 1871). Apparently, the island was covered with forests until at least 1502 when it was colonized by Europeans. However, subsequent farming and ranching changed the landscape drastically by the late 1800's (Haydock 1954, Benson 1950). It is likely that any passeriforms native to Saint Helena disappeared, along with any native forests, sometime after 1500 but well before 1800.

We conducted the morphological analyses in two ways, corresponding to the phylogenetic grouping seen in introductions (i.e., finches or all passeriforms), to avoid a J.P. Morgan effect (Colwell and Winkler 1984, see below). We first compared all passeriforms and then finches only. By including only species that are presumably more closely related (i.e., finches), and hence morphologically more similar, the chances of experiencing a J.P. Morgan effect are reduced (Colwell and Winkler 1984). A J.P. Morgan effect will occur when a species with an extreme morphology is included within a set of morphologically very similar species (e.g., including a flamingo within a set of warblers). This extreme species (or set of species) then serves to "clump" the phylogenetically similar species in morphological space. This obscures any possible patterns. Because most of the introductions on Saint Helena were finches, the inclusion of other species may reduce the chances of detecting patterns within the finch assemblage.

None of the 14 species released in 1929 were successful. We have no information on propagule sizes or sex ratios for these introductions. Moreover, all were introduced by a single individual whose methods of release may have, for some unknown reason, doomed all these species to failure. Thus, it could be argued that for our analyses to be conservative these species should be excluded. For this reason, we have conducted each test with and without these 14 species.

Methods

For each introduced species, we collected measurements on between 4 and 9 museum specimens located at the United States National Museum of Natural History, Washington D.C. Measurements taken were: wing chord (from the wrist to the tip of the longest primary); beak length (from the anterior margin of the nares to the tip of the upper mandible); beak depth and width (at the anterior nares) and tail length (from the base of the tail to the longest primary rectrice).

To be consistent with past analyses, we attempted to collect measurements on equal numbers of males and females to account for any size sexual dimorphism. It is difficult to asses what, if any, differences in morphology sexually dimorphic species exhibit for three reasons. First, most species included here were present in small numbers in museum collection (i.e., <5). Second, sex was unspecified in greater than 50% of all measured specimens. Third, there is a significant chance that specimens of monochromatic species are mis-identified in terms of sex (McClain et al. 1995). We are thus constrained to averaging any possible morphological sexual dimorphisms.

The characteristics measured are common in similar analyses (Ricklefs and Cox 1977; Miles and Ricklefs 198;, Moulton and Pimm 1983, 1986a, 1987; Moulton and Lockwood 1992; Lockwood et al. 1993; Lockwood and Moulton 1994) and it is believed that each is correlated with some aspect of avian

ecology. Thus, wing and tail length represent overall body size for inter-specific comparisons (Rising and Somers 1989, Freeman and Jackson 1990), whereas beak dimensions indicate the size and type of food taken (e.g., Ashmole 1968, Wilson 1975, Grant 1986, Ricklefs and Travis 1980, Benkman and Pulliam 1988).

The specimens measured typically were not taken from the island of Saint Helena, rather from their native ranges or established populations on mainlands (e.g., House Sparrow specimens typically were collected on the North American continent despite it's introduced status here). It is unclear if the species successfully established on Saint Helena have experienced shifts in morphology. Crowell (1962) tested for morphological shifts among the introduced birds of Bermuda and found none. Moreover, the vast majority of species introduced to Saint Helena did not survive long enough for any substantial changes to occur (i.e., fewer than 5 years).

We transformed the raw measurements by calculating their common logarithms. We then conducted a principal component analysis (PCA) by factoring the covariance matrix (Ricklefs and Travis 1980). Each individual of each species had as many principal component scores as raw measurements (i.e., five). We then calculated the means of the principal component scores for each species. We plotted each of the species introduced to Saint Helena in

the morphological space defined by the principal component scores that accounted for the most variability within the raw measurements.

Using Monte Carlo simulations, we constructed random or null communities for comparison to the observed. Null communities were constructed by randomly selecting M species from the pool of N species, where M is the number of successful species in the observed community and M-N is the number that failed. The size of the species pool varied in the different analyses. In the first simulation, only the passeriforms were included, thus the pool consisted of all 31 species introduced on Saint Helena. When we excluded species introduced in 1929, the pool consisted of only 17 species. For the finch-only analyses, we included only the 23 finch species in the pool or the nine finch species introduced before 1929. Wherever possible, we constructed 1000 null communities. In the analyses involving finches introduced prior to 1929, the pool included only nine species. We were thereby limited to only 126 null communities (there are only 126 ways of choosing 4 species from 9).

We compared the dispersion of the observed sets of surviving species to the random distributions generated by the simulations. When measuring the dispersion of sets of species in morphological space, we used the minimal spanning tree (MST). Essentially, the MST is the smallest sum of n-1 line segments connecting n points (Ricklefs and Travis 1980). Each point

corresponds to one of the species in the morphological space. Thus, the MST is an estimate of the sum of interspecies morphological differences. The set of surviving species on Saint Helena is morphologically overdispersed if the observed MST length exceeds a large proportion (e.g., 90 to 95%) of the 1000 random MST's comprising the null distribution.

A second indication of interspecific competition is unusually even spacing between the surviving set of species. We considered a community to be evenly dispersed within the morphological space if only a small proportion (e.g., 5 to 10%) of the random variations of the n-1 line segments were smaller than the observed (see Lockwood and Moulton 1994, Moulton and Pimm 1987). The variation of the interspecies line segments is positively correlated to the length of those line segments (Lockwood and Moulton 1994). Thus, we believe variation and MST considered in tandem is a better descriptor of any morphological pattern than either statistic considered in isolation (see also Lockwood and Moulton 1994).

Results

As is typical in principal component analyses using avian morphologies, the first two principal components accounted for most of the total variance (i.e., > 90%; Ricklefs and Travis 1980). Principal component I (PC I) was positively correlated with all the log-transformed raw variables. Regardless of which species we included in a particular analysis, the PC I axis represents a measure

of overall body size. However, the correlation between principal component II (PC II) and the various raw measurements depended on which species we included in the analysis. Thus, when all passeriform species were included, PC II was negatively correlated with the log of wing, tail and beak length and positively correlated with the log of the depth and width of the beak (table 2-1). However when only finches were included, the reverse occurred: log of wing, tail, and beak lengths were positively correlated with PC II and the log of beak width and depth were negatively correlated (table 2-2). In all cases, the

Table 2–1. Eigenvectors and Pearson product moment correlation coefficients between the first two principal components (PC I and PC II) and the log transformed variables when all 31 species are included.

	L wing	*L* culmen	*L* nd	*L* nw	*L* tail	Eigenvectors
PC I	0.92273	0.95972	0.86575	0.72814	0.80612	0.056149
PC II	-0.23236	-0.02618	0.41461	0.59733	-0.56370	0.014613

Table 2–2. Eigenvectors and Pearson product moment correlation coefficients between the first two principal components (PC I and PC II) and the log transformed variables when only the 23 finch species are included.

	L wing	*L* culmen	*L* nd	*L* nw	*L* tail	Eigenvectors
PC I	0.81576	0.92681	0.94182	0.93169	0.69161	0.027331
PC II	0.35976	0.06434	-0.05610	-0.09586	0.81932	0.007398

PC II axis in each of the figures give some indication of the shape and size of the beak in relation to the size of the body. All the species introduced, their date of introduction, and their first two principal component scores are listed in appendix A. When we interpret how all 31 passeriform species are disperin morphological space (figures 2–1 and 2–2), we see that species plotted in the upper right corner are typically large bodied and have relatively thick beaks.

Conversely, those plotted in the lower left corner are the smaller bodied species with relatively thinner and longer beaks. Not surprisingly, when all 31 species are included in the simulation the finches clump in space toward the mid– to upper–left corner of the graph, with the other species spreading

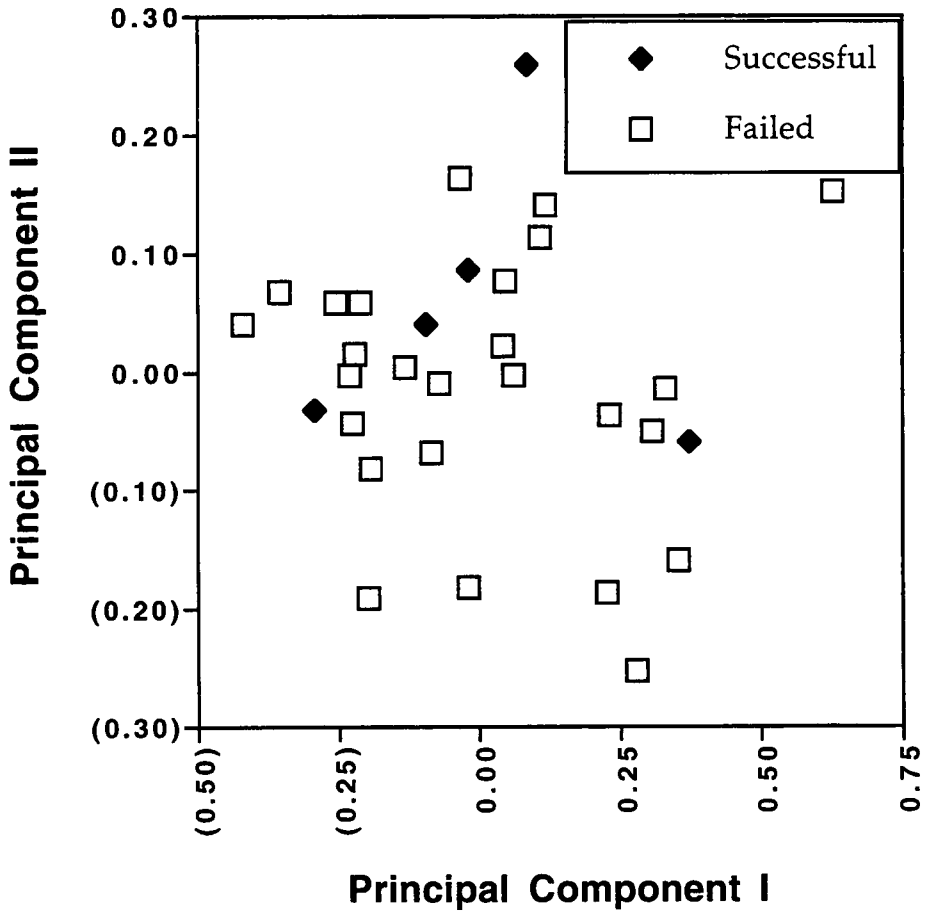


Figure 2–1. All passeriforms introduced on Saint Helena plotted according to their first two principal component scores. Principal component I indicates overall body size. Principal component II indicates the size and shape of the bill relative to body size.

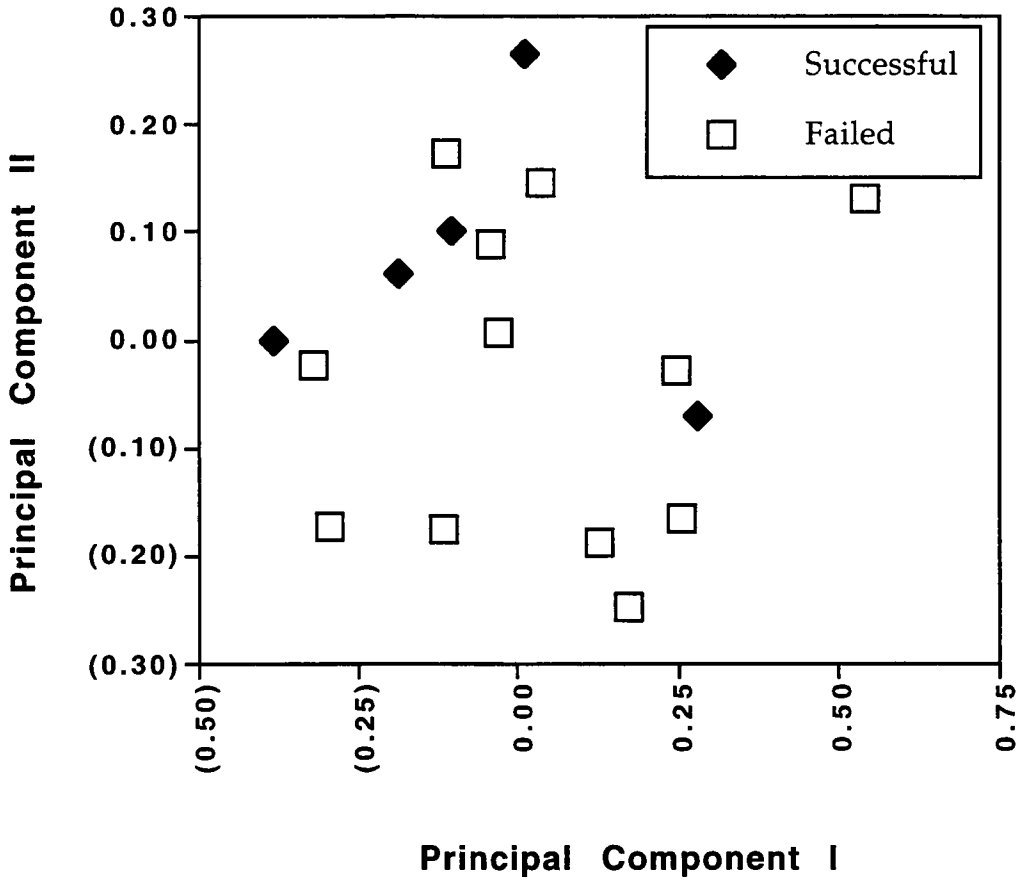


Figure 2–2. The passeriforms introduced on Saint Helena excluding the 14 species released in 1929. The axes in this figure represent the same morphological characteristics as in figure 2–1.

out accordingly. The Hill Myna (*Gracula religiosa*) is the one species which stands apart from the rest in the upper extreme right of the plots in figures 2–1 and 2–2. The Java Sparrow is the successful outlier species being plotted at the top midline of the graph.

In our first set of simulations, we included all passeriform species introduced to Saint Helena. The observed MST length was 0.920 and the variation of the interspecies segments was 0.014. Of the 1000 null communities, 282 had MST values as large or larger than the observed ($p = 0.282$). Of those 282, 139 had variances smaller than the observed ($p = 0.139$). When we exclude the introductions that took place in 1929, the observed MST value became 0.922 and the variance remained 0.014. Of the 1000 null communities, 492 had MST values as larger or larger than the observed ($p = 0.492$). Of those 492, 301 had variances smaller than the observed ($p = 0.301$). When we consider all species introduced to Saint Helena, the surviving set is not morphologically overdispersed. Moreover, this is true whether or not we include or exclude those species introduced in 1929.

We restricted our second group of simulations to the portion of the morphological space occupied by the finches (figures 2–3 and 2–4). In these plots the outlier in the upper extreme right is the Long-tailed Widdow

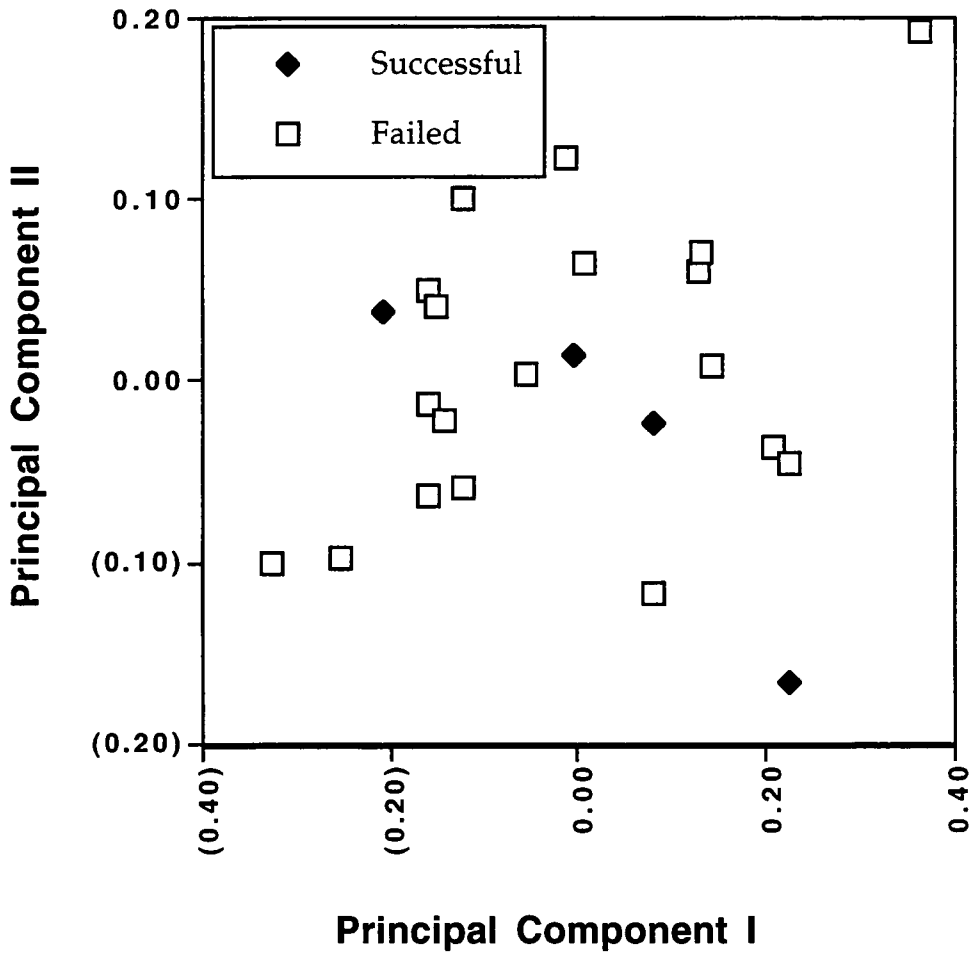


Figure 2–3. The 23 finch species introduced on Saint Helena plotted in the two–dimensional space defined by their morphological characteristics (PC I and PC II). Species plotted in the upper right corner are large bodied with relatively thin bills. Those plotted in the lower left corner are small bodied with thicker bills.

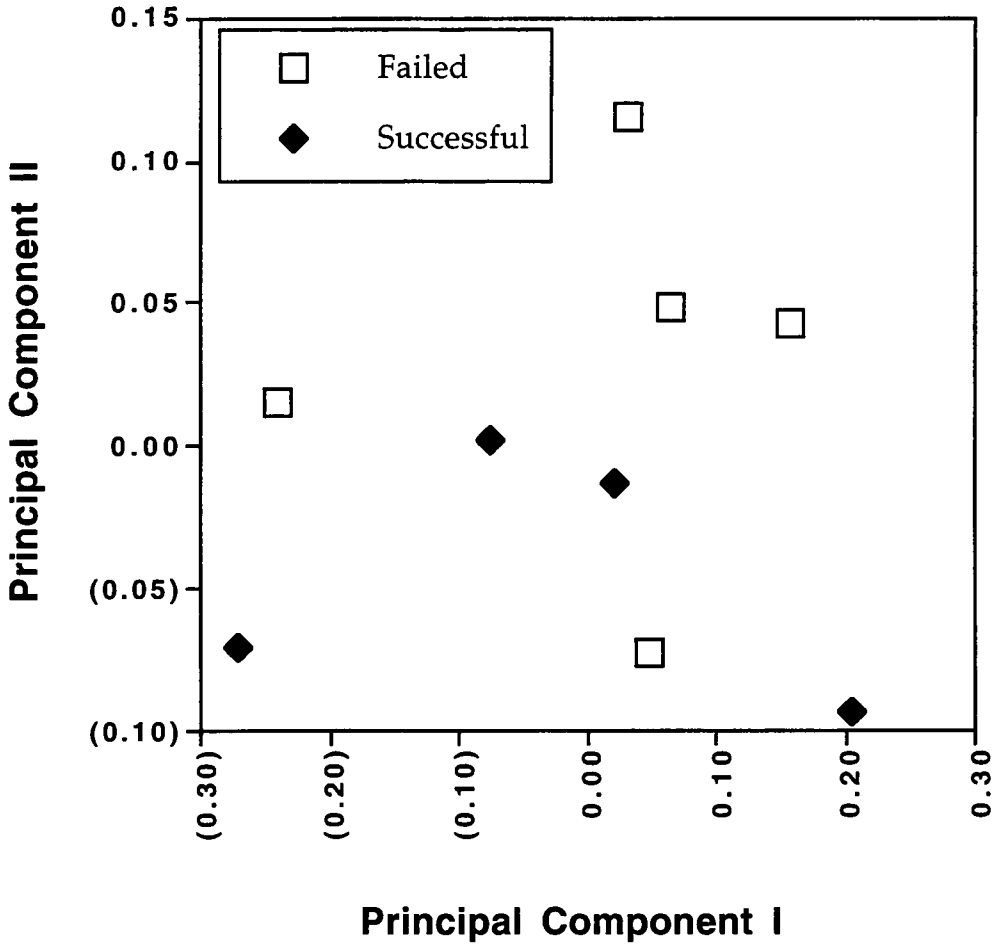


Figure 2–4. The nine finches introduced on Saint Helena before 1929. The axes in this figure represent the same morphological characteristics as in figure 2–3.

(*Euplectes progne*). The relative positions of each species changes when only finches are included in the species pool. This is a product of the reverse correlations for PC II. In this space, the species plotted in the upper right portion are again large bodied species as in figures 2–1 and 2–2. However, their beak shapes tend to be thin and long in relation to all other finches. Species in the lower left corner are small bodied with thick beaks. For example, the Java Sparrow moves from the top of the space defined by all 31 species to the bottom of the space defined by only finches and ceases to be an outlier.

In our second set of simulations, the observed MST value for the 23 finch species was 0.501 and the variation of the interspecies segments was 0.003. Of the 1000 null communities 439 had MST values as large or larger than the observed ($p = 0.439$). Of those439, only 92 had variances smaller than the observed ($p = 0.092$). When we exclude the 1929 introductions, the observed MST value becomes 0.506 and the variance remained 0.003. Of the 126 null communities possible, 49 had MST values as large or larger than the observed (37.6%). Of those 49, 10 had variations smaller than the observed (7.6%). Thus, the finches introduced to Saint Helena are simultaneously more spread out and more evenly spaced than 91% and 93% of all randomly constructed communities respectively.

Priority Effect

Methods

In the test for a priority effect, we calculated the number of species present at the time of introduction using the technique of Moulton (1993). Briefly, we ranked each species by release date and then summed the number of other introduced species present at the time of the release. The actual number of other species present at the time of introduction (or NSP) was obtained by subtracting the number of extinctions of introduced species from the total number of other introduced species. We then used a Kruskal-Wallis test to compare the number of other species present at the time of introduction for failed versus successfully established species. If extrinsic forces such as competition were not an influencing factor, then we would expect no significant difference in the mean number of other species present between groups. However, if these extrinsic forces were important, at the time of introduction the average number of other species present would be higher for the group of species which failed to establish than for the group that successfully established.

As a direct test of the alternative view of Simberloff and Boecklen (1991) which emphasizes intrinsic properties, we calculated an index of success for each species. The success index is based chiefly on data in Long (1981), updated using Lever (1987). We excluded any introductions for which the outcome was uncertain. Our calculation is based on the index used by

Simberloff (1991) and Moulton (1993). We calculated an index of success for each species by dividing the number of times that a species was successfully introduced, excluding Saint Helena, by the total number of places that species was introduced. Often a species was intentionally introduced on several occasions in one geographic location. Because information concerning multiple introduction events is unlikely for other species however, we counted each species as having only one attempt at invasion in one geographic location.

We were able to calculate a probability index of success, or P(success), for 21 of the 31 species released on Saint Helena: the remaining species were only released on Saint Helena. We then compared the mean success index value for the group of species that successfully colonized Saint Helena versus those that failed. If intrinsic properties influenced successful establishment, then those species successfully introduced outside Saint Helena should have a greater probability of success on Saint Helena. Similarly, if species tended to fail wherever introduced they will have tended to fail when introduced on Saint Helena. The introduction dates and success index values that we used are listed in appendix B.

In the analyses of the avian introductions on the Hawaiian islands, there is a tendency for the number of introduced species on the island to increase over time (Moulton and Pimm 1983, 1986a, 1986b, 1987). Thus, it is argued that

early introductions typically succeed because they encounter fewer competitors. The alternative is that these early introductions were intrinsically more successful — perhaps because only the most hardy species could survive the rigors of mid-nineteenth century sea transport or something of the like. The dynamics of species introductions to Saint Helena are different and do not show the same rough increase in species numbers over the years. The last addition, for example, was in 1850 while the Hawaiian islands may be continuing to accrue species. These differences in the timing of introductions allowed us to examine the effects of timing on success with what is essentially a different experimental design.

We can thus test another prediction of the "intrinsic colonization hypothesis" that early introductions are more likely to be successful due to intrinsic properties than later introductions. We compared the success values for early versus late introductions using the median and mean date of all introductions as our criterion for classification. In addition, we used a Spearman rank correlation of success index value against date of introduction. If intrinsic properties determine successful invasion, we would expect that in each of these tests, species introduced earlier are also the species with high success index values.

Results

Following the arguments presented above, we conducted these analyses with and without the passeriform species released in 1929. The failure of such a large proportion of the introduced species when the greatest number of other introduced species were present superficially appears to overwhelmingly support the "competition" hypothesis. Their exclusion makes the following tests conservative.

When we look at the number of other species present at the time of introduction and its influence on successful establishment, we see that successful species on average faced fewer potential competitors. (Kruskal-Wallis, approximate $\chi^2 = 10.99$; $p > \chi^2 = 0.009$). The mean number of species encountered by successful species on Saint Helena was 5.4 and for unsuccessful species 14.15. This result is consistent with the competition hypothesis: successful species, on average, faced fewer potential competitors when they were initially released. When all 1929 releases were excluded, we still observe a significant difference (Kruskal-Wallis, approximate $\chi^2 = 6.94$, $p > \chi^2 = 0.008$), with the mean number of species encountered for successful introductions being 5.4 and 9.67 for failed introductions.

Supporters of the idea that intrinsic properties are most important (e.g., Simberloff and Boecklen 1991) have predicted that the outcomes of several introductions of a given species into separate locales would be correlated. To

test this, we compared success index values between the group of successful versus the group of failed introduced species on Saint Helena. Ideally, this test would include success index values for all species however, this was not possible. Only 21 (all 5 of the successful species and 16 of the unsuccessful species) of the 31 passeriforms introduced on Saint Helena have also been introduced in some other locale. Ten of these species were introduced by H. Bruins-Lich in 1929 (Haydock 1954). Thus, most of the 1929 introductions (10 of the 14 species) were, by default, not included in this and the following tests. Following arguments made above however, we conducted this test with and without those four 1929 species.

We found that the success index values for the group of species that successfully established on Saint Helena did differ significantly from the group that failed. This was true regardless of whether we included the 1929 introductions (approximate $\chi^2 = 8.74$, $p > \chi^2 = 0.0031$) or excluded them (approximate $\chi^2 = 7.34$, $p > \chi^2 = 0.0067$). Thus, the species successfully establishing on Saint Helena tend to have a high success index value. This result superficially supports the "intrinsic colonization hypothesis" of Simberloff and Boecklen (1991). If we look closely at the results however, of the 16 species that failed, 13 had better than a 50% chance of succeeding elsewhere. For example, the generally extremely successful European Starling (*Strunus vulgaris*) and House Sparrow (*Passer domesticus*) failed when

introduced on Saint Helena. Thus, although there is a statistical tendency for intrinsic properties to influence successful establishment on Saint Helena, this result is somewhat negated on closer examination.

Finally, we can test a hypothesis advanced by Simberloff and Boecklen (1991) that species introduced earlier are simply more likely to succeed (perhaps for reasons not involving competition), while more recent introductions are more likely to fail. As indicated in appendix B, the first passeriform introductions occurred in 1776, whereas the last took place in 1929. In classifying introductions as being either late or early, we used the median and mean dates of all 31 introductions (see Moulton 1993). The median date for all passeriform introductions on Saint Helena was 1870, and the difference in probability of success values between early versus late introductions was not significant (Kruskal-Wallis, approximate $\chi^2 = 1.48$, $p > \chi^2 = 0.22$). In this test, 15 species were classified as "early" and six as "late". We also did this test using the mean date of all introductions (1874). In this test we did observe a significant difference in probability of success values between early and late introductions (Kruskal-Wallis, approximate $\chi^2 = 4.90$, $p > \chi^2 = 0.03$). In this test, the four species that were classified as "late" were the four introduced in 1929, which, as we have argued, are best excluded.

When we exclude the 1929 introductions, the difference in probability of success values between early and late introductions is not significant, whether

we use the mean date of 1829 (Kruskal-Wallis, approximate $\chi^2 = 0.00$, $p > \chi^2 = 0.99$) or the median date of 1820 (Kruskal-Wallis, approximate $\chi^2 = 2.04$, $p > \chi^2 = 0.15$). When using the median date of 1820, we classified all species introduced in 1820 as "late". However, if we had classified them as "early" the analysis is the same as using the mean date of 1829.

If earlier introductions were more likely to succeed, we would further expect a significant correlation between date of introduction and probability of success. We used a Spearman rank test, and observed no significant correlation (Spearman's ρ of = -0.39, P > absolute ρ= 0.08). A correlation excluding those species released in 1929 was also not significant (Spearman's $\rho = 0.098$, p > absolute $\rho = 0.71$).

Discussion

Overall, we contend that our results are consistent with the hypothesis that competition played a prominent role in influencing the fates of species introduced onto Saint Helena. Our results do not support the hypothesis that species successfully introduced onto Saint Helena were intrinsically destined to be so. We have three major results. First, species that were unsuccessful on Saint Helena were released when there were about two to three times as many species present than when the successful species were released. The criticism of our interpreting this result as indicating competition, is that the

successful species could be intrinsically successful and the unsuccessful species could be intrinsically unsuccessful. The relationship to the number of species present could just be spurious.

We can evaluate this criticism, because there are 21 species for which we were able to calculate a probability of success outside of Saint Helena. There is indeed a significant tendency toward species successfully introduced on Saint Helena to be those that had high probabilities for success outside of Saint Helena. However, 13 of the 16 species which failed to become established had overall probabilities of success at, or above, 50%. This can hardly be interpreted as supporting the hypothesis that these species were destined to fail no matter where introduced. Indeed, the chance that all 13 would fail is the same as tossing a coin 13 times and getting 13 heads, i.e. less than one in 2000. Thus, our second major result is that some species seem to have intrinsic qualities that make them superior invaders. Intrinsic factors are not however, prevalent enough to mask the effects of competition.

We found no support for the hypothesis that species successful early were intrinsically more likely to be so. Unlike Hawaii, species introduced earlier to Saint Helena (pre–1829, or pre–1870 depending on the analysis) were not more likely to succeed outside of Saint Helena than those released later. In addition, there was no trend for the probability of success elsewhere to decline with the date of introduction on Saint Helena.

Finally, we were able to detect a pattern of morphological overdispersion among the group of finches introduced on Saint Helena. This pattern suggests that the finch assemblage was structured by interspecific competition (Moulton and Pimm 1983, 1986, 1987; Lockwood et al. 1994). The degree of overdispersion observed however, is clearly not as profound as in similar studies (see Lockwood and Moulton 1994, Lockwood et al. 1993, Moulton 1993).

Although the effects of interspecific competition are notoriously difficult to prove in extant communities (Connell 1980), we can deduce these effects using the introduced communities on oceanic islands (for the benefits of such analyses see Moulton and Pimm 1983). Our results lend further evidence to support the hypothesis that extrinsic properties, specifically interspecific competition, strongly influence the success or failure of introduced species (Moulton and Pimm 1983, 1986a, 1986b, 1987; Moulton 1985, 1993; Lockwood and Moulton 1994, Lockwood et al. 1993).

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Appendices

Appendix A. Mean principal component scores (PC I and PC II) and dates of release for each of the 31 species introduced on Saint Helena. Principal component numbers given in parenthesis represent the new scores given when using only finch species. The first set of principal component scores are for simulations conducted with all species included. The second set of principal component scores are for simulations where the species introduced in 1929 were excluded. Successful species are designated by (S). Nomenclature follows Sibley and Monroe (1990).

Species	**Date Intro.**	**PC I**	**PC II**	**PC I w/o 1929**	**PC II w/o 1929**
Alauda arvensis	1820	-0.01785	-0.18194	-0.11598	-0.17628
Amandava sublava	1929	-0.42127 (-0.32691)	0.04111 (-0.10105)		
Carduelis chloris	1870	0.11782 (0.22442)	0.14038 (-0.04492)	0.03391 (0.15641)	0.14548 (0.04257)
Acridotheres tristis (S)	1820	0.37323	-0.06010	0.28030	-0.07090
Estrilda astrild (S)	1820	-0.29366 (-0.20868)	-0.03105 (0.03862)	-0.38560 (-0.27093)	-0.00048 (-0.07005)
Estrilda erythronotos	1929	-0.19156 (-0.12310)	-0.08121 (0.10067)		
Estrilda melpoda	1929	-0.35495 (-0.25179)	0.06727 (-0.09730)		

Euplectes albonotatus	1929	0.04275 (0.12910)	0.02271 (0.05974)		
Euplectes orix	1820	-0.03390 (0.07982)	0.16304 (-0.11701)	-0.11266 (0.04902)	0.17208 (-0.07273)
Euplectes progne	1929	0.30671 (0.36221)	-0.05097 (0.19276)		
Erithacus rubecula	1820	-0.19998	-0.19068	-0.29583	-0.17349
Fringilla coelebs	1820	0.05844 (0.13029)	-0.00210 (0.07039)	-0.03269 (0.03162)	0.00651 (0.11548)
Foudia madagascariensis (S)	1850	-0.02082 (0.08078)	0.08719 (-0.02323)	-0.10578 (0.02088)	0.10139 (-0.01267)
Gracula religiosa	1829	0.62554	0.15295	0.54100	0.12955
Passer domesticua	1870	0.04528 (0.14247)	0.07740 (0.00859)	-0.04281 (0.06366)	0.08937 (0.04868)
Padda oryzivora	1790	0.08369 (0.22356)	0.25844 (-0.16631)	0.00952 (0.20393)	0.26521 (-0.09357)
Mimus gilvus	1853	0.27673	-0.25310	0.17189	-0.24844
Ploceus melanocephalus	1929	-0.13431 (-0.05418)	0.00489 (0.00329)		
Ploceus velatus	1929	0.10697 (0.20653)	0.11371 (-0.03585)		

Serinus atrogularis	1929	-0.22417 (-0.14293)	0.01684 (-0.02180)		
Serinus canicollis	1850	-0.22858 (-0.15962)	-0.04374 (0.04949)	-0.32330 (-0.24059)	-0.02250 (0.01595)
Serinus flaviventris(S)	1776	-0.09716 (-0.00384)	0.04374 (0.01416)	-0.18735 (-0.07657)	0.05989 (0.00209)
Serinus mozambicus	1929	-0.21093 (-0.12204)	0.05271 (-0.05948)		
Sporopipes squamifrons	1929	-0.25632 (-0.15957)	0.05893 (-0.06376)		
Sturnus vulgaris	1852	0.32929	-0.01310	0.24638	-0.02967
Turdus merula	1820	0.35446	-0.15828	0.25646	-0.16507
Turdus philomelos	1820	0.22500	-0.18609	0.12622	-0.18797
Uraeginthus angolensis	1929	-0.22809 (-0.15021)	-0.03654 (0.04042)		
Uraeginthis granatina	1929	-0.08634 (-0.01349)	-0.06752 (0.06495)		
Vidua paradisaea	1929	-0.06981 (0.00750)	-0.00860 (0.06495)		
Vidua regia	1929	-0.23247 (-0.15844)	-0.00281 (-0.01192)		

Appendix B.
Species introduced to Saint Helena, followed by the date of introduction, present status on Saint Helena and calculated probability of success, P(success). All other places introduced and those introduction fates are listed as well. All information is taken from Long (1981) or Lever (1987).

Serinus flaviventris (Yellow Canary): 1776, Successful, P(success) = 1.00

Successful (1) - Ascension

Unsuccessful (0)

Padda oryzivora (Java Sparrow): 1790, Successful, P(success) = 0.81

Successful (25) - China, Hong Kong Island, South Vietnam, Singapore Island, Pinang Island, Myanmar, Sumatra, Lesser Sunda Islands, Pemba Island, Thailand, Sri Lanka, Borneo, Sulawesi, Moluccas, Philippines, Christmas Island, Cocos-Keeling Islands, Zanzibar, Hawaiian Islands, Fiji, USA, Puerto Rico, Tanzania, Japan, Taiwan

Unsuccessful (6) - Seychelles, Mauritius, Réunion, Archipel des Comores, New Zealand, Australia

Erithacus rubecula (European Robin): 1820, Failed, P(success) = 0.00

Successful (0)

Unsuccessful (4) - Australia, New Zealand, Canada, USA

Fringilla coelebs (Chaffinch): 1820, Failed, P(success) = 0.50

Successful (2) - New Zealand, South Africa

Unsuccessful (2) - Australia, USA

Euplectes orix (Red Bishop): 1820, Failed, P(success) = 0.60

Successful (3) - Australia, Puerto Rico, Hawaiian Islands

Unsuccessful (2) - Tahiti, Bermuda

Estrilda astrild (Common Waxbill): 1820, Successful, P(success) = 0.79

Successful (15) - Mauritius, Ascension, Rodrigues, Amirante Islands, Seychelles, Réunion, Cape Verde Islands, Tahiti, New Caledonia, Brazil, Puerto Rico, São Tomé, Portugal, Bermuda, Hawaiian Islands

Unsuccessful (4) - Fiji, Madagascar, Archipel des Comores, Principé

Turdus merula (Blackbird): 1820, Failed, P(success) = 0.50

Successful (3) - Australia, New Zealand, Tasmania

Unsuccessful (3) - South Africa, USA, Fiji

Turdus philomelos (Song Thrush): 1820, Failed, P(success) = 0.50

Successful (2) - Australia, New Zealand

Unsuccessful (2) - South Africa, USA

Acridotheres tristis (Indian Myna): 1820, Successful, P(success) = 0.92

Successful (22) - Australia, New Zealand, South Africa, Seychelles, Réunion, Rodrigues, Mauritius, Madagascar, Archipel de Comores, Chagos Archipelago, Ascension Island, Solomon Islands, Cook Islands, Fiji, New Caledonia, Society Islands, Hawaiian Islands, New Hebrides, Agalega Islands, Laccadive Island, Maldive Island, South Africa.

Unsuccessful (2) - USA, England

Alauda arvensis (Skylark): 1820, Failed, P(success) = 0.88

Successful (7) - New Zealand, Australia, Hawaiian Islands, Vancouver Island (Canada), Tasmania, Kangaroo Island, Lord Howe Island

Unsuccessful (1) - USA

Gracula religiosa (Hill Myna): 1829, Failed, P(success) = 0.75

Successful (3) - Hawaiian Islands, USA, Puerto Rico

Unsuccessful (1) - Christmas Island

Serinus canicollis (Cape Canary): 1850, Failed, P(success) = 0.33

Successful (1) - Réunion

Unsuccessful (2) - Mauritius, Tahiti

Foudia madagascariensis (Madagascar Weaver): 1850, Successful, P(success) = 1.00

Successful (7) - Amirante Islands, Seychelles, Chagos Archipelago, Mauritius, Reunion, Rodrigues, Agalega Islands

Unsuccessful (0)

Sturnus vulgaris (European Starling): 1852, Failed, P(success) = 0.50

Successful (6) - North America, Jamaica, South Africa, Australia, New Zealand, Puerto Rico.

Unsuccessful (3) - Cuba, Venezuela, Russia

Mimus gilvus (Tropical Mockingbird): 1853, Failed, P(success) = 0.75

Successful (3) - Colombia, Panama, Trinidad and Tobago

Unsuccessful (1) - Barbados

Passer domesticus (House Sparrow): 1870, Failed, P(success) = 0.85

Successful (29) - North America, South America, Easter Island, Falkland Islands, Cuba, St. Thomas, Bermuda, Hawaiian Islands, Australia, Norfolk Island, New Zealand, New Hebrides, New Caledonia, Senegal, Kenya, South Africa, Zanzibar, Archipel des Comores, Seychelles, Mauritius, Réunion, Rodrigues, Chagos Archipelago, Azores Islands, Cape Verde Islands, Amirante Islands, Puerto Rico, Java, Andaman Islands

Unsuccessful (5) - Greenland, Philippines, South Georgia, New Guinea, Jamaica

Carduelis chloris (Greenfinch): 1870, Failed, P(success) = 0.80

Successful (4) - Australia, New Zealand, Azores Islands, Uruguay and Argentina

Unsuccessful (1) - USA

Uraeginthus angolensis (Blue Waxbill): 1929, Failed, P(success) = 0.50

Successful (1) - Hawaiian Islands

Unsuccessful (1) - Tahiti

Amandava subflava (Orange Waxbill): 1929, Failed, P(success) = 0.00

Successful (0)

Unsuccessful (1) - Tahiti

Serinus mozambicus (Yellow—fronted Canary): 1929, Failed, P(success) = 0.75

Successful (6) - Mauritius, Réunion, Rodriques, Hawaiian Islands, USA, Puerto Rico

Unsuccessful (2) - Amirante Islands, Tahiti

Euplectes albonotatus (Whitewinged Widow): 1929, Failed, P(success) = 1.00

Successful (1) - Australia

Unsuccessful (0)

Introduced only to Saint Helena:

Estrilda erythronotos (Blackcheeked Waxbill): 1929 Failed

Estrilda melanotis (Yellow-bellied Waxbill): 1929 Failed

Euplectes progne (Longtailed Whydah): 1929 Failed

Pytilia melba (Green-winged Pytilia): 1929 Failed

Ploceus velatus (Redeyed Masked Weaver): 1929 Failed

Serinus atrogularis (Blackthroated Canary): 1929 Failed

Sporopipes squamifrons (Scalyfronted Finch): 1929 Failed

Uraenginthus granatinus (Grenadier Waxbill): 1929 Failed

Vidua paradisaea (Longtailed Paradise Widow): 1929 Failed

Vidua regia (Short-tailed Widow): 1929 Failed

Part 3

Introduced avifaunas as natural experiments in community assembly

Introduction

In 1975, Jared Diamond hypothesized a series of rules for assembling communities of birds on islands in the south Pacific. In large part these rules were based on incidence functions which dealt with the probability of species occurrence as a function of species richness (Diamond 1975). His work sparked a heated debate and the concept of "assembly rules" was largely put to rest (Connor and Simberloff 1979, Gilpin and Diamond 1982). Perhaps one of the most serious, and yet least appreciated, problems with applications of assembly rules is that they are in practice based principally, if not exclusively, on extant community membership (e.g., Wilson and Roxburgh 1994, Fox and Brown 1993). As Diamond (1975) noted, the principal goal in elucidating assembly rules is to discover why some species become members of a community and some do not. How can we decide the true criteria for inclusion in a community without knowledge of criteria for rejection?

In order to derive meaningful assembly rules, we argue that one must begin with knowledge of all species once present, but now missing, from communities. In natural communities, a knowledge of this depth is generally lacking, reducing the strength of tests for assembly rules. Communities of non–indigenous bird species represent a companion system in which to study the effects of various selection criteria for community membership. Within such communities we often have a very thorough

knowledge of which species failed to become community members enabling us to evaluate the influence of specific mechanisms of membership rejection.

We based the analyses described below on a data set that includes the passeriform species introduced on four oceanic islands; Oahu, Tahiti, Saint Helena, and Bermuda. Non–indigenous bird species have been accidentally or intentionally introduced for centuries on these islands (Long 1981). With the help of ardent bird watchers past and present, we have very clear records of which species were introduced, in what manner, and when, and if they became extinct (Moulton and Pimm 1983).

We reconstruct the assembly history of each island avian community using this information. With this reconstructed assembly trajectory we can build sensible null models with which to compare the extant assemblage. We built two of the tests below specifically to search for patterns produced by interspecific competition: one of the most often cited, and controversial, criterion for membership rejection (see reviews by Connell 1983, Schoener 1983). An alternate, and equally plausible criteria for rejection, is that a particular species simply is not intrinsically capable of surviving within the new environment (Simberloff 1992). Thus, we also look for patterns of

success associated with a species' native range size which is believed to reflect a species intrinsic ability to compensate for environmental variability (Williamson 1996).

Results of previous studies of introduced birds have been conducted mostly on an island by island basis (Lockwood and Moulton 1994, Brooke et al. 1995, Moulton 1993, Lockwood et al. 1993, 1996). Here, we attempt a much broader view of the phenomena of introduced avian community assembly by incorporating a large number of species (99) across four oceanic islands. We address each of the three patterns described above in more detail individually and completely before moving to the next. First, however we must describe the species introduced, the islands, and the circumstances surrounding the introduction events.

The Islands

All four islands are oceanic although they vary in degree of geographical isolation. Bermuda is perhaps the least isolated recording more than a hundred migrants every year (Wingate 1973). Oahu and Tahiti are members of archipelagos and thus may receive natural immigrants from other nearby islands, but not from any mainland source. Saint Helena is the most geographically isolated sitting alone over 2000 km off the Cape of Africa in the Atlantic Ocean. It is thus doubtful that Saint Helena is subject to any

regularly occurring attempts at natural colonization. Bermuda is temperate and relatively small (51 km^2). Tahiti and Oahu are tropical islands with sizes of 1057 km^2 and 1536 km^2 respectively. Saint Helena is also tropical but relatively small in size (122 km^2).

Each island has had a significant proportion of its native flora and fauna altered through human manipulation (Moulton and Pimm 1983, Brooke et al. 1995, Lockwood and Moulton 1994, Lockwood et al. 1993). There remain however, some physiographic differences between islands. For example, Bermuda and Saint Helena are relatively low relief islands in which nearly all native forest has been cleared (Wingate 1973, Benson 1950). Tahiti and Oahu are high relief islands that still retain a small, but significant, portion of their native forests (Moulton 1992, Lockwood et al. 1993).

Through field observations on each island it is our impression that most successful species are utilizing suburban or disturbed habitat rather than the remaining native habitat (R. Brooke, pers. com.). This is supported by others conducting avian surveys on each island (Scott et al. 1986, Crowell and Crowell 1976, Haydock 1954). Not only are the avian assemblages of human derivation, but so too are the habitats that sustain them. The introduced passeriforms on each island make their living from suburban lawns, parks, and city streets thus reducing the variability in habitat across islands.

The Formulation of the Species Pool

Perhaps the most important aspect of determining a criteria of rejection is determining which species one should include in the species pool. The pool consists of all species likely to have attempted establishment during the assembly history. The first step in formulating the pool is by far the easiest and most enjoyable: determining the composition of the extant community. In all the data sets described below, the extant community was determined by combining field observations by JLL, MPM or R. Brooke with recently published field guides (e.g., Pratt et al. 1987, Wingate 1973). The second step involves an in-depth exploration into the published literature. We compiled lists of species introduced from published references and references contained within the following: Saint Helena; Brooke et al. (1995), Tahiti; Lockwood et al. (1993), Bermuda; Lockwood and Moulton (1994), and Oahu; Moulton (1993).

The results of this search revealed that across all four islands a total of 99 species have been introduced incorporating 131 total introduction events (see appendix). Of the 24 species introduced on more than one island, only one, the Common Waxbill (*Estrilda astrild*), was introduced on all four islands. These islands are clearly not geographically close enough to exchange species. Thus, each island represents a relatively distinct assemblage with its own unique avifaunal assembly history.

These references were also the basis for decisions regarding when species were introduced as well as if and when they failed. On some occasions there was a significant lag between published references concerning which species were present on what island. For example, two species on Bermuda were introduced around 1800 but, were not referred to again until 1957 (Bourne 1957). In this account, Bourne indicated that these species had not established after initial introduction however, he gave no date of last sighting. Thus, we counted each species as being present between 1800 and 1957. Such difficulties do not influence our results as long as we can place each species' time of extinction relative to all others. In this case, no species introduced between 1800 and 1957 subsequently went extinct.

Of the 131 introduction events, we count 46 as successful and 85 as failed (35%). However, the individual island success rates varied considerably (see table 3–1). Saint Helena and Tahiti had similar overall success rates at 16% (5 of 31) and 17% (7 of 41) respectively. A total of 45 species were released on Oahu, 27 of those are currently considered successful (60%). On Bermuda there were 14 exotic species introductions and half of those were successful (50%). There is a slight tendency for the number of successful species to increase with island size ($P = 0.2668$, $R^2 = 0.538$, see figure 3–1).

The first two of our three tests are sensitive to various influences on the formation of the species pool. There is one criterion, however that we universally follow. We excluded species that invaded one of the islands naturally or in which only 5 or fewer individuals were known to have been released as these species' fates would more likely be determined by stochastic processes. The other influences include the phylogenetic variability seen within the species pool, the timing and method of introduction, and the presence or absence of a native avifauna. We deal with each in turn.

Table 3–1. Success rates for each island: the number of successful species out of the number of passeriforms introduced. Also, priority effect and morphological overdispersion results for each island avifauna.

Island	**Success Rate**	**Priority Effect**	**Morphological Overdispersion**
Saint Helena	5 out of 31 (16%) or 5 of 17 excluding 1929 intro.'s (29%)	Yes	Yes, in finches
Tahiti	7 out of 41 (17%)	Yes	Yes
Bermuda	7 out of 14 (50%)	Yes, if incl. natives	Yes
Oahu	27 out of 45 (60%)	Yes, if species intro. after 1960 excluded	Yes

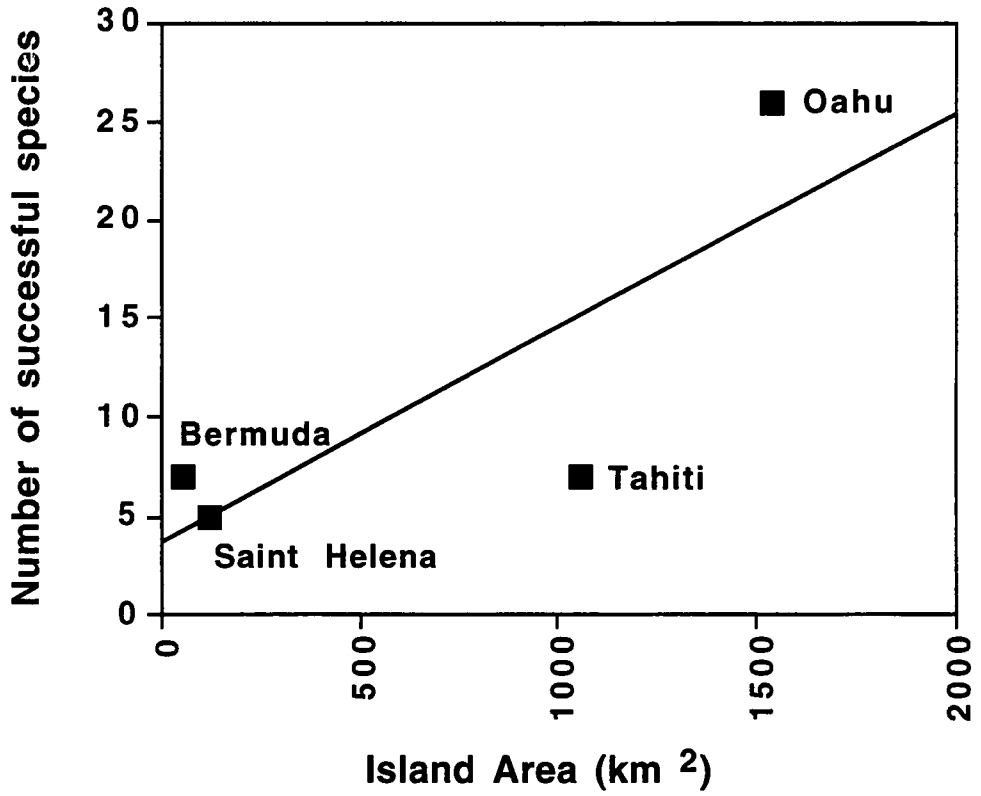


Figure 3–1. The number of species which successfully established on each island according to island area. The number of successful introductions increases broadly with island area.

Colwell and Winkler (1984) point to a potential bias in the formation of the species pool due to the amount of phylogenetic variability incorporated. Simply, if we include a species with an extreme morphology in the pool, the remaining species will appear clumped in any morphologically defined space. Since morphological characters are conserved within phylogenetic lineages, the likelihood of including an extreme morphology correlates with to the degree of variability seen within the species pool (Colwell and Winkler 1984). An extreme species (or group of species) included within a group of very similar species serves to obscure any pattern present.

We argued in Lockwood et al. (1996) that in order to avoid a J.P. Morgan effect we must look only within the group of finches introduced to Saint Helena. Finches make up the overwhelming majority of all species introduced (74%) and species that were successful (84%: Lockwood et al. 1996). Clearly, within this group competition will be the strongest as they all feed and nest in very similar fashion (Clement et al. 1993). The presence of distantly related species in the pool may obscure any competitively generated pattern.

The introduction events ranged in time from 1776 to the mid–1980's, with most occurring during the late 1800's to early 1940's. Recently introduced species (i.e., within the past 20 years) are often difficult to place as either successful or failed. This is especially true if some species are currently

present in small numbers or are restricted to a particular habitat. We should perhaps consider these species "the walking dead" (Simberloff 1992) rather than successful colonizers. This is the case with several species introduced to Oahu since 1960. However, most other species considered here were released several years before the present (e.g., the last species released on Saint occurred 67 years ago). The remaining few are very clearly successful (e.g., the Great Kiskadee was released on Bermuda in the 1970's and is currently one of the most common birds observed there; Wingate 1973).

The modes of introduction varied across islands however, we can classify them into the following categories: ship or airplane stow–a–ways, cage escapees, and purposeful introductions (Long 1981, Lever 1987). No individual or group introduced avian species on more than one of these islands. However, on two islands (Tahiti and Saint Helena) one individual was responsible for the release of the majority of species we included in the species pool. The circumstances surrounding each introduction event is unique and influenced how we constructed each pool differently.

On Tahiti, Eastham Guild released 85% (35 of 41) of all species introduced (Guild 1938, 1940; Lockwood et al. 1993). Only two of these survived, although we know Guild exerted considerable effort to ensure proper release (Guild 1938, 1940). Guild kept individuals in an aviary for some time after

their arrival allowing him to remove diseased or sick birds. Further, Guild and other island residents established feeding stations to enhance the bird's chances for success. For these reasons, we felt it appropriate to include in the pool all the species Guild released.

H. Bruins–Lich released 45% (14 of 31) of all species introduced on Saint Helena (Haydock 1954, Brooke et al. 1995). We have made the argument previously that these species should be excluded from the pool (Brooke et al. 1995) as we have very little information on the release methods. Further, none of the 14 species he released were successful. Thus, unlike Guild, we can not dismiss the possibility that he may have in some way inadvertently doomed all of these species to failure. For this reason, we conducted our analyses with and without these 14 species.

On all islands except Bermuda, the native passeriform fauna was either decimated before introductions occurred (Brooke et al. 1995) or severely restricted in range or numbers (Lockwood et al. 1993, Moulton 1993). Thus, on these three islands interactions between native and exotic passeriforms is minimal at best (Brooke et al. 1995, Lockwood et al. 1993, Moulton 1993). However, on the island of Bermuda three native passeriforms remain that are wide–spread and abundant (Wingate 1973, Lockwood and Moulton 1994). These are the Gray Catbird (*Dumetella carolinensis*), Eastern Bluebird (*Sialia*

sialis), and the White–eyed Vireo (*Vireo griseus*). We can not discount native–exotic interactions when looking for pattern within this community. We include the three native species on Bermuda where appropriate.

Priority Effect

If the group of species that successfully colonized a particular island did so when significantly fewer other species were present, we say this community exhibits a priority effect (Moulton 1993). Simply, species which arrive first are less likely to encounter competitors which may preclude their establishment. Once establishment is ensured, these same species are more likely to become competitively dominant over later arrivals (Alford and Wilbur 1985). We would expect this pattern if interspecific competition was the predominate criteria for membership rejection.

Methods

Moulton (1993) details the procedure for testing for a priority effect. Briefly, we rank each species introduced to a particular island according to its date of introduction. For each species, we calculated the number of other introduced species present on the island at the time of introduction. Using a Mann–Whitney U test, the mean number of other species present for failed introductions is compared to the mean for the group that was successful. We considered each island separately.

Results

All of our island avifaunas exhibits a priority effect (table 3-1). The most pronounced patterns are within the species introduced on Saint Helena and Tahiti. On Tahiti, the average number of other species present for successful species is 13.14, whereas for failed species it is 38.0 ($P > \chi^2 = 0.0032$). The average number of species faced by successfully introduced species on Saint Helena was 5.4 and for unsuccessful species 14.15 ($P > \chi^2 = 0.0009$: Brooke et al. 1995). As noted above, there is reason to exclude the 1929 introductions on Saint Helena. Their inclusion certainly inflates the priority effect. However, even if we exclude these species, the priority effect on Saint Helena still holds ($P > \chi^2 = 0.008$).

The Bermuda avifauna exhibits a priority effect when we include the native species as the first to arrive, which undoubtedly they were ($P < \chi^2 = 0.057$, mean successful = 5.6, mean failed = 9.14). However, we do not know how many other species the natives encountered when they first arrived. One could argue that we should exclude the natives from the analysis and only count them as 'other species present' in our calculations. If we 'fix' the natives into the analyses in this way, there is no evidence for a priority effect ($P < \chi^2 = 0.252$, mean successful = 7.14, mean failed = 9.14).

Moulton (1993) conducted tests for the priority effect among the introduced passeriforms of Oahu. Originally, Moulton and Pimm (1983) excluded species introduced to Oahu after 1960 as they believed the current status of these species was uncertain. If we examine only species introduced prior to 1960, as is in Moulton and Pimm (1983), we observe a priority effect ($P > \chi^2 = 0.009$, mean successful = 12, mean for failed = 19).

After more than 10 years of continued monitoring of these questionable species beyond 1983, we have a much better picture of which species have become established and which have not (Moulton 1993). When we updated the list to include introductions up to 1981 (thus still excluding very recent introductions due to their questionable status), there is no evidence for a priority effect ($P < \chi^2 = 0.235$, mean for successful = 17.5, mean for failed = 20).

Discussion

In four independent assemblies, we can statistically show the influence of a priority effect. This result is consistent with the hypothesis that interspecific competition was the predominate criteria of membership rejection in each assembly. A priority effect results if a species which establishes early encounters fewer competitors and has a greater chance of being competitively dominant than does a later arrival (Alford and Wilbur 1985).

With this in mind, it is not surprising that we do not consistently find evidence for a priority effect within the avifaunal assemblages on Oahu and Bermuda. In each case, we are saddled with a lack of sufficient knowledge concerning which species were truly 'early' and which of the 'late' arrivals failed to establish. We do not know what set of species may have been present when the three Bermuda natives first colonized the island. Similarly, we do not know how to classify the outcomes of species introduced recently on Oahu even though we do know the set of species they likely encountered. Our results depend on how we compensate for this lack of knowledge.
It is thus clear that insufficient information on the assembly history, and thus about the circumstances of membership rejection (i.e., competition or not), influences our perception of the assembly process.

Morphological Overdispersion

Morphological overdispersion will result if the species that successfully colonized a community are more spread–out in morphological space and more evenly positioned than what is expected by chance (Lockwood et al. 1993, Moulton and Pimm 1987). Overdispersion is also consistent with the hypothesis that interspecific competition determined community membership.

Methods

We measured several morphological variables (beak width, depth, and length and wing length) on all species introduced from museum specimens housed at the Los Angeles County Museum of Natural History or the United States National Museum of Natural History. We chose each morphological variable because of a known correlation with some aspect of avian ecology (Ricklefs and Travis 1980, Grant 1986). There are two possible approaches when deciding how many morphological variables to incorporate into such an analysis. The first is to include only one variable, and preferably one that reflects a multitude of ecological characteristics (for example body size). The second is to include several variables in the hopes of homogenizing any variability seen within any one correlation. Thus, if a species whose body size is not highly linked to its food preference, maybe its beak shape is, and in a multivariate analysis this would not go unnoticed (Ricklefs and Travis 1980, Karr and James 1976, Findley 1973, 1976).

These raw variables are then log-transformed to normalize the inherent variability of such measurements and a principal components analyses is conducted using the covariance matrix (Ricklefs and Travis 1980). The first two principal component scores invariably accounted for the majority of the variance seen within the raw data in our analyses (i.e. > 90%). The first principal component typically reflected body size and accounted for the

majority of the variability within the data. The second principal component typically reflected the size and shape of the beak relative to the body size and accounted for significantly less variance.

We then plot each species in two–dimensional space according to its first two principal component scores. The minimal spanning tree (MST) is used as a measure of dispersion within this morphological space and thus becomes our test statistic. The MST is the minimum sum of the lengths of n-1 line segments that connect n points such that no loops are created (Ricklefs and Travis 1980). We use the standard deviation (SDEV) of the MST line segments as a measure of how evenly positioned the species are in that space.

An MST is drawn for the extant set of species on each island and then compared to a null distribution of MST values derived from Monte Carlo simulations (Ricklefs and Travis 1980). Thus, if an introduced community comprises 10 species and we know 20 species were introduced, MSTs are calculated for 1000 random selections of 10 species from the pool of 20. We consider an observed community to be morphologically overdispersed if a large proportion (i.e., 90 - 95%) of null community MST values are simultaneously smaller and more evenly spaced than the observed. Again, we considered each island avifaunal assemblage separately.

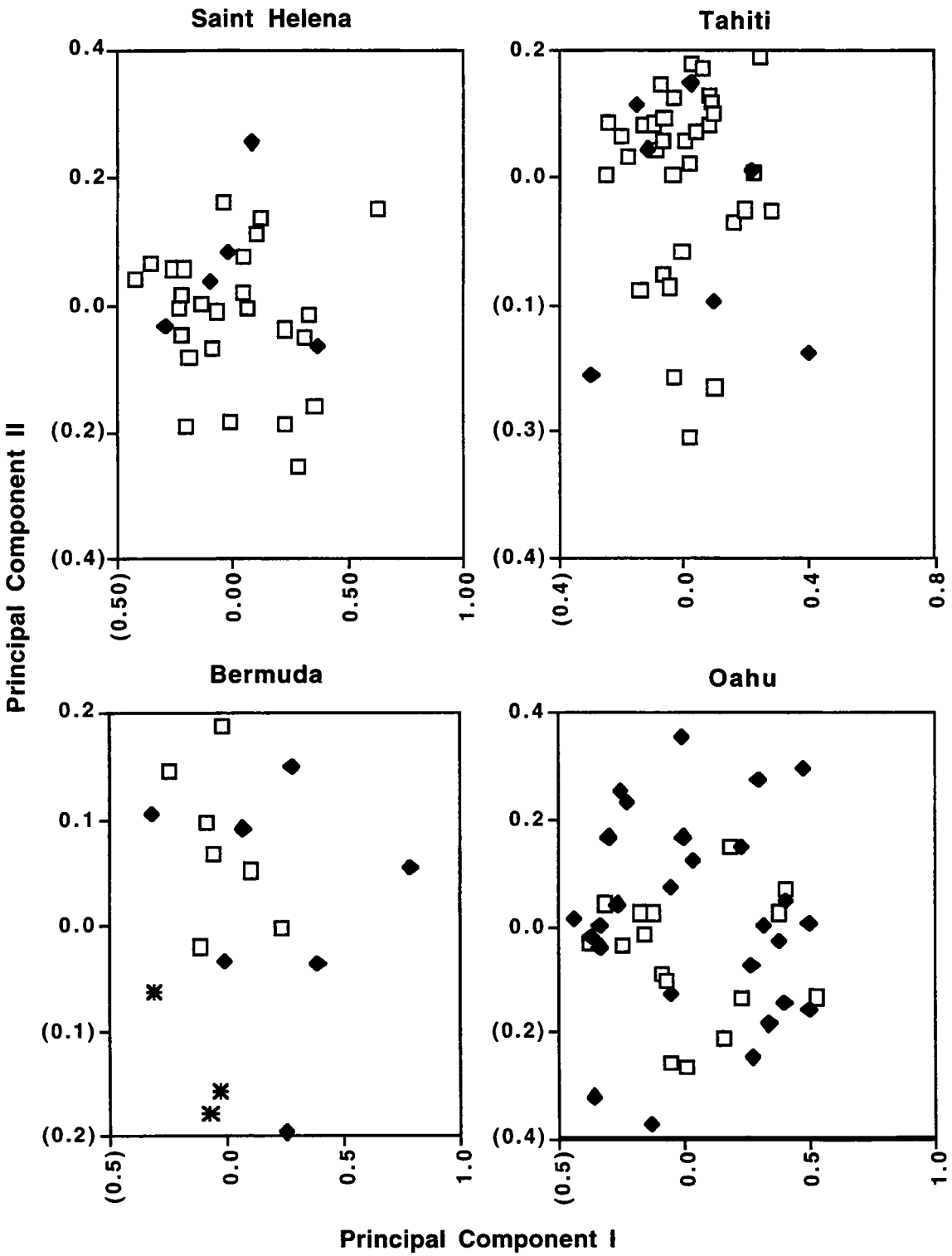
The observed passeriform communities on Bermuda, Tahiti and Saint Helena were all compared to 1000 randomly constructed communities (Lockwood et al. 1993, 1996; Lockwood and Moulton 1994). However, the extant assemblage on Oahu was compared only to 200 random communities (Moulton 1993). For a more detailed account of methods see Lockwood et al. (1993).

Results

Moulton and I have previously tested for morphological overdispersion among the successful passeriforms on all four islands (Lockwood et al. 1993, 1996; Moulton 1993, Lockwood and Moulton 1994). Here we provide only a brief review of our results (see figure 3–2 for all morphological spaces). Oahu, Tahiti and Bermuda all exhibited pronounced overdispersion while simultaneously being more evenly spaced among all successful passeriforms introduced (Oahu: $P = 0.035$, Tahiti: $P = 0.002$). On Bermuda, this is true regardless of whether or not we fixed the native species in the morphological space ($P = 0.006$) or considered them part of the species pool ($P = 0.014$).

On Saint Helena we searched for overdispersion among all introduced passeriforms and among only the group of finches to compensate for a potential J.P. Morgan Effect (see above). We show the group of introduced finches are morphological overdispersed ($P = 0.092$). As noted above, there are compelling reasons to exclude the 14 species released in 1929. The finches

Figure 3–2. The morphological spaces defined by the first two principal component scores for all island avifaunas considered. Principal component I is typically a measure of overall body size. Principal component II indicates beak dimensions relative to overall body size. Graphs are redrawn from: Lockwood and Moulton (1994), Lockwood et al. (1993), and Moulton and Pimm (1987), Lockwood et al. (1996). Closed diamonds represent successful species; Open squares represent failed species; Stars represent native species.


Saint Helena
Tahiti
Bermuda
Oahu
Principal Component II
Principal Component I
0.4
0.2
0.0
(0.2)
(0.4)
(0.50)
0.00
0.50
1.00
0.2
0.0
(0.1)
(0.3)
(0.4)
0.0
0.4
0.8
0.2
0.1
0.0
(0.1)
(0.2)
(0.5)
0.0
0.5
1.0
0.4
0.2
0.0
(0.2)
(0.4)
(0.5)
0.0
0.5
1.0

introduced prior to 1929 are still overdispersed (7.6%). However, the set of all species introduced are not overdispersed (P = 0.139), nor are the surviving species introduced before 1929 (P = 0.301).

Discussion

In all four independent assemblies, we see the pattern of morphological overdispersion. Overdispersion, like the priority effect, is consistent with the hypothesis that interspecific competition was the predominate criteria for species rejection. Thus, using two methodological approaches, we come to the same general conclusion: competition between existing community members and those that are newly released often determines the fate of new colonizers.

Morphological overdispersion will only result if two criteria are met. First, interspecific competition must be strong enough to drive one of the competitors to extinction. Second, competition must be wide-spread enough to effect all the species included in the species pool (Moulton and Pimm 1987). Thus, determining the composition of the species pool takes on added importance. A balance must be struck between including all species in the community and only those that are likely to compete intensely and extensively enough to perhaps produce pattern. This balance is sometimes

tenuous as is the case with the introduced avifauna of Saint Helena. It is not clear if the 8 phylogenetically (and thus morphologically) distinct species released on Saint Helena significantly altered the chances that the set of finches released would successfully colonize. Clearly, how we answer that question influenced the results we obtained.

We simultaneously solve many problems by defining the species pool as all the passeriforms introduced onto an oceanic island (i.e., we know who, how, and why species attempted colonization on the island). This is a luxury that those working within natural systems do not enjoy. Indeed, the lack of predators, native species and natural colonizers on oceanic islands makes the definition of an island community all the easier. However, it does not solve all problems of definition. Our results indicate that the definition of the species pool, and the extent of the community itself, can play a considerable role in how we determine a rejection criteria.

Size of Native Range

Finally, we test a hypothesis set forth by Moulton and Pimm (1986) and Daehler and Strong (1993) that species which have expansive native ranges will more likely successfully colonize a new locale after introduction. Species with larger range sizes may exhibit greater inherent ecological or physiological flexibility or may be better dispersers (Williamson 1996, Brown

1995). These species thus may be pre-disposed to be successful invaders no matter where released or what other species may be present (for the alternate view see Hanski et al. 1993). This is consistent with the 'All or None' hypothesis of Simberloff and Boecklen (1991) which has been put forth as an alternative explanation for patterns observed above. Thus, we explore the same data set to test this hypothesis as well.

It is important to note here that we can test this hypothesis directly. In the above tests, we were forced to build null models to compare with extant assemblages. Here, we can simply estimate the range size and the number of times a species was successfully introduced and look for correlations between the two variables.

Methods

We estimated native range sizes from maps in Long (1981) following the methods of Moulton and Pimm (1986). We placed a grid over each map and counted the number of intersecting points within the native range specified by Long (1981). We then divided the number of intersections by the number within the continent of Australia to standardize range sizes between maps (there were two map sizes). Thus, we calculated relative range sizes and not exact range sizes. All species were ranked according to their relative range size and grouped as either successful or failed. We compare mean range sizes for each group using a Mann–Whitney U test. We consider all introduction

events in this analysis across all islands. Thus, if the same species was introduced on two or more islands, each introduction was counted as an independent event. We further tested for effects of range size on an island by island basis.

Results

There were 131 independent introduction events (99 species) recorded as occurring on the four islands. However, there were 12 species for which Long (1981) provided no native range maps. We thus excluded any introduction events associated with these species. Of the remaining 118 introduction events (87 species), 41 were successful and 77 failed. The average relative range size of the 41 successful species was 0.96, whereas the average relative range size for failed species was 1.09. There was no statistical difference between these two means ($P > \chi^2 = 0.617$).

It may be that the species comprising one or more island communities do show increased chances for success based on their native range sizes if the island communities are considered independently. Our result above may mask effects present at the island level. Thus, we conducted the above test on an island by island basis. None of the island communities showed significant correlations between successful establishment and large native range (see table 3–2).

Table 3–2. Island by island analyses of the effect of native range size on the probability of successful establishment after introduction. None of the islands showed an effect. In addition, there is no effect shown when each species' introduction is considered an independent event. Thus, a large native range does not appear to be a dominant influence on the successful establishment of a species in an assembling community.

Island	**Average range size of successful species**	**Average range size of failed species**	**Associated probability**
Saint Helena	0.589	1.44	P = 0.1054
Tahiti	0.687	0.491	P = 0.2912
Bermuda	2.35	1.23	P = 0.1792
Oahu	1.04	0.736	P = 0.5541

Discussion

To some degree, all species that strive for membership in a community face a novel situation. The species they encounter will likely not be the same as those present in the community from which they originated. The variability in abiotic conditions will also not be the same. This is certainly more pronounced when we consider human mediated introductions. These species are often transported to remote areas and released (Long 1981, Lever 1987). Thus, we may expect that patterns regarding native range size will be more pronounced within species introduced by human actions.

Our results however, indicate that range size in itself is not a good predictor of successful establishment within an assembling community. There are clearly species–specific attributes that will influence establishment within a particular context. Indeed, there is a growing sub-discipline surrounding the topic (see volumes by Drake et al. 1989, Williamson 1996 , Kareiva 1996). It is not clear that any one, or even a small suite, of these characteristics will consistently determine a species fate when attempting to enter a community (Williamson and Fritter 1996, Gilpin 1990). In other words, species–specific attributes may predict success under some circumstance but not all. Our results indicate this is true if such attributes are used as predictors within a unique assembly (within an island community) or across several independent assemblies (across several island communities). Thus, we suggest that assembly rules based on these attributes are subsumed by broader rules operating at the community level (e.g., priority effects).

We again point to the deficiency of natural experiments in determining a true criterion of rejection even when directly testing the predictive ability of species-specific attributes in introduction success. The attribute of a generalist as a good 'invader' has persisted for some time (Williamson 1996). However, it is difficult to decide if this a true assembly 'rule' when we do not know how many generalists (and specialists) did not successfully invade a community.

Summary and Conclusion

We suggest that the determination of 'rules' that govern the assembly of natural communities is riddled with several methodological flaws. The first of which is the inability to determine a true criteria of rejection when looking only within an extant community (Drake 1991). However, our results indicate that even when we use companion systems of introduced avifaunas we can not always gain a clear picture of those criteria. There remain questions concerning introduction timing and the definition of the species pool. Most analyses of natural communities uniformly ignore such questions.

Our results, some new and some summarized here, indicate that interspecific competition can play a deciding role in which species will become community members. They also point to a deficiency in the predictive ability of species–specific attributes in determining success. Any criteria, if it is to prove useful as an assembly rule, must provide an acceptable predictive ability across many assembly scenarios. As yet, we believe neither of these two hypothesized rules completely fits the bill.

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Appendix. All species introduced on Oahu, Tahiti, Saint Helena or Bermuda. DI = Date of introduction. F = Failed. S = Successful. Oahu dates taken from Moulton (1993), Tahiti from Lockwood et al. (1994), Saint Helena from Brooke et al. (1995), and Bermuda from Lockwood and Moulton (1994).

SPECIES	Oahu	DI	Tahiti	DI	Saint Helena	DI	Bermuda	DI	Relative Range Size
Pitangus sulphuratus							S	1950	1.76923076
Corvus brachyrhynchos							S	1876	2.30769230
Rhipidura leucophrys	F	1926							1.30769230
Grallina cyanoleuca	F	1922							1.23076923
Dumetella carolinensis							N	native	
Sialia sialia							N	native	
Sialia mexicana			F	1938					0.46153846
Turdus merula					F	1820			2.84615384
Turdus philomelos					F	1820			2.84615384
Cyanoptila cyanomelana	F	1929							
Erithacus rubecula					F	1820			2.07692307
Luscinia akahige	F	1929							
Luscinia komadori	F	1931							
Copsychus malabaricus	S	1939							1.23076923
Copsychus saularis	F	1932							
Sturnus vulgaris					F	1852	S	1950	3
Acridotheres tristis	S	1872	S	1908	S	1820			0.40909090
Gracula religiosa	S	1960			F	1829			0.61538461
Mimus gilvus					F	1853			0.46153846
Mimus polyglottos	S	1928	F	1938			F	1983	1.07692307
Parus varius	F	1928							0.23076923
Pycnonotus cafer	S	1966	S	1979					0.53846153
Pycnonotus jocosus	S	1965							0.46153846
Zosterops japonicus	S	1929							0.30769230
Zosterops lateralis			S	1938					0.30769230
Cettia diphone	S	1929							0.53846153
Garrulax caerulatus	S	1947							
Garrulax canorus	S	1900							0.38461538
Leiothrix lutea	S	1928	F	1938					0.30769230
Alauda arvensis	S	1847			F	1820			4.53846153
Passer domesticus	S	1871			F	1870	S	1870	5.90909090
Passer montanus							F	1800	3.45454545
Sporopipes squamifrons					F	1929			0.23076923
Ploceus capensis							F	1970	0.15384615

Ploceus velatus					F	1929			1.15384615
Foudia madagascarensis					S	1850			0.07692307
Euplectes albonatus					F	1929			0.38461538
Euplectes progne					F	1929			0.30769230
Euplectes orix			F	1938	F	1820	F	1970	1.15384615
Pytilia melba					F	1929			1.15384615
Lagonosticta senegala	F	1965	F	1938					1.69230769
Estrilda astrild	S	1981	S	1908	S	1820	F	1970	1.38461538
Estrilda caerulescens	S	1965							
Estrilda erythronotus					F	1929			0.46153846
Estrilda melpoda	S	1965	F	1938			S	1970	0.53846153
Estrilda melanotis					F	1929			0.61538461
Estrilda troglodytes	F	1965	F	1938					0.38461538
Uraeginthus angolensis	F	1965	F	1938	F	1929			0.46153846
Uraeginthus bengalus	F	1965	F	1938					0.92307692
Uraeginthus cyanocephala	F	1965							0.07692307
Uraeginthus granatinus					F	1929			0.53846153
Amandava amandava	S	1900	F	1938					0.46153846
Amandava subflava			F	1938	F	1929			1.30769230
Stagonopleura guttata			F	1938					
Erythrura psittacea			F	1938					0.07692307
Erythrura cyaneovirens			F	1938					0.07692307
Erythrura prasina			F	1938					0.30769230
Erythrura trichroa			F	1938					0.07692307
Neochmia modesta			F	1938					
Neochmia ruficauda			F	1938					0.23076923
Neochmia temporalis			S	1899					
Poephila acuticauda			F	1938					0.07692307
Taeniopygia bichenovii			F	1938					
Chloebia gouldiae			F	1938					0.07692307
Lonchura oryzivora	S	1964			S	1790			
Lonchura castaneothorax			S	1899					0.23076923
Lonchura cucullata			F	1938					1.38461538
Lonchura fringilloides			F	1938					1
Lonchura malabarica	S	1984							1.15384615
Lonchura malacca	S	1936	F	1938					0.53846153
Lonchura punctulata	S	1883	F	1938					0.76923076
Vidua macroura	F	1962							1.76923076
Vidua paradisea					F	1929			0.76923076
Vidua regia					F	1929			0.38461538
Fringilla coelebs					F	1820			2.38461538
Serinus atrogularis					F	1929			0.76923076
Serinus canaria							F	1968	0.07692307
Serinus canicollis					F	1850			0.15384615
Serinus flaviventris					S	1776			0.30769230

Serinus leucopygius	F	1965							0.30769230
Serinus mozambicus	S	1964	F	1938	F	1929			1.07692307
Carduelis carduelis							S	1800	2.40909090
Carduelis chloris					F	1870			1.84615384
Carduelis tristis			F	1938			F	1800	1.30769230
Carpodacus mexicanus	S	1870							0.76923076
Paroaria coronata	S	1928							0.30769230
Paroaria dominicana	F	1931							0.15384615
Tachyphonus rufus			F	1938					1.23076923
Ramphocelus bresilius			F	1938					0.15384615
Ramphocelus carbo			F	1938					0.92307692
Ramphocelus dimidiatus			S	1938					0.07692307
Thraupis episcopus			F	1938					0.84615384
Tangara arthus			F	1938					0.23076923
Tangara larvata			F	1938					
Cyanerpes cyaneus			F	1938					1.23076923
Sicalis flaveola	S	1965							0.76923076
Tiaris olivacea	S	1974							0.23076923
Passerina cyanea	F	1934							0.61538461
Passerina leclancherii	F	1941							0.07692307
Sturnella neglecta	F	1931							1.07692307
Cardinalis cardinalis	S	1929					S	1800	0.53846153
Vireo griseus							N	native	
Total Introductions	**45**		**41**		**31**		**17***		
Total Successes	**27**		**7**		**5**		**7**		

* includes native species

Nomenclature follows Sibley and Monroe (1990)

Part 4

Assembling ecological communities in time and space

Abstract

Ecological communities do not spring into existence overnight, but develop during the process we call assembly. As in other complex systems, random assemblies may generate surprising patterns. In previous models, sequential invasion and extinction moved successive species mixes toward a persistent one. Other species present in the pool could not invade this persistent mix. Chance events early in the assembly produced persistent mixes of different compositions. Most model species survive somewhere by belonging to one or more alternative persistent mixes. We show that with more rapid invasion, communities move through complex cycles of composition, where each species gets its turn. These complementary views offer insights into the diversity of natural communities. Importantly, they have practical implications for those attempting to restore diversity to damaged ecosystems.

Introduction

Community assembly, the addition and subtraction of species through time, can produce several surprising patterns (Diamond 1975; Drake 1990, 1991; Drake et al. 1993; Pimm 1991; Kauffman 1993). In early models, sequential invasion and extinction moved successive species mixes toward a persistent one. Other species present in the pool could not invade this persistent mix. Chance events early in the assembly produced persistent mixes of different compositions (Robinson and Edgemon 1988; Wilson 1992; Drake 1990, 1991;

Drake et al. 1993). Most model species survived somewhere by belonging to one or more alternative persistent mixes in a spatially extended system (Drake 1990, 1991, Drake et al. 1993, Wilson 1992). We know this algorithm has flaws (Morton et al. 1996). Species mixes developed sequentially – losing or gaining only one species at a time – because numerical integration of the intervening changes in population densities was too slow for the computers of the time. Using such numerical integration, we show that the same patterns still emerge for slow, sequential invasions. Our novel result is that with more rapid invasion, communities move through complex cycles of composition, where each species gets its turn.

Early models of community assembly employed Lotka-Volterra systems of differential equations with hundreds of parameters (Post and Pimm 1983; Drake 1990,1991; Drake et al. 1993; Wilson 1992). The large array of guessed parameters and untested assumptions begged our asking which features of assembly are model independent? One solution comes from experiments with microcosms (Drake 1991, Drake et al. 1993, Robinson and Edgemon 1988). A theoretical solution comes from scoring species as only present or absent and ignoring the detailed population dynamics (Luh and Pimm 1993).

This 'minimalist' view employs a hypercube as a metaphor for the assembly process (Luh and Pimm 1993). We can envision the 2^n different mixes of n

species as the corners of the n-dimensional hypercube. With sequential invasion and extinction, the temporally adjacent mixes are along the cube's edges. With three species, A, B, and C, the mix (just) B can change only to A+B, B+C or B can go extinct. Diagonal moves, say to mix A+C, are prohibited. Assign the direction of change between adjacent mixes as if by a coin toss. Either B can invade A or A excludes B; the probability of both events is $1/2$. A species mix will persist only if all the moves from the n temporally adjacent mixes are in its direction. The probability of this is $(1/2)^n$. The expected number of persistent mixes is the number of possible mixes times this probability = $2^n.(1/2)^n = 1$.

Only adjacent mixes are dependent: if mix B is persistent, mixes (no species), B+C and A+B cannot be, but mixes A, C and A+B+C may or may not be (figure 4–1). For large n, the small probability that any mix is persistent is independent of whether the many (= 2^n–n–1) other, non-adjacent mixes are persistent. Consequently, the frequency distribution of persistent mixes should be nearly Poisson, a prediction that simulations confirm for ($4 < n < 12$). Thus ~37% of assemblies (= $1/e$) have one persistent mix, ~14% (=$1/e^2$) have two persistent mixes, and so on (Luh and Pimm 1993).

The preponderance of persistent mixes and the commonness of alternative persistent mixes are thus not a consequence of the details of the Lotka–Volterra models. Rather, they are general features of community assembly.

Interestingly, this simple analysis shows how crucial is the assumption of sequential invasion to obtaining persistent community states. If we allow diagonal moves within the hypercube (i.e., simultaneous invasions and extinctions), each mix becomes temporally adjacent to a much greater number ($\leq 2^n$-1) of possible other mixes than with sequential invasion (n). The probability that every one of these changes would be towards a given mix (and hence a persistent one) becomes vanishingly small.

As the extent of simultaneous invasion increases, it becomes increasingly probable that some set of species can invade, so driving other sets of species to extinction in the process (figure 4–1). We thus expect community persistence to vanish as the rate of species invasions increases. As the historical events of 1066 illustrate, a community may resist one invasion per year, but not two.

Our view of nature as consisting of alternative persistent communities (Drake 1990, 1991; Drake et al. 1993, Pimm 1991, Wilson 1992) may then represent only part of the theoretical picture. Such a landscape may be dependent on having sequential additions and subtractions of species throughout the assembly process. It is not likely that assemblies in nature

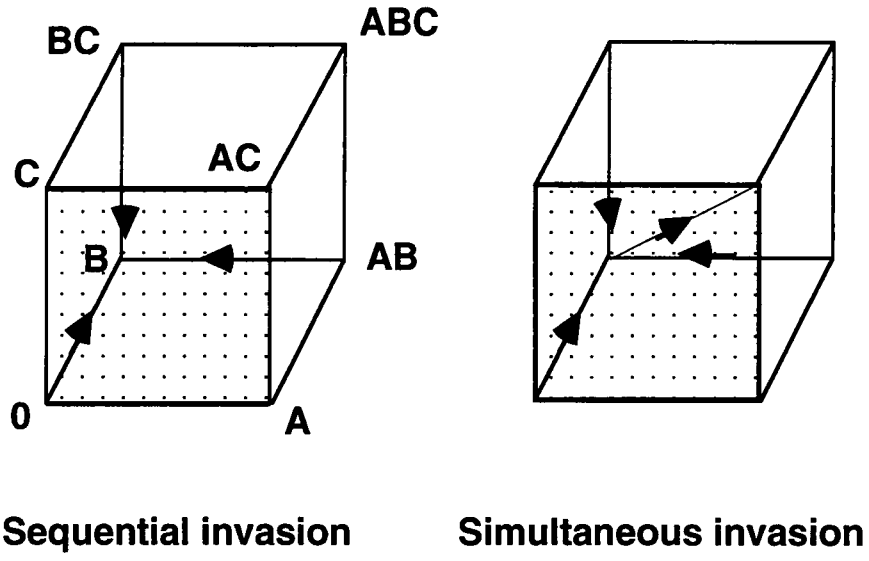


Figure 4–1. Hypercubes illustrating the effect of multiple invasions on the expected number of persistent community states. Under sequential invasion (left), the probability that a mix consisting of only species B is persistent is $(1/2)^3 = 1/8$. With 8 possible mixes, one persistent community is the expected number. Although B may exclude A and C separately, under simultaneous invasion from both (right), it may succumb.

proceed in this manner. Natural colonization rates are variable. They reflect how often, how easily, and how many individuals are released as propagules by neighboring individuals. How do these variations influence our view of community assembly? We suggest that, at the very least, communities experiencing rapid invasions will not be persistent and alternative states will be rare.

The Model

Similar to past modeling efforts, we create systems of Lotka–Volterra equations, $dX_i/dt = X_i(b_i - \Sigma a_{ij}{}^*X_j)$, with sensible ecological constraints. Parameters are chosen randomly and uniformly over ecological sensible intervals specified thus: the 20 species of carnivores (i = 41 to 60), and the 20 species of herbivores (i= 21 to 40) cannot survive in the community unless a food item is present, so $-1 < b_i < 0$. Plants (i= 1 to 20) survive on resources external to the model, so $1 > b_i > 0$. The effect of a species eaten (X_i) on the growth rate of what eats it (X_j) is chosen $0 < a_{ji} < 1$, and the reverse effect, $-1 < a_{ij} < 0$. We define specialist, generalist, and oligothrophic species by limiting the number of other species they can utilize as a food resource. Thus, specialists feed on only one of the species present in a lower trophic level, generalists feed on five species, and oligothrophs feed on three species. Similar to past efforts (Drake 1990, 1991; Drake et al. 1993), the species pool

created above is finite (for the alternate approach see Roberts and Tregonning 1981 or Post and Pimm 1983).

Unlike previous efforts (Post and Pimm 1983, Drake 1990,1991; Drake et al. 1993) however, we determine the fate of each invasion, and that species' effect on the community, by integrating the equations. We employ a simple rectangular integrator with a small but fixed step size. This ensures reasonably accurate estimations of each species' density after each iteration. Numerical integrations using variable step sizes and predictor-corrector methods can certainly portray the differential equations' behavior more accurately (Case 1991, Morton et al. 1996). These methods are extremely time-consuming. Moreover, we question whether they portray the underlying ecological dynamics. Births and deaths are discrete events; at some small time interval rectangular integration is the ecologically correct assumption.

Similarly, while equations permit species to persist at unrealistically small densities, we set a density (X_i = 0.005) below which populations become extinct. This density is higher than the seed density, so populations must grow quickly after initial invasion or fail to become established. This, too, mimics nature (Pimm 1991).

A potential invader can come from any trophic level and is 'seeded' into the existing community matrix at an arbitrarily low density (X_i = 0.001). It is possible for a species already present in the community to be an invader

(when we add 0.001 to the existing density). Species that become extinct may re-invade during any future invasion event. Assemblies proceed for 24,000 'years' (= 1.2×10^6 iterations, with a time step of 0.02).

We initially set the invasion rate at one species per 100 years. This slow rate of invasion allows the community to approach any possible equilibria between invasions. We designed this infrequent invasion scenario to mimic previous models in which species sequentially attempted colonization. We then set the invasion rate at one species per 1 year thus, likely preventing any possible equilibira between colonization attempts. We replicate each assembly scenario (i.e., one species/100 yr and one species/1 yr) three times and calculate the mean and standard deviations of duration that each species persists.

Results

With infrequent invasion, over all replicates 38 of 60 species (65%) will become a community members. The set of species that are successful varies considerably between replicates. Those that do successfully invade the community, persist for long periods of time and effectively exclude other species. In each replication, a set of species arrives early and comes to dominate. Yet, this set varies. Species that persist long periods at high abundances in one replication are typically unsuccessful in others.

An alternative way to represent this variation is in the coefficients of variation of persistence times over three replicate simulations. They are very high: 75%, 87%, and 82% for plants, herbivores, and carnivores respectively. Both these results mirror previous studies that found alternative persistent species mixes (Drake 1990,1991; Drake et al. 1993). The specific mix one obtains depends on random events early in the assembly process.

In contrast, under frequent invasion, only 7% of the species do not successfully invade. Thus, 56 species will be a part of the community at some time — a higher richness than those observed in infrequently invaded communities. Moreover, it was almost always the same 56 species. Fifty-five species are always successful and only three species always fail. No species persists for long periods of time and composition constantly changes. Species' persistence times across replicate simulations are remarkably constant: their coefficient of variations are 15%, 33%, and 33% for plants, herbivores and carnivores respectively. Species that do well in one replicate, will do well in all. High rates of invasion thus reduce the influence of chance historical events on community composition.

A species that persists for long periods in under one scenario does not necessarily fare as well under the other. Within each trophic level in figure 4–2, species numbering is arbitrary and sorted (bottom to top) in descending order of persistence for the slower rate of invasion. The duration that a plant

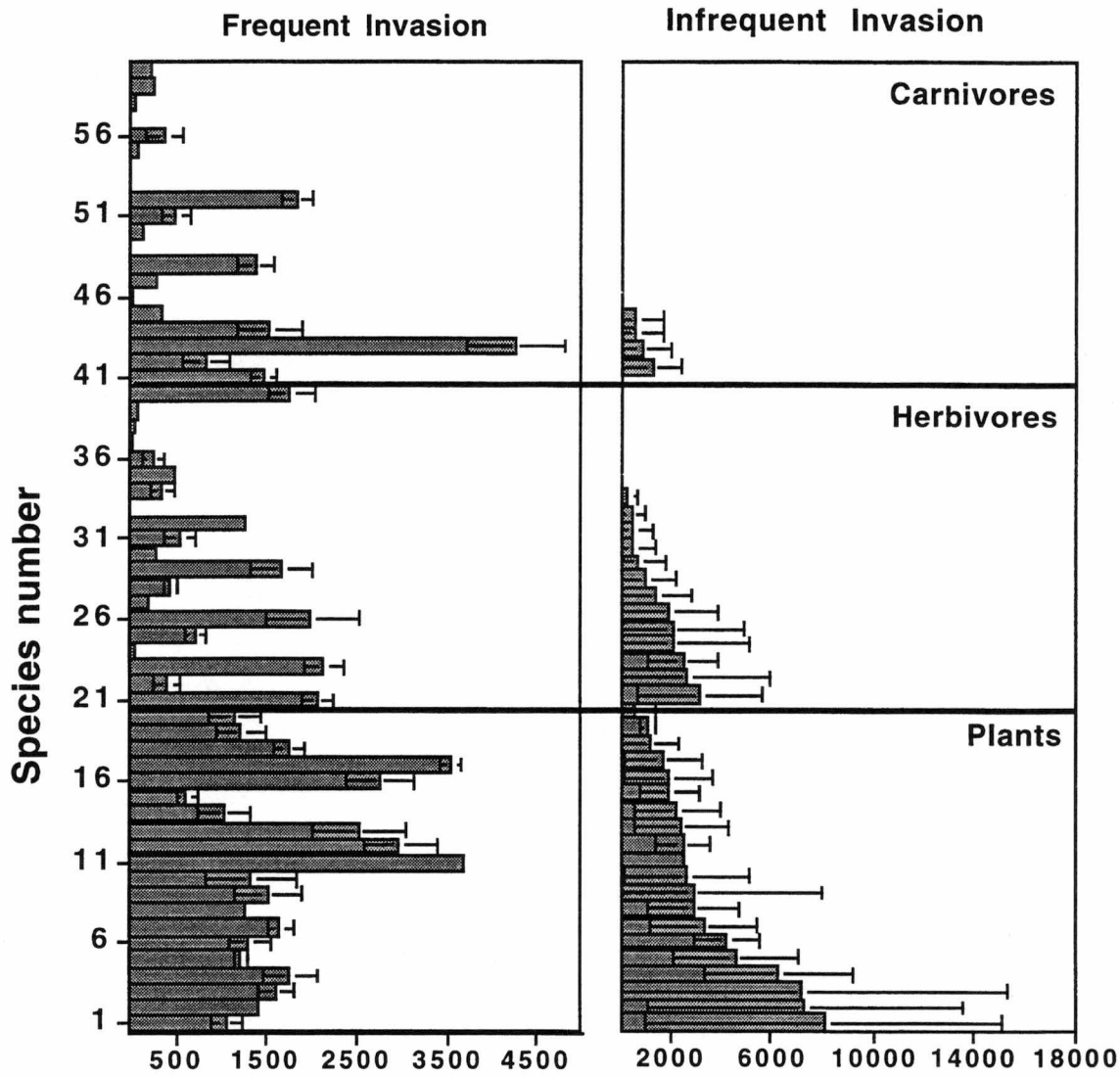


Figure 4–2. Two assembly scenarios. At the right, the invasions rate is 1 species per 100 yr. At the left, the invasion rate is 1 species per 1 yr. We replicate each assembly scenario three times and show the mean and standard deviations of duration that each species persists. Within each trophic level, species numbering is arbitrary and sorted (bottom to top) in descending order of persistence for the slow rate of invasion.

species persists under frequent invasion is uncorrelated with how long it persists under infrequent invasion ($r^2 = 0.04$). For the herbivores and carnivores the correlations are only slightly larger ($r^2 = 0.2$ and $r^2 = 0.28$, respectively)

.Discussion

We have three results. First, alternative persistent community compositions is a result dependent on sequential invasion. Second, the number of species that persist within a community increases as the rate of invasion increases.

Third, and perhaps most unexpectedly, species that do well in one assembly scenario do not necessarily do well in the other. Invasion rate thus becomes a niche dimension for these model species. Across a gradient of invasion rates, some species might occupy different parts of that gradient and not others.

The first of these results is consistent with the expectations stemming from Luh and Pimm (1993) – community persistence and the existence of alternative states is dependent on the rate at which invasions occur. If we view the replicates as a landscape or meta—community (*sensu* Wilson 1992), a frequent invasion rate across all communities produces a homogenous, but ephemeral, biotic environment. This is in direct contrast to what one would expect if the invasion rate across the landscape was slow. Here we would

expect a heterogeneous environment containing distinct community compositions that, after an initial building period, never change.

Together, these complimentary views of community assembly provide new perspective on two very basic conservation concerns – biodiversity and restoration. First, these results resolve a nagging dilemma that emerges from food web theory. As the number of species in a model increases (say to >10), it typically takes tens of thousands of attempts to create one model with a dynamically stable, ecologically feasible equilibrium from a set of species created with random, yet ecologically sensible parameters (Roberts and Tregonning 1981; Tregonning and Roberts 1979; May 1971, 1972; Pimm 1982). So how do large numbers of species coexist in nature? First, these results show that most model species survive either somewhere — in alternative persistent mixes — or sometime — in an ephemeral community.

A community (or more precisely a meta-community) fed by an unchanging species pool, will allow increased species co-existence by simply incorporating a variable invasion rate across space and through time. This is independent of the increased co-existence allowed from physical or other disturbance events that may 're-set' the assembly process in small patches within that community (Pickett and White 1985). What we have not explored are community assemblies where the colonists come not from a central,

unchanging pool, but from other pools that also undergo assembly. We defer this to a later paper.

Further, we had expected that there would be clear winners. By the random draw, some species should have parameters that always allow them to do well — high birth rates, for example. Similarly, others should always do badly. This is clearly not the case. This uncovers a mechanism of species coexistence we believe to be new, and call the "1066-effect". Some species can only invade because others are invading simultaneously. That is, they exemplify the same bad sportsmanship as the French invading England in the same year as another invasion. (Otherwise, they would clearly have been defeated.)

Second, we can provide a novel approach to building, or more practically re-building, complex natural assemblages. Such constructions (or re-constructions) are common goals in the restoration of degraded ecosystems (Berger 1990).

Under infrequent invasion, most species will belong to one of many persistent communities across the landscape. Establishing different assembly histories across a restored site should ensure that all or most of the desired species persist somewhere, if not exactly in their original places and original mixes. Under frequent invasion, every species will have its "day," but no species will dominate. Symmetrically, establishing different assembly

histories across a restored site should ensure that all or most of the desired species persist at some time, even if at one place their presence is fleeting. The diminishing space over which we can play these independent games of restoration does not bode well for our attempts to save species (Pimm et al. 1995).

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Part 5

When does restoration succeed?

Introduction

How effective have been our efforts to restore nature? Have we ever successfully restored a degraded site, species for species, or function for function? We attempt to answer these key questions of restoration ecology by reviewing 87 published studies. We also try to relate our results to ecological theory, which may strike the reader as overly ambitious. Our ambition stems from prior experience of assembling other scattered and highly subjective descriptions of nature — food webs. On reading these early compilations, many field workers felt (correctly) that they could collect much better data. As a consequence, the quality and quantity of new studies improved (Pimm et al. 1991) and served to refine food web theory considerably.

Obviously, all restoration ecologists wish for more and better data. We hope our ideas will suggest specific choices from the bewildering array of observations for them to report. The theories we present will surely need improvement; indeed, we may need to abandon them completely. Theories improve most when we confront them with data, even data as ill-defined as subjective accounts of restoration's successes and failures.

The simplest division in the expressed goals of restoration is between function and structure. By "function" we mean ecosystem processes, such as primary productivity, water clarity, soil erosion, and the loss or retention of nutrients. By "structure" we mean measures of species composition. These

range from a complete list of an area's original inhabitants, to such qualitative terms as "wildlife habitat". Function and structure are unlikely to be independent, of course. What does theory suggest about the likelihood of restoring function or structure?

On getting function

Large-scale surveys of ecosystem processes reveal consistent patterns. We can predict terrestrial primary productivity from evapotranspiration (Rosenzweig 1968), secondary productivity from primary (McNaughton et al. 1989, Cyr and Pace 1993), the stocks of soil carbon and nitrogen from a site's Holdridge life-zone (Post et al. 1985) and many other features (Schulze and Mooney 1993). These patterns are broadly independent of the species the ecosystems contain. This does not mean that species composition does not matter, for much scatter remains about these statistical relationships. It does suggest however, that nature achieves these relationships using a vast array of possible species combinations.

To restore ecosystem functions we may not even need the original number of species. The connections between the number of species an area supports and its ecosystem processes are tenuous. Clearly, with no species there can be no functions. Yet, except for systems with unrealistically few species, there is as-yet little evidence for a relationship between structure and function (Naeem

et al. 1994, Lockwood and Pimm 1994). Finally, restoration of ecosystem function does not even require native species (Aronson et al. 1993).

Simply, particular ecosystem functions appear to be consistent with a range of species numbers and such broad arrays of species compositions that they need not even include the area's native species. Metaphorically, the restoration of function should be an easy target to hit.

On getting structure

In contrast, the restoration of the original species composition, or any particular species composition, must surely require a close approximation to the original ecosystem processes. For example, without fire some prairies will become forests. Although restoration of the ecosystem functions may be necessary, surely they are not sufficient. Simply burning an area may still not restore the original prairie's composition. Differences in species composition in prairies may be determined in part by biotic interactions superimposed on the template of ecosystem processes. Metaphorically, structure will be a hard target to hit, because more constraints must be satisfied.

Critics will argue that we have overstated this case: subtle differences in environmental condition may drive *all* differences in species composition. Afterall, not all prairie fires are the same. Restore these exact conditions and perhaps the original species composition will return.

The experience of restoration provides a test of these competing hypotheses. If nature is so sloppy as to accommodate a wide variety of species compositions within a narrow range of ecosystem conditions, then function should be much easier to restore than structure. There will be many pathways to the former and few to the latter.

Partial or complete structure

Critics will now (rightly) notice that we have applied a double standard. By "structure" we mean some precise measure of species composition—often the original! By "function" we are content with some rough measures of productivity, nutrient retention, and so on. Society often imposes these different standards upon restoration. There are circumstances when it does not. Some *partial structure* may be the goal; by this we mean a particular group of species but not a particular set of species — for example hardwood trees or prairie plants, ground cover, "habitat for wildlife" and so on.

Following earlier arguments, function and partial structure should be equally easy to restore: there are multiple ways to achieve both. There are a variety of species compositions that will include the suitable "habitat for wildlife" or a group of prairie plants. Similarly, one might define, say, a prairie as easily by its partial structure (grasses, forbs, but no trees) as by its processes (low rainfall, episodic fires). Ease of definition may also equate to ease of

restoration: the more precise an object's definition, the more difficult it will be to create.

Secondary succession or community assembly?

So far, we have derived a crude theory of the likely patterns in the success of a restoration. It is based on the number of acceptable endpoints and thus the number of pathways that will lead us there. Our analogy begs the question: what if there are few pathways, but they are easy, well-worn ones? Perhaps familiarity is more important than number. Long-held ideas on secondary succession suggest that community composition moves along pathways towards a final end–point with goal–driven determination.

Communities assemble by the addition of species through sequential invasions and by the loss species through extinctions. In this sense, a pathway is the sequence of species invasions and extinctions that leads to a particular species composition. Succession, by its very name, implies that the pathways are traditional. Metaphorically, species of early sucessional stages know that their local extinction is inevitable, but that in other places, their destined hour is yet to come. Some restorations may be able to use these traditions, so mimicking natural processes of disturbance and recovery.

Unfortunately, there is no guarantee that desired species ***A*** need follow our introduction of species ***B***. We may neither have kept "every cog and wheel" (Leopold, 1948), — all the species, nor the "assembly instructions" — the

ecological history of the site. In ecological succession, species follow a time-worn path through community assembly. In many restorations, the pathways may be obscured and the map lost.

What does the theory of community assembly tell us?

If the familiar pathway is obscured, what does ecological theory tell us to expect from community assembly? Computer simulations and small scale experiments now recognize two endpoints along a continuum of possible behaviors (Drake 1988, Luh and Pimm 1993, Lockwood et al. in review). The rate at which species are allowed to invade a community determines the nature of the community turnover. Communities that are invaded often churn through species regularly and quickly. Virtually all species in the species pool (i.e., the group of species that potentially could be community members) become members of the community at some point during the assembly process. Each species persists for only a very short period of time; no species come to dominate.

Communities that are invaded much less often will show a greater persistence, and may in fact become completely invasion resistant. By "persistent " we mean no (or, in practice, little) turnover is species composition. A small set of all species in the pool will successfully become community members and they will persist for long periods.

This may seem a less democratic outcome than the previous circumstance where each species has its day. Interestingly, the theory also suggests that from any initial set of species, several states, each with different species compositions, are possible (Drake 1988, 1990; Luh and Pimm 1993). The presence of a species early in the development of the community may have profound effects on the species composition at any selected point in the assembly history. Communities are not just the result of processes that operate today, but are also the products of a long, capricious history. The historical sequence in which species are added to, and removed from, a community determine its extant structure.

Given that different places will likely experience different histories, each species has its chance somewhere, rather than sometime, as at the other end of the continuum.

Practically, we may restore a community but not always the desired one. At the high invasion end of the continuum, any desired community will be ephemeral. Indeed, the repeat of any exact mix of species may be statistically improbable.

At the low invasion end, the historically contingent idea of community composition allows the impossibility of restoring a community from its constituent species (Drake 1988, 1990; Pimm 1991, Luh and Pimm 1993). This Humpty-Dumpty effect (Pimm 1991), holds that species important in

determining structure may not be present in the community composition we see today. There is no guarantee that practical restoration can repeat a community's history even if all the species of the extant community are available for re-introduction, these re-introductions are sufficiently sequential and abiotic conditions are sufficiently replicated.

In sum, we argue that the restoration of ecosystem functions and partial structure should be relatively easy. The restoration of a particular species composition, such as the site's original, will not be easy, it may be impossible, and it may be transitory, except when the restoration can employ the natural patterns of secondary succession.

Restoration as Ecological Experimentation

The most difficult bridge between ecological theory and practice will likely remain the similarity of their words and the contrariety in their meanings (Pimm 1984). We now try to translate the vocabulary of practical restoration into our theoreticians' lexicon.

Restoration often involves the manipulation of the physical and chemical environment. These may involve major changes and we do not underrate their difficulty. A restoration attempt is also an uncontrolled experiment in assembling a community (Pimm 1991, Luh and Pimm 1993). Species are added ("seeded") into the community either by planting or inoculating the restoration site with a chosen set of species or by natural colonization of

species from adjacent sources. Species are removed ("weeded") either through active removal (often actual weeding) of unwanted species or from the unintended loss of all individuals of a species that is purposefully introduced.

A restored community becomes persistent when the turnover in species composition falls to a sufficient low level. Ideally, those responsible for management will cease to weed and seed when this happens. (The alternative is to constantly tinker with the species composition.) The species composition of a persistent community may or may not satisfy any of the other structural or functional goals of the project.

We can review restoration projects and identify them as either "successes" or "failures" in terms of these two major features. We understand that these terms are loaded with meaning. Here, we assume that practitioners hope to restore some attribute(s) of the original community and have these attributes persist for long periods of time. First, they are either "weeding and seeding" or else they have achieved a sufficiently low level of species turnover that this is not deemed necessary. Second, they either achieve or fail to achieve other goals. Only a completely successful project satisfies all projected biological goals and achieves persistence as defined by the cessation of management.

Using these translations of practical to theoretical terms, we judge a project as successful or failed based on the knowledge gained from published reports. Some of these reports appear in peer-reviewed journals. Others do not, and may not be so carefully scrutinized. Yet others are second-hand reports from compilations of case studies. Wherever possible, we obtained the primary source along with other corroborating publications. We recognize however, that not all publications have passed through equally stringent publication guidelines and that relying on second-hand interpretations may mis-represent results. We will compare the results from peer-reviewed and not peer-reviewed plus compilation publications to assay the effects of data quality.

Our criteria of success and failure incorporate several biases associated with the sociology of restoration efforts. We rely on the authors' judgment of whether or not a specific goal was met. There is likely a bias toward optimistic judgments on the part of some authors. This bias is difficult to assess, but will likely inflate the ease with which goals are reached. When management ceases, we will assume this is because changes in species composition are minimal enough to require no further intervention. This is likely not always true. Individuals responsible for an expensive, legally-mandated restoration efforts, for example, may "declare victory and go home," ceasing to assume responsibility regardless of the site's still changing species composition. Although we can identify some projects that potentially

fit this class, we cannot reliably estimate the size of this bias nor correct for it. Thus, we are also likely over-estimating the ease at which persistence is achieved. We thus accept that our criteria, although not perfect, will consistently err on the side of optimism.

The Literature Base

We gathered literature using computer databases, citation indexes, and bibliographies. To include a project, it had to satisfy three constraints. First, each project must have intended goals. Second, we excluded projects in which clearly non-native species were purposefully used. By doing this, we have narrowed the scope of the review to include only those projects that seek to restore some portion of the native ecosystem. We excluded projects in which the damaged ecosystem is assigned a new use, through exotic species introduction or physical manipulation (Aronson et al. 1993, Bradshaw 1988). Third, each project was subjected to at least some initial management intervention. This may include simply the cessation of pollution or some other source of degradation, but most often was some physical manipulation of the site over time.

Eighty-seven restoration projects met our criteria. We incorporated projects as we found them, so our sample represents how easily they could be found. Thus, if projects describing wetland restorations in the continental United States were easier to find than those for forests in central Siberia, we were

more likely to include them in our analyses. Our review does include a variety of community types however, and they are located around the world. The compilation of restoration efforts is representative, not exhaustive.

We list all the projects in the appendix. It includes the author(s) of the publications, the location of the project, the success category (see below), and the author(s) judgment of whether or not each goal was met. We also include three descriptive variables: duration, system type, and size. We calculated the duration of each project by subtracting the date of initial management from the date of latest publication. Thus, each project is judged during the time period for which we have information and not beyond. For many recent projects, this information is necessarily preliminary. Projects range in duration from 1 to 53 yr with the average being 6.3 yr. Duration is categorized as short-term (1–5 yr), medium-term (6–20 yr) , and long-term (> 20 yr). We classified each project broadly according to system type. "Freshwater" includes rivers, streams and lakes (15 studies), "marine" includes seagrass beds, rocky subtidal areas, and artificial reefs (18 studies), "terrestrial" includes prairies and woodlands (23 studies) and "wetland" includes any area which is partially or periodically flooded (31 studies). The size of the site where the restoration takes place is a grouped into three categories: small (1–10 ha), medium (11–50 ha), and large (> 51 ha). There are 59 small , 20 medium, and only 8 large sites.

Classifying the goals

Structural goals include anything that pertains to the return of species. We are interested in the success rates of returning a community species-for-species (full structure) versus just sets of appropriate species (partial structure), so we report these goals separately.

For example, consider two projects intended to restore a freshwater wetland. One may list the establishment of a "sufficient diversity of freshwater plants" as its goal. The second lists the return of each of the species observed at the site prior to disturbance. The first desires the return of diversity *per se* and thus pays less attention to the original species composition nor even to the use of only original species (although not exotics). Some may never return, nor are they encouraged to do so, but the finished product still resembles a freshwater wetland. The return of partial structure is sufficient for success. The second project demands the return not only native species but most of the original species composition. Here, those responsible are very concerned about which species are present and which are not. Full structure is desired and required for success.

Functional goals comprise variables that ecologists consider under the broad umbrella of ecosystem processes. Functional goals, like partial structure, do not require the return of a specific set of species. Functional goals may call for similar intervention as for structural goals. For example, a functional goal

might by the planting *Spartina* to control erosion but the goal is that process and not *Spartina* and its associated biota.

Classifying the results

Unsuccessful. In 17 projects, management neither ceased nor were all the biological goals achieved. Commonly, projects under this category faced physical restraints. For example, improper turbidity in a seagrass restoration prevented the long term establishment of underwater vegetation (Teas 1977), or previously unknown contaminants uncovered during restoration operations caused the die-off of large portions of the newly planted marsh vegetation (Josselyn et al. 1990).

Partially Successful. This class includes the majority of the projects considered (53). There are two sub–classes of partial success:

(1) *All goals met but management continues.* In 11 studies, management continues in efforts to control for unwanted species or species are continually added to the site, but the other goals are met.

For example, in many prairie restorations when other than a desired species enters, it is actively removed. If a desired species fails, or becomes only poorly established, it is repeatedly introduced. It is possible to achieve intended goals while management continues. In one case, the goals of establishing a few dominant prairie grasses and controlling erosion were both met (Kramer

1980). Although those responsible were concerned about species composition and continued to manage the site to direct which species established, the goals stated at the outset of the project were apparently met by the current, if changing, species composition.

Also included in this class are restorations where management continues in efforts to correct problems with physical characteristics of the site but not necessarily to control for unwanted species. These projects often face the difficulties associated with restoring water quality, soil properties or elevation characteristics. For example, when large river systems or lakes are considered for restoration those responsible must improve water quality by stopping non-point pollution sources (Berger 1992, Markarewicz and Bertram 1991). Often such improvements are achieved allowing for the return of many native fish. However, the continuation of this function (i.e., providing fish habitat) is dependent on the continued improvements in water quality through constant management. Here, functions are restored without much regard to the exact species composition that supports that function (i.e., as long as fish have something to feed on they will survive, it is not necessary to return the set of species that the fish *originally* fed on).

(2) *Management stops but not all goals are met:* This type of project is the most common in our review, with 42 case studies. Typically, some of the desired species persist and some, but not all functions are restored. For

example, the Salmon River salt marshes were restored through a series of projects initiated in the early 1980's (Frenckel and Morlan 1990). The project was successful in restoring a diversity of plants typical of salt marshes and biomass production. The native species richness of the site was not restored. Since all three goals were mentioned and only two achieved, we classify this project as partially successful.

There is a subset of 13 projects in which management ceased but the reasons for the cessation are not clearly detailed or expected. Most often, management ceased despite none of the stated goals having been met. An unusual example involves a wetland which, after years of neglect, was set for restoration in mitigation for construction on a nearby site (Josselyn et al. 1990). As their goals, the authors listed restoring a diversity of wetland plants and the use of the area by birds. Neither goal was met. Inadvertently, the area did provide habitat for an endangered plant, the Humboldt Bay Owl's clover (*Orthocarpus castillejoides var. humboldtiensis*) causing those responsible to cease management (at least temporarily).

Complete Success. In this class, are 17 projects that satisfied all prescribed goals and management ceased. For example, a project in Florida to mitigate marsh habitat destruction due to phosphate mining listed as its goals the establishment of a diversity of trees and shrubs common to freshwater wetlands in the area (Erwin 1985). Both of these goals were met and

management was no longer necessary, thus we consider this project completely successful.

Results

(1) An equal percentage (20%) of all projects are completely successful or unsuccessful; most projects are only partially successful (60%) (see table 5–1).

(2) There is no difference in the success rates reported from publications from peer reviewed journals and publications from non-reviewed or compiled sources. In 24 peer reviewed publication, 4 projects were judged complete successes, 4 failed, and 16 achieved partial success. In 63 non-reviewed sources, 13 were considered complete successes, 13 failed and 37 were partially successful. These proportions are almost identical, ($\chi^2 = 0.16$, 2df) and we henceforth discount biases between sources.

(3) Of the 184 goals given, 97 (52%) were achieved (see table 5–2). Functional goals were listed a total of 80 times and considered restored by the author(s) in 49 of those attempts (61%). Structural goals were listed 104 times with success occurring in 48 of those attempts (46%).

(4) Most of the successes under structure however, came from restoring diversity *per se* or establishing the dominant species (46 out of the 48 successes) rather than a specific species composition (see table 5–2). Restoring at least a portion of the native community species-for-species was listed 34

Table 5–1. Summary of restoration project results according to our classification system. Only 17 (20%) of the projects in our literature base are completely successful. Within those 17 projects, 32 goals were given. Only one of those was the restoration of at least a portion of the native community species for species.

Characteristics of the project	**Total number of projects that fit characterization**	**Which of these are successful under our first criterion**	**Type of goals listed**
Persistent and met all biological goals	17	Successful	13 functional goals 18 partial structure 1 complete structure
Persistent and not all goals met	42	Partially Successful	41 functional goals 32 partial structure 25 complete structure
Not persistent and all goals met	11	Partially Successful	13 functional goals 10 partial structure 0 complete structure
Not persistent and not all goals met	17	Unsuccessful	13 functional goals 10 partial structure 7 complete structure

Table 5–2. Biological goals listed by all projects. There are two types of goals: functional and structural. We divide the structural goals into those that are restoring only partial structure (i.e., diversity *per se*) and those that are restoring complete structure (i.e., portions of the community species for species). The number of successes and failures are listed beside each goal type. Function and diversity *per se* are more often returned than the species for species native diversity.

Function	Successful	Failed	Total
Water Quality	11 (92%)	1	12
Sustaining habitat	16 (73%)	6	22
Productivity	13 (38%)	21	34
Erosion control	9 (75%)	3	12
Totals	49 (56%)	31	80
Structure			
Partial	46 (66%)	24	70
Complete	2 (6%)	32	34
Total	48 (46%)	56	104

times but only 2 attempts considered successful (6%). Thus, function and partial structure are considered restored at least 10 times more frequently than species-for-species restoration ($\chi^2 = 17.76$, $P < .001$).

(5) When we consider the subset of projects deemed "completely successful" only one listed among its goals the return of full structure (Southward 1979, Hawkins and Southward 1992). The other goals, function and partial structure, where mentioned 13 and 18 times respectively. The restoration of complete structure is considerably under-represented among this group of completely successful projects ($\chi^2 = 7.1$, $p < .05$). We find that those projects that wish to restore a diversity of the appropriate species are at least as likely to be included in our complete success category as those who wish to restore function. However, those projects which attempt to restore the original community species-for-species are far less frequently considered completely successful.

(6) We found no χ^2 association between projects deemed completely successful and any descriptive variables (see table 5–3). This is likely the result of combining a large number of projects that incorporate many temporal and spatial scales.

Table 5–3. Summary of chi-square correlations between complete success and descriptive variables. No association existed between complete success and such descriptive variables as duration, size or type of system.

	Duration	**Size**	**System Type**
Complete Success	$\chi^2 = 1.565$, df = 2, P = 0.457	$\chi^2 = 2.346$, df = 2, P = 0.3094	$\chi^2 = 0.153$, df = 3, P = 0.9849

(7) We consider 59 of 87 attempts (61%) achieved persistence. This rate falls to 48% if we exclude the set of 17 projects in which it is unclear why management ceased.

Discussion

We have purposefully taken a broad-scale view of the practice of restoration in order to search for patterns. We have found two. First, those who practice restoration (or who evaluate restoration projects) are frequently pleased with efforts to restore such features as water quality, habitat structure suitable for deer, a substantial biomass of grasses or trees, or the normal loss of soil. In contrast, only a very few are pleased with efforts to restore a particular species composition. Thus, function and partial structure are indeed considered restored more often than species composition.

Second, in a total of 34 deliberate attempts, only two restored original species composition. In these projects, those responsible were likely utilizing still extant secondary successional pathways (Gore and Johnson 1981, Southward 1979, Hawkins and Southward 1992). In one project a river was diverted along a 2.5km stretch while coal was mined from under the original bed. Restoration then proceeded by re-enforcing the natural bed, controlling erosion and diverting the water flow back along its original course. The up-stream portion of the river served as the source pool for colonizing invertebrates and eventually that set of characteristic species established (Gore and Johnson 1981). The second successful attempt was comparable. After an oil-spill and its clean-up along a rocky tidal coastline, the invertebrate sessile community was destroyed. Eventually, the species typical of the area returned after the remaining oil and solvent disappeared. Again, the source for the colonizing species was presumably an undisturbed adjacent coastline since no re-introduction of species was attempted (Southward 1979, Hawkins and Southward 1992). Thus, it may be that original species richness will only be restored when secondary successional pathways are still available for exploitation.

We have outlined above two theoretical explanations for why these two patterns may exist. The first emphasizes the necessity of replicating original physical conditions. The second is the nature of community assembly

dynamics: even given identical physical conditions, restoration of a particular species composition may be impossible, at best improbable, and even then, only transitory. The exception is where we can use the historically familiar, frequently explored pathways of secondary succession.

We report a relatively high rate of persistence — which we equate with the cessation of management. This may be the product of the relatively short average duration of the projects we include here (6.3 yr). It remains to be seen whether persistence is indeed achieved despite the cessation of management. The level of persistence achieved by most restoration projects is important beyond satisfying political and economic requirements. Collecting long-term community turnover data from restoration projects may be the only way to distinguish which of the two assembly scenarios described above (i.e., constant species turnover or achieving alternative persistent states) best describe most restoration attempts.

No matter which assembly model proves the best descriptor of most restoration attempts, incorporating several separate restoration protocols within any one site may be most efficacious at restoring lost species. Restoring original composition is a worthy goal, of course. Those who practice restoration should accept that the communities they build might be functional replicates, but — our models predict — they will not be structural

replicates. Any attempt at hitting that one "target" will almost surely fail for the reasons given above. We claim that building many "targets" into the restoration protocol will increase the numbers and variety of species the site will support. Each "target" will produce a variant of the original in species composition and in function. Together, a mosaic of different restorations methods, planting sequences, and so on, should lead to alternative endpoints. In their totality, these alternatives may be the best way to ensure that most original species are restored. To our knowledge, this suggestion has not yet been explored by any restoration.

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Appendix. Here we list all projects considered listed by author. Also included are location, achievement of persistence and all goals, success according to both criteria, and the intended goals. We categorize each project under three descriptive variables: duration (D), system type (S T), and size (S).

Author(s)	Peer?	Location	Persists?	All Goals?	Compl Suc?	Type of Goal	Goal attained?	D	S T	S
Berger, John J.	no	Williamette River, OR	No	No	No	Functional Partial	(1) yes (2) no	1 1	Freshwater	2
Berger, John J.	no	Mattole River Watershed, CA	No	No	No	Functional Functional	(1) yes (2) no	2 2	Freshwater	3
Berger, John J.	no	Blanco River, CO	Yes	Yes	Yes	Partial	(1) yes	1	Freshwater	2
Buckner and Wheeler	no	Freshwater marsh, Front Range, CO	Yes	Yes	Yes	Partial Functional	(1) yes (2) yes	1 1	Wetland	1
Erwin, K.L.	yes	Agrico phosphate mine restoration, FL	Yes	No	Partial	Partial Partial	(1) no (2) yes	1 1	Wetland	2
Fonseca et al	yes	Eelgrass bed, NC	Yes	No	Partial	Complete Complete	(1) no (2) no	1 1	Marine	1
Hutchinson D.E.	no	Prairie restoration at Homestead Monument, NE	No	Yes	Partial	Partial	(1) yes	3	Terrestrial	2

Pritchett, D.A.	no	Vernal Pools in Santa Barbara,CA	Yes	No	Partial	Complete	(1) no	1	Freshwater	1
Josselyn et al	no	Vernal Pools in San Diego County, CA	Yes	No	Partial	Complete	(1) no	1	Freshwater	1
Josselyn et al	no	Hayward Regional Shoreline, CA	Yes	No	Partial	Functional Partial Functional	(1) no (2) yes (3) no	1 1 1	Wetland	1
Josselyn et al	no	Bracut Marsh, CA	Yes	No	Partial	Partial Functional Partial	(1) no (2) no (3) no	2 2 2	Wetland	1
Josselyn et al	no	Lincoln Street Marsh, CA	No	Yes	Partial	Functional Functional Functional Functional Functional Partial	(1) yes (2) yes (3) yes (4) yes (5) yes (6) yes	1 1 1 1 1 1	Wetland	1
Levin and Willard	no	The Harbor Project, Sandusky Bay, OH	Yes	Yes	Yes	Partial Functional	(1) yes (2) yes	2 2	Wetland	1
Levin and Willard	no	Lack Puckaway, WI	Yes	No	Partial	Functional Partial Functional Functional	(1) yes (2) yes (3) yes (4) no	1 1 1 1	Freshwater	2
Moss et al	yes	Norfolk Broadland Lakes, UK	Yes	Yes	Yes	Functional Partial	(1) yes (2) yes	1 1	Freshwater	1
Butler et al	yes	Lake Tohopekaliga, FL	Yes	No	Partial	Complete	(1) no	1	Freshwater	2

Josselyn et al and Roberts L.	no	Sweetwater Marsh, CA	Yes	No	Partial	Partial Functional Functional Partial	(1) yes (2) no (3) no (4) no	2 2 2 2	Wetland	1
Thorhaug, A.	yes	Florida Keys seagrass bed, FL	Yes	Yes	Yes	Partial	(1) yes	1	Marine	1
Erwin, K.L.	yes	Agrico phosphate mine second site, FL	Yes	Yes	Yes	Partial Partial	(1) yes (2) yes	1 1	Wetland	1
Mclaughlin et al	yes	Turkey Point seagrass bed, FL	Yes	No	Partial	Functional Complete	(1) yes (2) no	2 2	Marine	1
Asuquo Obot, E	yes	Nigerian freshwater wetland	Yes	No	Partial	Complete	(1) no	2	Wetland	2
Smith et al	yes	Seagrass bed, NC	Yes	No	Partial	Functional	(1) no	1	Marine	1
Anderson and Ohmart	no	Lower Colorado River Test plots	Yes	No	Partial	Partial Complete	(1) yes (2) no	1 1	Terrestrial	1
Childress and Eng	no	Canyon Ferry Resevoir, MT	Yes	Yes	Yes	Partial Functional	(1) yes (2) yes	1 1	Wetland	2
Hueckel et al	yes	Elliott Bay, Puget Sound rocky intertidal	Yes	No	Partial	Functional Complete	(1) yes (2) no	1 1	Marine	1
Jessee et al, Carter et al	yes	Pendelton Artificial Reef, CA	Yes	No	Partial	Functional Functional	(1) no (2) yes	1 1	Marine	1
Teas, H.J.	yes	Mangrove shorelines, FL	No	No	No	Functional Partial	(1) no (2) no	1 1	Wetland	1

Cammen, L.	yes	Salt Marsh, NC	Yes	No	Partial	Functional	(1) no	1	Wetland	2
						Functional	(2) no	1		
						Functional	(3) yes	1		
Gore and Johnson	yes	Tongue River, WY	Yes	No	Partial	Complete	(1) yes	1	Freshwater	1
						Complete	(2) no	1		
						Functional	(3) no	1		
Brunori, C.	no	Freshwater marsh along Elk River, MA	No	Yes	Partial	Functional	(1) yes	1	Wetland	1
Brunori, C.	no	Freshwater marsh on Bohemia River, MA	No	Yes	Partial	Functional	(1) yes	1	Wetland	1
Bontje, M.P.	no	Salt Marsh, NJ	Yes	No	Partial	Partial	(1) no	1	Wetland	2
						Partial	(2) yes	1		
						Partial	(3) yes	1		
						Partial	(4) no	1		
						Partial	(5) no	1		
Brown and Gibson	yes	Grassland in UK	Yes	No	Partial	Complete	(1) no	2	Terrestrial	2
Broome, S.W.	no	Saltwater Marsh at Pamlico estuarary, NC	No	No	No	Functional	(1) no	1	Wetland	1
Carangelo, P.D.	no	Hog Island mitigation, TX	No	No	No	Partial	(1) no	1	Marine	1
Carangelo, P.D.	no	Huffco Project, TX	Yes	No	Partial	Functional	(1)no	1	Marine	1
						Functional	(2) no	1		
Carangelo, P.D.	no	Petrus-Hughes project, TX	No	No	No	Functional	(1) no	1	Marine	1
Carangelo, P.D.	no	Clark Island Project, TX	No	No	No	Functional	(1) no	1	Marine	1
Bragg, T.B.	no	Allwine Prairie Transplants, NE	No	No	No	Complete	(1) no	1	Terrestrial	1
Bragg, T.B.	no	Allwine Prairie seeded, NE	No	Yes	Partial	Partial	(1)yes	2	Terrestrial	2

Steigman, K.L. and L. Ovenden	no	Heard Wildlife Sancturary transplants, TX	No	No	No	Complete	(1) no	1	Terrestrial	1
Nichols, O. et al.	no	Jarrah forest of Western Australia	Yes	No	Partial	Functional Complete Functional	(1) no (2) no (3) yes	1 1 1	Terrestrial	3
Hayes, T.D. et al.	no	Rolling Plains Prairie of north-cental Texas	No	Yes	Partial	Partial Partial	(1) yes (2) yes	2 2	Terrestrial	2
Southward, A.J.	no	Rocky Shores of West Cornwall, U.K.	Yes	Yes	Yes	Complete	(1) yes	2	Marine	2
Pickart, A.J.	no	Dune revegetation at Buhne Point, CA	Yes	No	Partial	Complete Functional Functional	(1) no (2) yes (3) no	1 1 1	Terrestrial	1
Kramer, G.L.	no	Prairie establishme nt, IA	No	Yes	Partial	Functional Partial	(1) yes (2) yes	1 1	Terrestrial	1
Drake, L.D.	no	Prairie establishme nt, IA	Yes	Yes	Yes	Functional Partial	(1) yes (2) yes	1 1	Terrestrial	1
Holler J.R.	no	Microfungal community in Prairie, WI	No	No	No	Complete Functional	(1) no (2) no	1 1	Terrestrial	1
Woehler, E.E. and M.A. Martin	no	Prairie, WI	Yes	No	Partial	Complete	(1) no	1	Terrestrial	1
Dale, E. E. Jr. and T.C. Smith	no	Prairie at Pea Ridge National Military Park,AR	No	No	No	Partial	(1) no	1	Terrestrial	1

Kirt, R.R.	no	Prairie at College of DuPage, IL	Yes	No	Partial	Complete	(1) no	1	Terrestrial	1
Webb, J.W. and C.J. Newling	yes	Salt Marshes Galveston Bay, TX	Yes	No	Partial	Functional Functional Functional	(1) yes (2) yes (3) no	1 1 1	Wetland	1
LaGrange, T.G. and J.J. Dinsmore	yes	Freshwater wetlands, IA	Yes	No	Partial	Partial Functional Partial	(1) yes (2) yes (3) no	2 2 2	Wetland	1
Shisler, J.K, and D.J. Charette	no	Salt Marshes, N.J.	Yes	No	Partial	Partial Partial Functional	(1) no (2) no (3) yes	1 1 1	Wetland	1
Beeman, S.	no	Salt Marsh, FL	No	Yes	Partial	Functional Partial	(1) yes (2) yes	1 1	Wetland	1
Gilio, J.L.	no	Marshland, FL	No	No	No	Functional Partial Functional	(1) yes (2) no (3) yes	1 1 1	Wetland	1
Goforth, H.W. Jr. and M. Williams	no	Mangrove shorelines, FL	Yes	No	Partial	Functional Partial	(1) yes (2) no	1 1	Wetland	1
Newling, C.J. et al.	no	Saltwater marsh in Apalach. Bay, FL	Yes	Yes	Yes	Functional Functional Partial Functional	(1) yes (2) yes (3) yes (4) yes	1 1 1 1	Wetland	1
Lewis, R.R. III and K.C. Haines	no	Mangrove restoration St. Croix, Virgin Islands	Yes	No	Partial	Functional Partial	(1) no (2) no	1 1	Wetland	2

Lewis, R.R. III and R.C. Phillips	no	Seagrass bed at Craig Key, FL	Yes	No	Partial	Partial Functional	(1) no (2) no	1 1	Marine	1
Kenworthy, W.J. et al.	no	Seagrass bed in Back Sound, NC	Yes	No	Partial	Functional Partial Functional	(1) yes (2) yes (3) no	1 1 1	Marine	1
George, D.H.	no	Lagoon at Cape Canaveral, FL	Yes	Yes	Yes	Partial Partial	(1) yes (2) yes	1 1	Wetland	1
Hoffman, R.S.	no	Eelgrass bed at Mission Bay, CA	Yes	No	Partial	Complete Functional	(1) no (2) no	1 1	Marine	1
Harrison, P.G.	no	Eelgrass bed southwest. British Columbia, Canada	Yes	Yes	Yes	Functional Partial	(1) yes (2) yes	1 1	Marine	1
Nitsos, R.	no	Eelgrass transplants in Morro Bay, CA	Yes	Yes	Yes	Partial Functional	(1) yes (2) yes	1 1	Marine	1
Merkel, K.W.	no	Eelgrass bed in Chula Vista Wildlife Reserve, CA	Yes	No	Partial	Partial	(1) no	1	Marine	1
Frenkel, R.E. and J.C. Morian	no	Salmon River Salt Marshes, OR	Yes	No	Partial	Complete Functional Partial	(1) no (2) yes (3) yes	2 2 2	Wetland	2
Allen, H.H. and Webb J.W.	yes	Saltmarsh in Mobile Bay, AL	No	No	No	Partial Functional	(1) no (2) no	1 1	Wetland	1

Lewis, R.R. III	no	Needlerush marsh, FL	Yes	No	Partial	Partial Functional	(1) yes (2) no	1 1	Wetland	1
Berger, John J. and Kent, M. et al.	no	Kissimmee River demo. project, FL	Yes	No	Partial	Complete Complete Complete Complete	(1) no (2) no (3) no (4) no	1 1 1 1	Wetland	3
Sperry, T.M./ Zimmerm J.H. and	yes	University of Wisconsion Arboretum Prairie, WI	Yes	No	Partial	Complete Partial	(1) no (2) yes	3 3	Terrestrial	2
Woehler, E.E. and M.A. Martin	no	Prairies on public land, WI	Yes	No	Partial	Partial Partial	(1) no (2) yes	1 1	Terrestrial	1
Wombacher J. and R. Garay/ Burton, P.J. et al.	no	Prairie at Knox College, IL	No	No	No	Partial Complete Complete	(1) no (2) no (3) no	3 3 3	Terrestrial	1
Burton, P.J. et al./ Schulenberg, R.	no	Morton Aboretum, IL	No	No	No	Partial Complete Partial	(1) no (2) no (3) yes	3 3 3	Terrestrial	1
Makarewicz J.C. and P. Bertram/ Charlton M.N. et al	yes	Lake Erie	No	No	No	Functional Partial	(1) no (2) yes	2 2	Freshwater	3
Urabe, J.	yes	Japanese Pond	Yes	Yes	Yes	Functional Functional	(1) yes (2)yes	2 2	Freshwater	1
Lutz, K.A.	no	Prairie, OH	Yes	No	Partial	Complete Partial	(1) no (2)yes	2 2	Terrestrial	1

Edwards, R.D. and Woodhouse W.W. Jr.	no	Saltwater Marsh in Pamlico Esturary, N.C.	Yes	No	Partial	Complete Partial Functional	(1) no (2) yes (3) yes	1 1 1	Wetland	1
Haynes, R.J. and L. Moore	no	Bottomland forest in the Southeast. U.S.	Yes	Yes	Yes	Partial Functional Partial	(1) yes (2) yes (3) yes	2 2 2	Terrestrial	2
Vassar, J.W. et al.	no	Prairie in Mark Twain National Forest, MO	Yes	Yes	Yes	Partial	(1) yes	1	Terrestrial	2
Kilburn, P.D.		Prairies, IL	Yes	Yes	Yes	Partial	(1) yes	1	Terrestrial	1
Keller, W. and N.D. Yan	yes	Sudbury Lakes,Ont., Canada	No	No	No	Functional Complete	(1) yes (2) no	2 2	Freshwater	3
Gameson, A.L.H. and A. Wheeler	no	Thames Estuary, UK	No	Yes	Partial	Functional Partial	(1) yes (2) yes	3 3	Wetland	3
Sparks, R.	no	Illinios River	No	Yes	Partial	Functional Functional Partial	(1) yes (2)no (3)yes	3 3 3	Freshwater	3
Edmondson W.T.	no	Lake Washington WA	Yes	No	Partial	Functional Functional Partial Partial	(1) yes (2) no (3) no (4) yes	2 2 2 2	Freshwater	3
Moore, D.C. and G.K. Rodger	yes	Garroch Head, Isle of Bute, Scotland	No	Yes	Partial	Partial Functional	(1) yes (2) yes	2 2	Marine	2
Olmstead, L.l. and D.G. Cloutman	yes	Mud Creek, AR	Yes	No	Partial	Complete Functional Functional	(1) no (2) yes (3) no	1 1 1	Freshwater	1

Vita

Born September 17, 1968, Julie Lynn Lockwood was the last of three children produced by G. Robert and Dianne G. Lockwood. She arrived somewhere within South Fulton General Hospital which is itself located within the sub-urban sprawl of Atlanta, Georgia. She attended Evoline C. West elementary within the public school system of Fulton County, Georgia. She then attended Sweetwater Middle and Berkmar High schools within the public school system of Gwinnett County, Georgia. Most of her youth was spent swinging bats and shooting basketballs (and drinking beer). After graduating she accepted a four year athletic scholarship to attend Georgia Southern College in Statesboro, Georgia. While there she majored in Biology. After graduating in 1990, she continued at Georgia Southern University (as it was now called) in order to receive her Master's degree. This degree, with a major in biology, was conferred in August of 1991. Her advisor was Michael Moulton. Julie then roamed the countryside for a year working mostly at the Naval Air Station Atlanta. She began attending the University of Tennessee in the spring of 1992. After a year chasing birds on Maui, HI she finished her Ph.D under the supervision of Stuart Pimm. She majored in Zoology and graduated in May 1997. She is currently (still) at the University of Tennessee completing a two–year post–doctoral research associateship with Dan Simberloff, but now watches others swing bats and shoot basketballs (she still drinks beer though).