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Abstract

General opinion in the contemporary literature is that disturbance strongly influences patterns of species diversity, and that diversity is greatest at intermediate levels of disturbance. However, empirical evidence is equivocal, and quantitative predictions about the strength of diversity–disturbance relationships are lacking. Using Markov models of dynamics of real communities, I derived predicted changes in diversity when communities are subjected to quantified disturbance gradients. I also derived predictions regarding effects of sampling intensity and species selectivity of disturbance on diversity–disturbance relationships. My models predict peaked relationships should be relatively rare, variation in diversity over disturbance gradients typically should be low, and relationship shape varies with sampling intensity. These results are broadly consistent with a review of published diversity-disturbance relationships. A meta-analysis of 197 published diversity–disturbance relationships was performed to determine how frequently observed relationships are peaked; how strong, in general, relationships are; and whether various attributes of a study influence the observed shape and strength of a relationship. Non-significant relationships were the most common, and peaked responses were reported in only 16% of cases. Variation in diversity explained by disturbance was variable, but averaged ~50%. Results suggest that strong and/or peaked relationships may arise from procedural artifacts. I conclude that there is little evidence to support the belief that disturbance should have a consistently important role in determining patterns of diversity, or that diversity–disturbance relationships are typically peaked.

Anthropogenic habitat loss is often cited as the most important cause of recent species' extinctions. Recent studies identifying hot spots of imperiled species have suggested

that habitat loss is the primary factor threatening the survival of imperiled species. However, interpretation of such hot spots is not practical without knowledge of where imperiled species have been lost. I determined distributions of richness and losses of imperiled species in Canada, and statistically examined the relationship between species' losses and various landuse variables. Several hot spots of losses were identified in southern regions of Canada. The combination of frequent and intensive insecticide applications, routine herbicide use, and habitat loss due to agricultural development appears to be the most important threat to imperiled species.

Résumé

L'opinion générale dans la littérature contemporaine est que la perturbation influence fortement les patterns de diversité d'espèces, et que la diversité est la plus élevée aux niveaux intermédiaires des perturbations. Cependant, l'évidence empirique est équivoque, et les prévisions quantitatives concernant l'importance des rapports de diversité-perturbation manquent. En utilisant des modèles Markoviens de la dynamique de communautés réelles, j'ai dérivé les changements prévus de la diversité quand les communautés sont soumises aux gradients mesurés de perturbations. J'ai également dérivé des prévisions concernant les effets de l'intensité d'échantillonnage ainsi que la sélectivité des perturbations sur les rapports de diversité-perturbation. Mes modèles prévoient qu'un maximum de diversité aux niveaux intermédiaires de perturbations ne devrait s'observer que rarement. De plus, la forme de cette relation devrait changer avec l'intensité de l'échantillonage. Ces résultats sont largement conformes à un examen des rapports déjà publiés de diversité-perturbation. Une méta-analyse de 197 rapports publiés a été réalisée pour déterminer la fréquence des relations à pic versus des relations monotones, et pour déterminer quelle proportion de la variance de la diversité peut être reliée à la fréquence et à l'intensité des perturbations. J'ai vérifié si les divers attributs d'une étude influencent la forme et la force observées d'une relation. Les rapports non-significatifs étaient les plus communs, et des réponses à pic ont été enregistrées dans seulement 16% des cas. La variation expliquée de la diversité était variable, mais les résultats étaient ramenés à une moyenne de ~50%. Les résultats suggèrent que les rapports forts et/ou à pic puissent résulter d'artefacts procéduraux. Je conclus qu'il y a peu d'évidence pour supporter l'hypothèse que les perturbations devraient avoir un rôle uniformément important sur les patterns de diversité, ou que des

rapports de diversité-perurbation possèdent typiquement un pic.

La perte anthropique d'habitat (un genre extrêmement intense et chronique de perturbation) est souvent citée comme la cause la plus importante des extinctions récentes d'espèces. Les études récentes identifiant les sites ayant un nombre important d'espèces en péril ont suggéré que la perte d'habitat soit le facteur primaire menaçant la survie de ces espèces. Cependant, l'interprétation de tels sites n'est pas pratique sans la connaissance des lieux de la perte d'espèces en péril. J'ai déterminé des distributions de richesse et de perte des espèces en péril au Canada, et j'ai statistiquement examiné le rapport entre les pertes d'espèces et les diverses variables d'utilisation de terrains. Plusieurs sites des pertes importantes ont été identifiés dans des régions méridionales du Canada. La combinaison des applications fréquentes et intensives de pesticides, ainsi que la perte d'habitat due au développement agricole, semblent être la menace la plus importante aux espèces en péril au Canada.

Table of Contents

List of Tables

List of Figures

Definitions of Key Terms

DISTURBANCE – A temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass. By directly or indirectly changing the availability of substrate and/or other resources, disturbance creates an opportunity for new individuals to become established (Connell 1978, Sousa 1984, White and Pickett 1985).

SPECIES DIVERSITY – There are two uses of "species diversity" in this thesis. The primary use of species diversity throughout the thesis is as a general term indicating the species composition or variation of species present in a given community, habitat, or area. This variation of species can be measured in many different ways, and three terms are commonly used to distinguish different kinds of species diversity metrics:

1) SPECIES RICHNESS – the number of species in a sample or area.

2) SPECIES EVENNESS – a measure of the relative abundance of individuals of each species in a sample, or the distribution of abundance among species. If all species in a community contain an equal number of individuals, species evenness would be high; and, if individuals are very unevenly distributed among species, evenness would be low. Many measures of evenness are currently in use (e.g. Pielou's *J* (Pielou 1975), several conversions of Simpson's dominance index to compensate for the effect of species richness (e.g. Pielou 1969, Pielou 1977); see Smith and Wilson (1996) for a review of evenness indices).

3) SPECIES DIVERSITY – unfortunately, one of the three groups of diversity metrics has been given the same terminology as the general concept of species diversity, leading to potential confusion when both are discussed in the same work (as in Chapter 2). The spe-

cific metric of species diversity incorporates both the number of species in a sample and the relative abundance of individuals among those species. As with species evenness, several measures of species diversity are commonly used (e.g. Shannon-Weiner's H′ (Shannon and Weaver 1949), Simpson's D (Simpson 1949)).

PEAKED RELATIONSHIP – a relationship between, in this case, some measure of species diversity and disturbance, where maximum observed species diversity is at some intermediate or moderate level of disturbance. Commonly used synonyms are unimodal and hump–shaped

Introduction

Species diversity – a measure of the number and/or relative abundance of species that co-occur – varies greatly through space and time. Natural patterns of species diversity occur at a broad spectrum of spatial and temporal scales and have been hypothesized to be influenced by many factors (Palmer 1994). Some patterns, however, can not be explained by natural mechanisms; instead, they are a result of anthropogenic factors.

This thesis addresses the effects of disturbance – a temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass – and human landuse on patterns of species diversity. Habitat loss is a kind of large-scale disturbance, and the effects of habitat loss resulting from extensive and chronic human landuse go beyond the effects of local disturbance. When a community is exposed to small-scale local disturbance, there is some loss of biomass, individuals, and/or habitat. With most such natural disturbances, losses of biomass or individuals are temporary. The empty spaces created by disturbance are often quickly recolonized by new individuals arriving from nearby undisturbed communities. When habitat is lost or severely degraded by natural disturbances (e.g. shoreline erosion from storm wave action, landslides flowing into streams), it becomes largely uninhabitable by the original species. If the affected area is large and slow to return to an inhabitable state, recolonization is delayed. Habitat loss from human landuse is generally very extensive and intensive (e.g. large urban centers, agricultural croplands). Logically, the effect of widespread habitat loss or degradation is extensive loss or displacement of many individuals and taxa. The chronic and large-scale nature of human landuse prevents many lost species from ever recolonizing; the effect is permanent until the land is abandoned or rehabilitated.

Species Diversity–Disturbance Relationships

Disturbance is widely believed to be one of the main factors influencing variations in species diversity (Noss 1996). Extant literature is virtually unanimous in postulating that species diversity is a peaked function of disturbance (i.e., species diversity is greatest at intermediate levels of disturbance). The Intermediate Disturbance Hypothesis (IDH; Grime 1973, Horn 1975, Connell 1978, Huston 1979, 1994) postulates that physical disturbance prevents competitively dominant species from excluding other species from the community, and that there is a trade-off between species' ability to compete and their ability to tolerate disturbance. In the absence of disturbance, competitive exclusion reduces diversity to minimal levels as communities approach equilibrium. When disturbances are very intense or frequent, few species can persist or repeatedly colonize after every disturbance, which also results in low diversity. At intermediate intensities or frequencies of disturbance, it is predicted that conditions favour the coexistence of competitively dominant species and disturbance–tolerant species: many species are able to tolerate the disturbance regime, and competitive exclusion is slowed or prevented, allowing competitively subordinate species and competitive dominant species to coexist. Thus, a peak in diversity should occur at intermediate intensities and frequencies of disturbance, as well as at intermediate times since the last disturbance.

From the IDH, one would predict that, along gradients of diversity, disturbance would explain a significant proportion of the variation in diversity. Additionally, one would expect that diversity undergoes large changes along disturbance gradients. However, a cursory examination of the disturbance literature reveals that diversity–disturbance relationships are neither consistently strong nor consistently peaked. And, when peaked

relationships are observed, the change in diversity is generally not large.

A Quantitative Theoretical Approach

Discrepancies between predictions from the IDH and observations of diversity–disturbance relationships led to questions regarding the consistency of published observations with current theory: 1) Are the observations in the literature consistent with current theory? 2) Do models predict that diversity–disturbance relationships should account for large amounts of the variation in richness, or only small amounts? 3) Do models predict that the relationship is consistently peaked (i.e., species diversity is greatest at an intermediate level of disturbance)?

The main theoretical treatments of the diversity–disturbance relationship are qualitative (e.g. Grime 1973, Huston 1979, Petraitis et al. 1989). Predictions are presented in figures with axes that lack dimensions, or as verbal models. There is little indication to what extent diversity might actually be expected to vary in response to disturbance. Theory is also ambiguous about the shape of diversity–disturbance relationship that one would expect to observe. The qualitative predictions of extant theory are such that virtually any observed relationship between diversity and disturbance is consistent with them, whether the relationship be peaked, negative monotonic, or positive monotonic.

Additionally, it is unclear to what extent the strength of an observed diversity–disturbance relationship is dependent upon either sampling intensity or the species selectivity of disturbance. Because observed species richness increases as a function of the number of organisms counted (MacArthur and Wilson 1967), non-exhaustive methods for estimating species richness will detect rare species to an extent that varies with sampling

intensity. Disturbances can be non-selective with respect to which individuals or species they remove (e.g. landslides), or they can selectively remove individuals of particular species (e.g. predation). Disturbance selectivity is believed to influence the shape of a diversity–disturbance relationship (Lubchenco 1978, Huston 1994), but extant theory does not indicate how strong the effects of disturbance–selectivity should be.

In the first chapter of this thesis, I develop quantitative models of community dynamics in the face of disturbance, and I derive quantitative predictions regarding the relationships between disturbance and two measures of species diversity (richness and evenness). The models are individual-based Markov matrix models developed from published transition matrices for forest, heathland, alpine cushion, and three coral reef communities. Some of the questions I address with these models are:

i) How strongly is diversity predicted to vary with disturbance intensity or frequency?

ii) Is the predicted shape of relationship consistently peaked?

iii) To what extent does the shape of predicted diversity–disturbance relationships depend upon sampling intensity?

iv) To what extent are predicted diversity–disturbance relationships affected by the selectivity of disturbance.

A Meta-Analytic Approach

When a cursory examination of the disturbance literature indicated considerable inconsistencies in the shape and strength of species diversity–disturbance relationships, I was compelled to ask the following questions: 1) How frequently are observed species diversity–disturbance relationships peaked? 2) How strong are species diversity–disturbance relationships?

Equivocal published data regarding the IDH indicate a need to determine why there is so little consistency in both the shape and strength of observed species diversity–disturbance relationships. There are several possible situations where it may be expected that peaked and strong relationships are not the rule. These include communities where post-disturbance succession is not driven by competitive hierarchies (Reice 1985, Chesson and Huntly 1999); communities where productivity (or population growth rates or rate of competitive displacement) is very low or very high (Huston 1979, 1994); and communities composed of motile, versus sessile, species (Fuentes and Jaksic 1988, Wootton 1998). Additionally, strong peaked relationships may also not be the norm in studies of disturbances that are predictable and moderate, versus unpredictable, severe, and episodic (Reice et al. 1990); studies that thoroughly sample the disturbed communities (Mackey and Currie 2000); and studies that examine species diversity within homogeneous patches of large-scale disturbance, vs. studies that examine species diversity in heterogeneous mosaics of multiple patches created by small-scale disturbances (Wilson 1994).

In the second chapter, I perform a meta–analysis of published species diversity–disturbance relationships to answer the following questions:

i) How much variation in species diversity is explained by disturbance?

ii) Does the strength of the relationship depend upon attributes of the study?

iii) How frequently are species diversity–disturbance relationships peaked?

iv) Under what conditions are peaked relationships most likely to occur?

To answer these questions, I searched the published literature for studies examining effects of disturbance on species diversity. I tested the extent to which the strength (explained variation) and shape of observed relationships were related to characteristics of the community, the habitat, the disturbance, and the sampling design.

Habitat Loss and Distributions of Imperiled Species

Expansion of the Canadian human population during the past 150–200 years has coincided with many changes in the natural patterns of species diversity across the country. Some places that used to be speciose are now relatively depauperate of species (e.g. the prairies of southern Alberta, Saskatchewan, and Manitoba). Similar changes are occurring in other regions around the world, and there is little disagreement that humanity is contributing to the current global wave of species extirpations and extinctions. Several anthropogenic factors are considered to have adverse effects on species diversity: habitat loss, pollution, introduction of exotic species, and overexploitation are thought to be the major factors (Soulé 1991, Wilson 1992, Flather et al. 1998, Wilcove 1998, Chapin et al. 2000).

Habitat loss due to human activity is widely believed to be the most important cause of recent species extinctions and the primary threat to endangered species (e.g. Wilson 1989, Soulé 1991, Wilson 1992, Wilcove 1998, Chapin et al. 2000). Case studies of

individual endangered species virtually always conclude that some aspect of anthropogenic habitat loss is a threat to the species in question; 85% of all imperiled taxa in the United States are threatened by habitat loss and degradation (Wilcove 1998). Broader-scale, multi-species approaches have also suggested that hot spots (relatively high numbers or concentrations) of endangered species richness coincide with habitat loss (Sisk et al. 1994, Dobson et al. 1997, Flather et al. 1998).

The presence of hot spots of endangered species in particular regions could be interpreted two ways. First, some factor(s) in these regions may be causing species to undergo losses and become imperiled. Alternatively, hot spots of endangered species may represent areas with desirable attributes that promote the survival of endangered species that have been lost elsewhere. To distinguish between the two possibilities, one must know where species have been lost, versus where they remain.

The third chapter addresses the following two questions:

i) Are there hot spots of species' losses in Canada?

ii) Are species' losses correlated with anthropogenic attributes of the landscape?

I compare historic and current distributions of imperiled species listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; the body that officially determines the conservation status (e.g., threatened, endangered) of species in Canada), and determine quantitative distributions of both imperiled species richness and losses of imperiled species. I also statistically examine the relationship between species' losses and many human landuse and landscape attributes.

Chapter 1: A Re-examination of the Expected Effects of Disturbance on Species Diversity

INTRODUCTION

The number of different species that co-occur – species richness – varies by orders of magnitude through time and space. A very large number of factors have been hypothesized to account for this variation (Palmer 1994). There is at least anecdotal evidence consistent with most of these hypotheses (Begon et al. 1996). Yet, a lengthening list of factors that can influence species richness under some circumstances does little to answer the question of which factors actually do account for the bulk of the variation in species richness in nature.

Disturbance is often cited as one of the main factors controlling species richness and other measures of species diversity. According to Noss (1996), "One notable generalization of modern ecology is that moderate levels of disturbance maximize the diversity of habitats and species in a landscape." Huston (1979, 1994) proposed a general theoretical model of species diversity variation, which postulates that disturbance and competitive exclusion are the two fundamental processes controlling species diversity. The role of disturbance has been emphasized (albeit often qualitatively) in many particular systems, such as tropical rain forests (Connell 1978), coral reefs (Connell 1978, Karlson and Hurd 1993), herbaceous vegetation (Grime 1973), temperate forests (Horn 1975), and algal communities (Lubchenco 1978). Although there are many definitions of disturbance (e.g. Grime 1973, Connell 1978, Huston 1979, White and Pickett 1985), it can, in general, be described as a force, often abrupt and unpredictable, with a duration shorter than the time between disturbance events, that kills or badly damages organisms and alters the

availability of resources.

The qualitative effect of disturbance on species richness is usually presented as follows (e.g. Grime 1973, Horn 1975, Connell 1978, Huston 1979, Petraitis et al. 1989, Huston 1994). In the absence of disturbance, systems approach equilibrium and competitive exclusion reduces species diversity to minimal levels. When disturbances are very intense or very frequent, few species can persist or repeatedly colonize after every disturbance, which also results in low species diversity. When disturbances are of intermediate frequency or intensity, there are opportunities for re-establishment of more species after disturbance, and persistence of competitive subordinates that would otherwise be outcompeted if the system were allowed to approach equilibrium. Thus, maximum species diversity should occur at intermediate frequencies and intensities of disturbance (the Intermediate Disturbance Hypothesis: IDH), as well as at intermediate times since the last disturbance. The shape of this form of relationship is referred to as peaked, hump–shaped, or unimodal.

At least two predictions can be derived from the hypothesis that disturbance is a major factor controlling species diversity. First, one would expect that, along gradients of species diversity, a significant proportion of the variance in species diversity would be statistically related to measures of disturbance. Second, one would expect that models of the species richness-disturbance interaction would predict large changes of species richness along disturbance gradients.

Empirical evidence regarding the statistical relationship between species richness and disturbance is very mixed. Some published species richness–disturbance relationships are peaked (Sousa 1979, Thorp and Cothran 1984, Bowers 1993), and some are not

(Armesto and Pickett 1985, Wilson and Tilman 1991, Fox 1992). In a set of 116 published studies relating species richness and disturbance reviewed in Chapter 2, only 16% exhibited the peaked pattern predicted by the IDH. Among the significantly peaked relationships, variation in species richness along the disturbance gradient was typically small: a median of 4.0 species, representing less than a two-fold variation in species richness (e.g. Thorp and Cothran 1984). These results suggest that peaked species richness responses to disturbance gradients may not be general responses in natural communities, and when they do occur, they are not large.

Are these results consistent with current theory? Would one expect the species richness–disturbance relationship to account for large amounts of the variance in species richness, or only small amounts? Would one expect the relationship to be consistently peaked?

The main theoretical treatments of the species richness–disturbance interaction are entirely qualitative. Theoretical treatments have gone beyond the basic IDH presented above, postulating interactions between disturbance frequency and intensity (Miller 1982, Malanson 1984), and between disturbance and rates of productivity or competitive exclusion (Grime 1973, Huston 1979, 1994), in both equilibrium and non-equilibrium situations (Petraitis et al. 1989). However, in all of these cases, predictions are presented as verbal models, or in figures with axes that lack dimensions. Reviews of disturbance effects and experimental studies designed to test them typically cite only the general qualitative prediction of a peaked relationship between species diversity and disturbance (e.g. Karlson and Hurd 1994, Sommer 1995). There is little indication to what extent species richness might be expected to vary in response to a particular disturbance.

Theory is also ambiguous about the shape of species diversity–disturbance relationships that one would expect to observe in practice. If a particular study involved only one end of a disturbance gradient, then the relationship could appear to be monotonic. Since the axes of extant models are not parameterized, one cannot know whether a particular range of disturbance is broad enough to capture a peak. Further, Huston's (1979, 1994) models suggest that species diversity is relatively insensitive to disturbance when rates of competitive displacement (and/or population growth or productivity) are either very low or very high, but very sensitive at moderate rates of competitive displacement and population growth. However, there is no way to know *a priori* over what range of measured productivity one would expect species diversity to be insensitive to disturbance. Thus, the predictions of extant theory are sufficiently broad that essentially any relationship between species diversity and disturbance is consistent with them.

Logically, the strength of species richness-disturbance relationships must also depend upon sampling intensity, but it is not clear to what extent. Observed species richness increases as a function of number of organisms counted (MacArthur and Wilson 1967). Thus, any non-exhaustive methods for estimating species richness such as point sampling, line transects with point intercepts, or point quadrats will detect rare species to an extent that varies with sampling intensity.

Finally, species selectivity of disturbance (i.e., selective mortality of a particular species by a disturbance) can also affect the species richness–disturbance pattern. Experimental removal of predators that selectively prey upon dominant species has often been observed to result in decreased species richness; no longer limited by predation, dominant species exclude inferior competitors (Paine 1966, Menge and Sutherland 1976). Removal

of predators or disturbances that affect the rare or competitively inferior species should result in increased species diversity (Lubchenco 1978, Huston 1994). Disturbances that affect the dominant competitor(s) are more likely to result in peaked species richness–disturbance relationships than disturbances that affect only the least dominant competitors (Lubchenco 1978). Again, extant theory gives little indication of how strong these effects would be expected to be.

In this study, I examine models of community dynamics in the face of disturbance, and I derive quantitative predictions regarding the relationships between species richness, species evenness, and disturbance. Specifically, I address the following questions:

1) How strongly are species richness and species evenness predicted to vary with disturbance intensity? Is the variation likely to be orders of magnitude, or just a few percent?

2) How strongly are species richness and species evenness predicted to vary with disturbance frequency?

3) To what extent do the shapes of the predicted species richness– disturbance and species evenness–disturbance relationships depend upon the intensity of sampling (i.e., the number of individuals counted)?

4) To what extent is the selectivity of disturbance predicted to affect the predicted species richness– and species evenness– disturbance relationships?

METHODS

Model Overview and Calibrating Data

To answer these questions, I used modified Markov models of succession in six real communities, based on published transition probability matrices. Even though some assumptions associated with Markov models (e.g. stationarity, the assumption that transition probabilities do not change over time) are not necessarily satisfied in all communities, Waggoner and Stephens (1970), Horn (1975), and Lough et al. (1987) concluded that Markov models make reasonably accurate predictions of community dynamics through time. Markov models were chosen for this project because of their simplicity, their ability to be modified by incorporating disturbance, and because they have been tested and found successfully to predict succession in many different kinds of communities.

Markov models postulate that when an individual dies during succession, that individual may be replaced by another individual of the same species, by an individual of another given species, or by empty space. A transition matrix contains the probabilities of each of these possible transformations, based on the observed frequencies of transformations in real communities. The models assume that these transition probabilities do not change through time.

I located published transition matrices for trees of a temperate deciduous forest (Horn 1975), a low alpine cushion/tussock/shrub community in southeastern New Zealand (Lough et al. 1987), heathland vegetation of northeastern Netherlands (Lippe et al. 1985), and three subtropical, shallow water coral reef communities (Tanner et al. 1994) (see Appendix 1 for transition probability matrices). These six matrices were used to build simulation models of succession interrupted by disturbance (see Appendix 2 for an

example of a model).

When communities are composed of many species, transition matrices become very large and difficult to compose. Researchers therefore commonly combine species into morphological or taxonomic groups when dealing with speciose communities (e.g. Tanner et al. 1994). The coral reef transition matrices used in this study were composed of seven coral groups (a total of 72 coral species) and one algal group (nine species). Therefore, rather than calculate species richness, coral models calculate taxon or functional group richness for the coral communities. Taxon, rather than species, richness is also more applicable to for the alpine cushion community (Lough et al. 1987), which was categorized into three species of shrubs, one species of grass, and multi-species groups for each of cushion-forming species and mat-forming species. Since both the heathland and forest communities contained relatively few species, the successional patterns of individual species, rather than groups of species, were distinguished in the transition probability matrices.

Transition probabilities were not calculated identically for all six communities. Tanner et al. (1994; coral reef communities), Lough et al. (1987; alpine cushion), and Lippe et al. (1985; heathland) calculated transition probabilities by censusing permanent quadrats several times over the course of many years (28, 32, and 19 years, respectively). Thus, their matrices represent observed transition probabilities per unit time. In contrast, Horn's (1975) transition probabilities were calculated by counting the numbers of saplings of each species found under each canopy tree species. By assuming that every sapling under a canopy tree has an equal chance of replacing the tree, the transition probabilities were estimated from the proportions of each sapling species under each canopy species.

Horn's transitions are, therefore, not transitions during a specific length of time, but rather from generation to generation. To use his matrix in my study, Horn's transition probabilities were converted to transitions per unit time by incorporating estimates of the average generation time for each species (Horn 1975). Further, while the transition probability matrices for the coral, heathland, and alpine cushion communities all included the probability of transition to bare space (points containing no individual), Horn's forest matrix did not. For the forest matrix, bare space resulted only from disturbance. Trees that die for other reasons (e.g. reaching their expected life span) are replaced immediately by an individual already present in the sub-canopy, as described by the succession matrix. Assuming that pioneer species would be more likely to fill bare space than other species, I identified which species in the community were pioneer species (Elias 1980). The three pioneer species were assigned the highest probabilities of colonizing bare space. The remaining species were all assigned low probabilities. I tested a range of possible transition probabilities for bare space; all of them yielded qualitatively similar model predictions.

We examined predicted successional changes at 10-year time intervals for the forest community, since trees are relatively long-lived. For the other five communities, I used transition time intervals equal to the mean time interval between the field censuses that the original authors used to calculate transition probabilities. For alpine cushion, the interval was ten years, for heathland, one year, and for coral reefs, 26 months (exposed pools and exposed crest) and 19 months (protected crest).

Model Specifics

Disturbance intensity and frequency gradients were incorporated into the model. I define disturbance intensity as the proportion of the individuals in a community, or of a particular species, that is killed. A non-selective disturbance with an intensity of 50% will kill 50% of each species in the community. A selective disturbance of this intensity will kill 50% of a particular species. Disturbance intensities were varied from 0% to 100% mortality at increments of 10%. Disturbance frequency represents the probability of a disturbance occurring in any given time interval. It ranged from 0 to 1 disturbances per transition time interval, and it was varied in increments of 0.1.

Each model community consisted of 5000 cells, with each cell containing either one individual or empty space. The state of the community vector at the initiation of each simulation was standardized at 5000 cells of bare space. Random numbers determined whether a disturbance would occur in a given time interval, and which transition each cell would undergo (given the transition probabilities). When a disturbance occurred, the mortality rate (i.e. disturbance intensity) chosen for the series of simulations was applied to the target species. The community space occupied by disturbed individuals was immediately changed to bare space. Then, each of the 5000 cells in the community underwent a transition. The number of individuals of each species and number of species were then counted. This order of events simulates a situation in which a community is disturbed at the beginning of a time interval, transitions occur over the span of that time interval, and the community is censused at the end of the interval.

Species richness was calculated after each transition and averaged over the whole simulation, which ran for 100 transition intervals. Pielou's evenness index

($J = -\sum p_i \log_2 p_i / \log_2(S)$, where p_i is the proportion of all individuals belonging to species i and S is the number of species) was also calculated after each transition time interval and averaged. For each community, 20 replicate simulations were performed at each combination of disturbance frequency and intensity. Average species richness, species evenness, and standard errors were calculated. This process was repeated for each of three types of disturbance: non-selective mortality, selective mortality of the most dominant species, and selective mortality of the least dominant species. The most and least dominant species in each community were determined by running the simulation over time without disturbance, and observing which species became most abundant, and which became extinct most quickly or the rarest, respectively.

Species richness and species evenness were calculated for a series of different sampling intensities. A geometric series containing the following 12 sampling intensities (number of cells censused out of the 'community' of 5000 cells) was examined: 5000, 2500, 1250, 625, 313, 156, 78, 39, 20, 10, 5, and 3. For each sampling intensity, a random number generator was used to select which cells would be censused.

All modeling was performed using Matlab® version 4 (The Mathworks Inc.). More descriptive accounts of model structure and procedures are located in Appendix 2.

RESULTS

Non-selective Disturbances and Patterns of Species Richness

The standard errors of the species richness estimates among replicate simulations were very low, typically ≤ 0.025 species, with an overall maximum value of 0.06 (forest

community). The standard errors of the species evenness estimates were also very low, with values generally ≤ 0.002. Due to such low variability, I do not show error estimates on the graphs.

In most simulations, the predicted patterns of species richness along the two different gradients of disturbance (intensity and frequency) were similar to one another (Fig. 1a): the response surface is bilaterally symmetrical. This similarity was also usually predicted for species evenness (Fig. 1b). The most common deviation from this symmetric pattern was observed in simulations that predicted peaked relationships between species richness or species evenness and disturbance. In these simulations, the peaked pattern was usually somewhat more pronounced along the disturbance intensity gradients than along the frequency gradients (Fig. 2).

Basically, my simulations predict that species richness is not very sensitive to disturbance gradients. Across the entire range of possible disturbance frequencies and intensities (0% to 100%), in all the communities for which data were available, the median range of variation of species richness (among all simulations) was 3% (Fig. 3). Species richness was never predicted to vary by more than a factor of 2 along any disturbance gradient. Although my simulations do predict that species richness should covary with disturbance, they predict further that the amount of variation explained should be quite small.

The predicted shape of the species richness–disturbance relationships varied with sampling intensity for every community I studied (Fig. 3). For example, in the heathland community (Fig. 4), the model predicted no relationship between species richness and disturbance at the highest sampling intensities (100% of individuals sampled), negative monotonic relationships at moderate sampling intensities (12.5% - 50% of individuals

sampled), a unimodal pattern at one low sampling intensity (e.g. 6.3% sampled), and positive monotonic relationships at very low sampling intensities (e.g. 0.2% - 3.1% sampled). Though not all four of these patterns were predicted in all of the communities, the patterns at low sampling intensities were always different from those predicted at high sampling intensities.

Peaked species richness–disturbance relationships were predicted only at low sampling intensities (≤6.25% of individuals sampled). At high sampling intensity (25% - 100% of cells), species richness was typically independent of disturbance (Fig. 3 and Fig. 4a). There were, however, two exceptions: a very subtle decline in species richness was predicted at the lowest levels of intensity and frequency in forests (Fig. 5a), and a more dramatic decline at high levels of intensity and frequency in alpine cushion (Fig. 5b).

The greatest change in species richness over a disturbance gradient was also typically predicted at low to moderate sampling intensities (Fig. 3). The only exception to this is the positive relationship predicted between the change in the number of species and the sampling intensity for the alpine cushion community (Fig. 3f).

Selective Disturbances and Patterns of Species Richness

When disturbances selectively removed the numerically dominant species, the relationship between species richness and disturbance was generally similar to that observed with non-selective disturbance (Fig. 3), but more subtle. The single prominent exception is in alpine cushion, where a strong response to non-selective disturbance was predicted (Fig. 3f), but only a weak response to selective disturbance.

When the disturbance selectively removed only the numerically least dominant

species, the qualitative species richness–disturbance patterns were similar in all communities (Fig. 3). Species richness was predicted to be independent of disturbance at the highest sampling intensities in all but the forest community, in which the relationship was negative monotonic. At low sampling intensities, species richness was independent of disturbance in all six communities. At moderate sampling intensities, the species richness–disturbance relationship was typically negative monotonic (e.g. Fig. 3) or flat. No unimodal or positive monotonic patterns were predicted.

Patterns of Species Evenness

Our models predicted that species evenness should be more sensitive to gradients of disturbance than is species richness (Fig. 6). The gradients are still not large: the median range of species evenness predicted along disturbance gradients was a factor of 1.06. At the highest sampling intensity, the species evenness–disturbance relationship was typically peaked or monotonic positive, although when disturbance selectively removed the least dominant species, species evenness was independent of disturbance patterns.

DISCUSSION

species diversity often varies by orders of magnitude across landscapes or regions (e.g. Aronson and Shmida 1992, Nichols et al. 1998). Disturbance is often postulated to be one of the main processes controlling patterns of species diversity (Huston 1994, Noss 1996). However, published relationships between species diversity and disturbance are not consistently strong or consistent in form (Chapter 2). Theoretical models of the

interaction (Petraitas et al. 1989; Huston 1979, 1994) predict that peaked relationships should exist, but that these may appear monotonic if disturbance gradients are short, or if species assemblages are growing very slowly. Published models give little hint whether one would expect strong relationships or not.

To examine this problem, I chose to use Markov models, based on observed species dynamics in six real communities. In principle, I could have used models based, for example, on Lotka-Volterra style interactions among species (Huston 1979), immigration and extinction probabilities (Petraitis et al. 1989), or spatially-explicit patch dynamics (Caswell and Cohen 1991). I chose Markov models because they have been shown to capture the dynamics of real communities reasonably well (Waggoner and Stephens 1970, Horn 1975, Lough et al. 1987), because the community dynamics appear to be virtually unchanged by disturbances (Tanner 1996), and because published transition probability matrices provide a means to build models based on data from several different real communities. It is possible that other, more complicated, models might identify conditions under which disturbance is predicted to have a greater effect on species diversity than that observed here.

My models predict that variation in species richness to be expected across wide disturbance gradients is generally quite small. Occasionally, the predicted range is as much as a factor of 2. In comparison, the median range of variation in published studies reviewed in Chapter 2 is 1.52. Thus, the effects of disturbance on species diversity are probably real, but modest, in most cases. In contrast, order-of-magnitude variations in spatial patterns of species richness have been related to the factors that determine productivity (Wright et al. 1993).

Earlier qualitative models predict further that the true species diversity–disturbance relationship is peaked, although it may appear to be monotonic when disturbance gradients are short. Our models predicted peaked relationships should be observed only occasionally (in 12% of the cases I modeled), even across long disturbance gradients. More commonly, species richness was predicted to be independent of disturbance (36%), a monotonic negative function of disturbance (32%), or a positive monotonic function of disturbance (20%), depending mainly on the sampling intensity. These frequencies are close to those observed in published studies: among 116 published species richness-disturbance relationships I reviewed (Chapter 2), I found that 16% were peaked, 35% flat, 21% negative, and 25% positive. Thus, in contrast to earlier qualitative models, my simulations suggest that relationships between species diversity and disturbance along long disturbance gradients should not generally be peaked.

The effect of sampling intensity on species richness–disturbance relationships is partly intuitively obvious, and partly very surprising. Species richness can only covary with disturbance if species are extirpated from the study area. If disturbance results only in some species becoming rare but not extirpated, then as the number of individuals sampled increases, the probability of including individuals of rare species increases, such that species richness becomes essentially insensitive to disturbance if sampling is extensive enough. At lower sampling intensities, species richness appears to respond to disturbance because some species are overlooked in the census. Thus, my models suggest that the shape of species richness–disturbance relationships are very dependent upon sampling intensity. More surprising, the shape of the relationship can qualitatively change forms – between peaked, positive monotonic, and negative monotonic – along gradients of

sampling intensity. This is mainly because observed species richness is a biased estimator of true species richness: as sample size increases, estimated species richness systematically increases. This affects the shape of observed species richness–disturbance relationships. Since the shape of the relationship changes with the number of individuals censused, the observed shape of a species richness–disturbance relationship at any particular sampling intensity is probably not very informative.

There are two processes that may counteract competitive displacement: disturbance (which is usually assumed to remove individuals of all species non-selectively), and predation (which is assumed to be selective) (Petraitas et al 1989, Huston 1994). I examined both selective and non-selective removal of individuals in this study to determine how the predicted effects on species richness differ. Note that my question was not whether disturbances of various sorts affect species diversity differently (c.f. Lubchenco 1978), but rather, whether the effect is likely to be large. In general, I observed that removal of the numerically least dominant species is predicted to produce very little change in species richness, while removal of the most dominant leads to patterns that are similar to those for non-selective removal, but more subtle. Thus, while selectivity of disturbance may influence fine points of species richness patterns, my models predict that the broad trends are unlikely to be much affected.

In contrast to species richness, my models do predict that species evenness is sensitive to disturbance and that species evenness–disturbance relationships should vary with species–selectivity of disturbances at high sampling intensities. Non-selective and dominant-selective disturbances produced positive or peaked relationships even with complete sampling. Similarly, Rogers (1993) concluded that hurricanes cause less change in coral

species richness than species evenness, and in fact, often have no significant or consistent effect on coral species richness. Changes in species evenness across a disturbance gradient may be perceived as a change in species richness when sampling intensity is too low to detect rare species in the community. The species richness patterns observed with less complete sampling generally reflect the species evenness patterns observed with complete sampling (Fig. 7). In other words, my models predict that the true effect of disturbance is mainly on species evenness (although even this is subtle); effects on species richness derive largely from sampling effects.

Why, then, are the species diversity changes predicted by my models so modest? First, in all of the published transition matrices I used but one (alpine cushion), every species has a finite probability of recolonizing empty space. When sampling intensity is reasonably high, most species are eventually found, and thus species richness depends little on disturbance. In the alpine cushion transition matrix, three species have zero probability of recolonizing bare space and thus become extinct at high levels of disturbance (Fig. 5b). Presumably, in species assemblages where many species have no or very low probability of colonizing empty space, disturbance effects would be stronger. It is not clear how often this is the case in real communities. A second reason that the trends I observed were fairly subtle may be that rates of natural mortality were reasonably high in these assemblages. In the six transition matrices that I examined, the median probability that a species would be replaced by a different species or by empty space is 0.65 (per time interval). Perhaps high rates of natural mortality reduce interspecific competition sufficiently so that disturbance has little additional effect (cf. Petraitis et al. 1989, Huston 1994). However, there is no evidence to suggest that the rates of natural mortality in these transition

matrices are atypical of species assemblages in general. Perhaps this is why disturbance effects are not generally strong under natural conditions.

Huston's (1994) model suggests another possible explanation why the responses to disturbance that I observed were very modest. His model suggests that disturbance and productivity interact such that strong effects on species diversity are observed when both disturbance and productivity are at intermediate levels. Productivity does not appear explicitly in my models; rather, the transition matrices I used came from real communities with whatever productivity levels occurred naturally. I do not know the location of my systems on the biomass gradient controlled by productivity and disturbance; perhaps none of these six communities had productivity levels that would favor strong responses to disturbance. This is a possibility, but there is no reason to think that these six communities are atypical of ecological communities in general. Perhaps communities exist in which species diversity responds strongly to disturbance, but there is no evidence to suggest that this is generally the case.

There are further similarities among all six transition matrices, and communities not exhibiting these traits may behave differently. First, transition matrices can only be applied to communities of non-motile species. Our predictions may therefore not apply to communities of motile species. Further, in all but the alpine cushion community, virtually all species in my model communities had at least a small probability of replacing any other species during one transition time interval, preventing species from being eliminated. That is, model complexity (ratio of the number of observed transitions : maximum number of possible transitions; Tanner et al. 1994) was very high (0.76 - 0.91) and no species competitively excludes other species completely, even when disturbance levels were

very low. The species richness of communities with a low complexity (e.g. alpine cushion, model complexity = 0.59) should decline at low levels of disturbance.

In conclusion, if one is interested in explaining the variation of species richness in nature, my models suggests that disturbance is unlikely to account for more than small amounts of variance. Moreover, the form of the relationship may well interact with sampling intensity and community type in ways that are not intuitively obvious. While effects of disturbance have been incorporated into qualitative models in intuitively appealing ways (Grime 1973, Connell 1978, Huston 1979, 1994), I suggest that, as a general explanation of species diversity patterns, its merits have yet to be demonstrated.

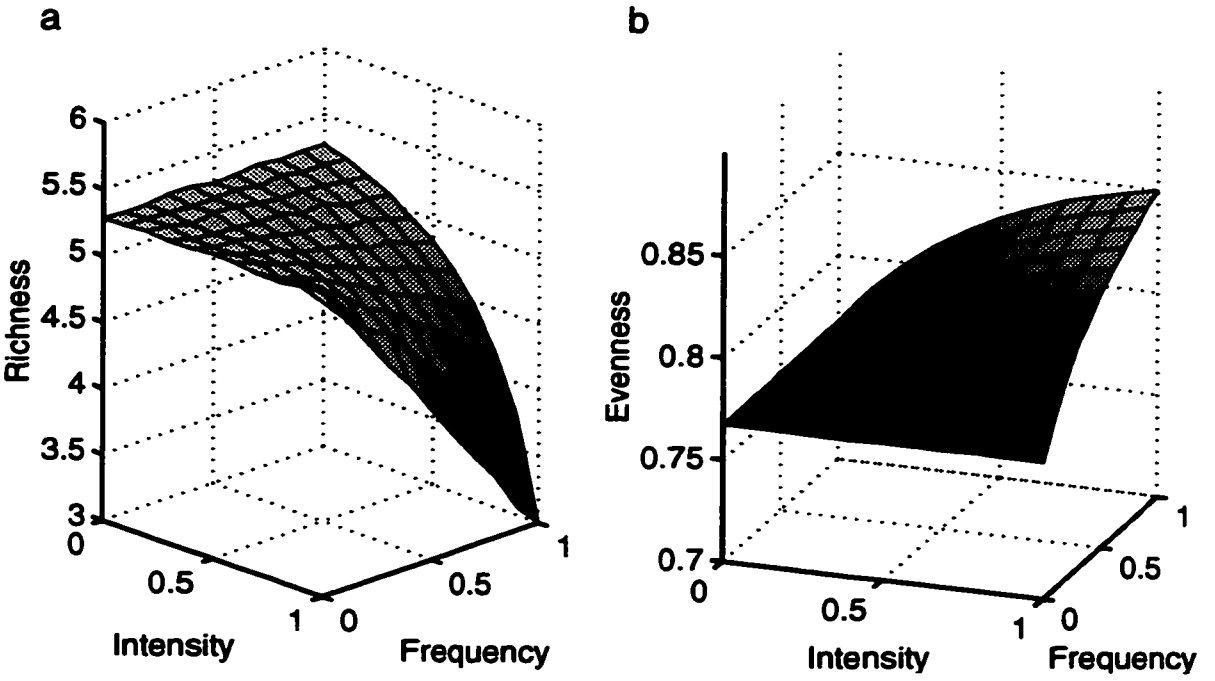


Figure 1: The predicted effects of disturbance on either species richness or species evenness were typically similar along the two types of disturbance gradient (frequency and intensity). a) Species richness of the alpine cushion community with non-selective disturbances at a sampling intensity of 625 cells, or 12.5% of the community. b) Species evenness of an exposed coral pool community with non-selective disturbances at a sampling intensity of 5000 cells, or 100%.

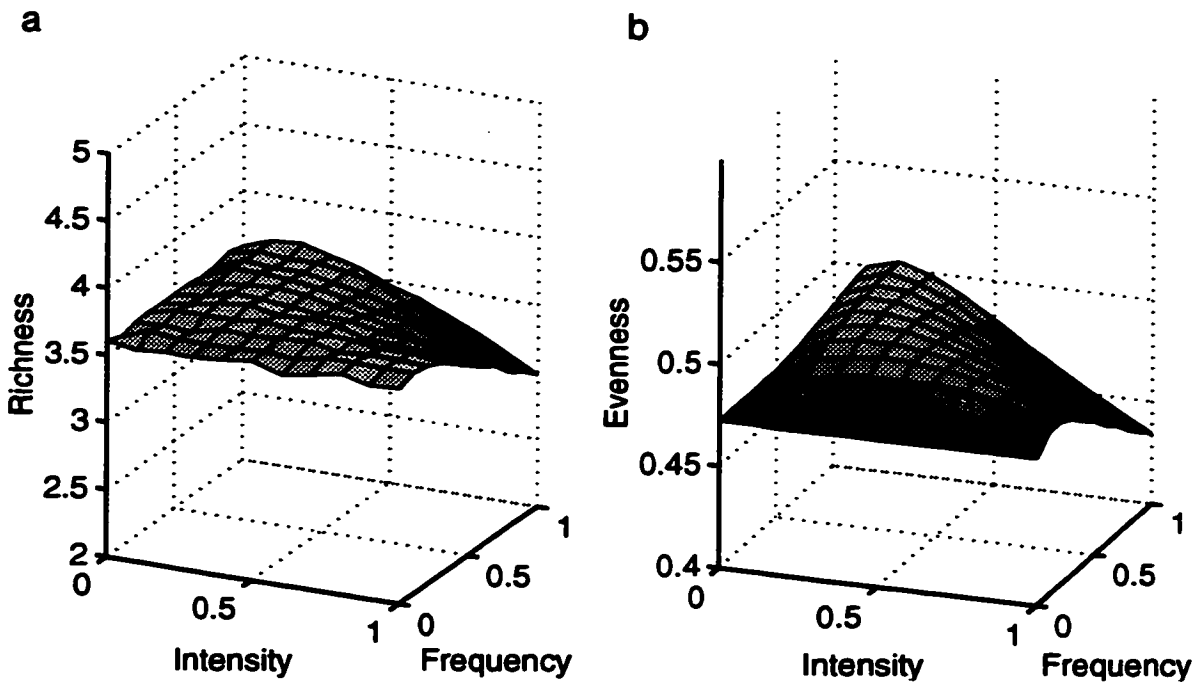
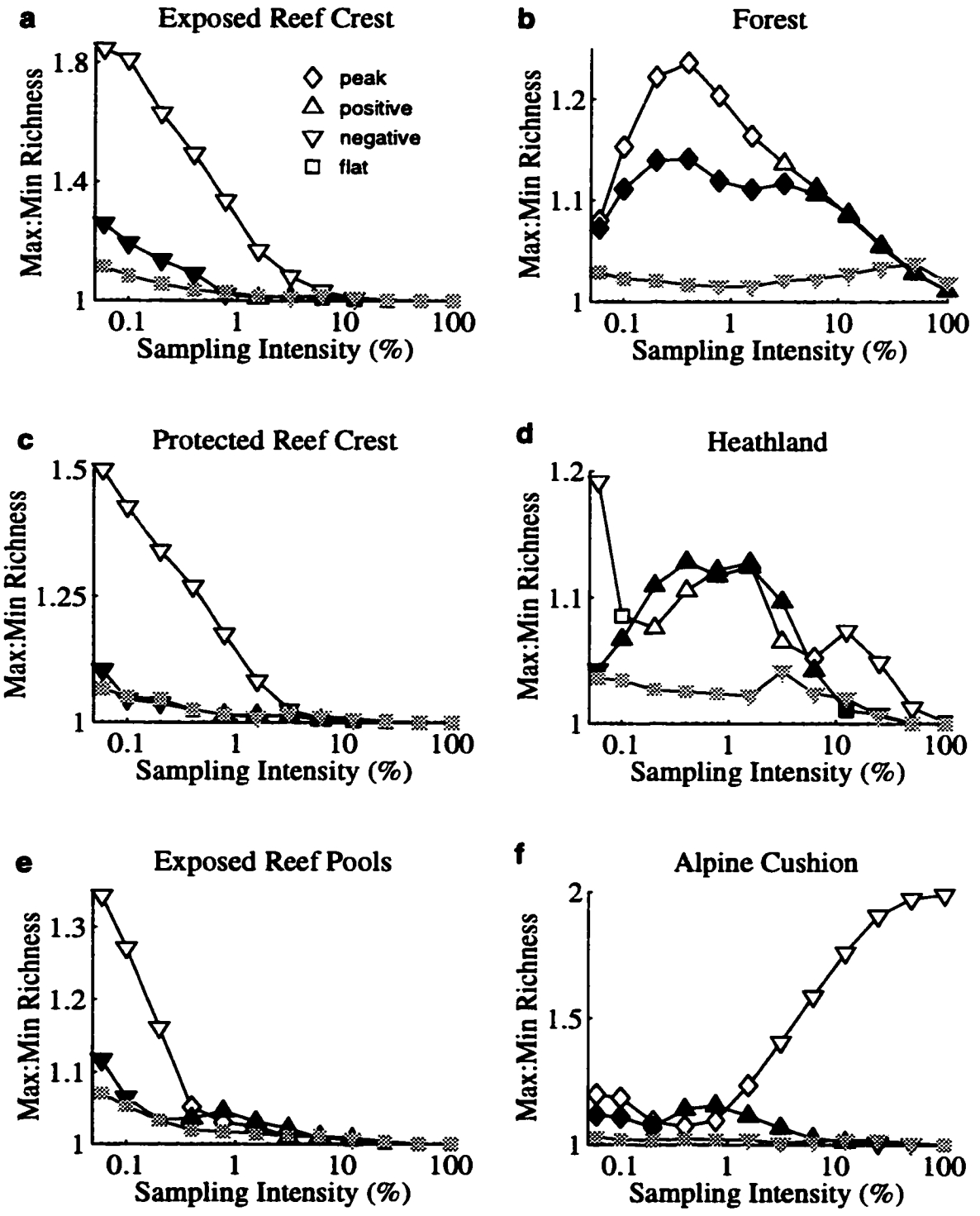


Figure 2: For simulations that predicted unimodal relationships between species richness or species evenness and disturbance, the peaked pattern was sometimes more pronounced along the disturbance intensity gradient than the frequency gradient. a) Species richness of the heathland community with non-selective disturbances at a sampling intensity of 313 cells, or 6.3% of the community. b) Species evenness of the alpine cushion community with dominant-selective disturbances at a sampling intensity of 5000 cells, or 100%.

Figure 3: Summary plots of the predicted range of species richness over the complete gradient of disturbance frequency (0% probability of occurrence per time interval, to 100%), expressed as the ratio of the highest observed species richness to the lowest (Max:Min). The different symbols indicate the shape of the pattern. Sampling intensity is the number of individuals censused out of a total model community of 5000. Data are presented for non-selective disturbance (open symbols), and for selective disturbance that targets the numerically most dominant species (black symbols), and the numerically least dominant species (gray symbols). Panel a): exposed coral reef crest with a maximum of 8 taxa; b) forest community, 11 species; c) protected coral reef crest, 8 taxa; d) heathland, 8 species; e) exposed coral reef pools, 8 taxa; f) alpine cushion, 6 taxa. The results from the disturbance intensity gradients are very similar to those indicated here and are therefore not presented. Note: at high sampling intensities, overlapping points sometimes give the appearance of missing data.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Exposed Reef Pools
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Sampling Intensity (%)
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Alpine Cushion
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10
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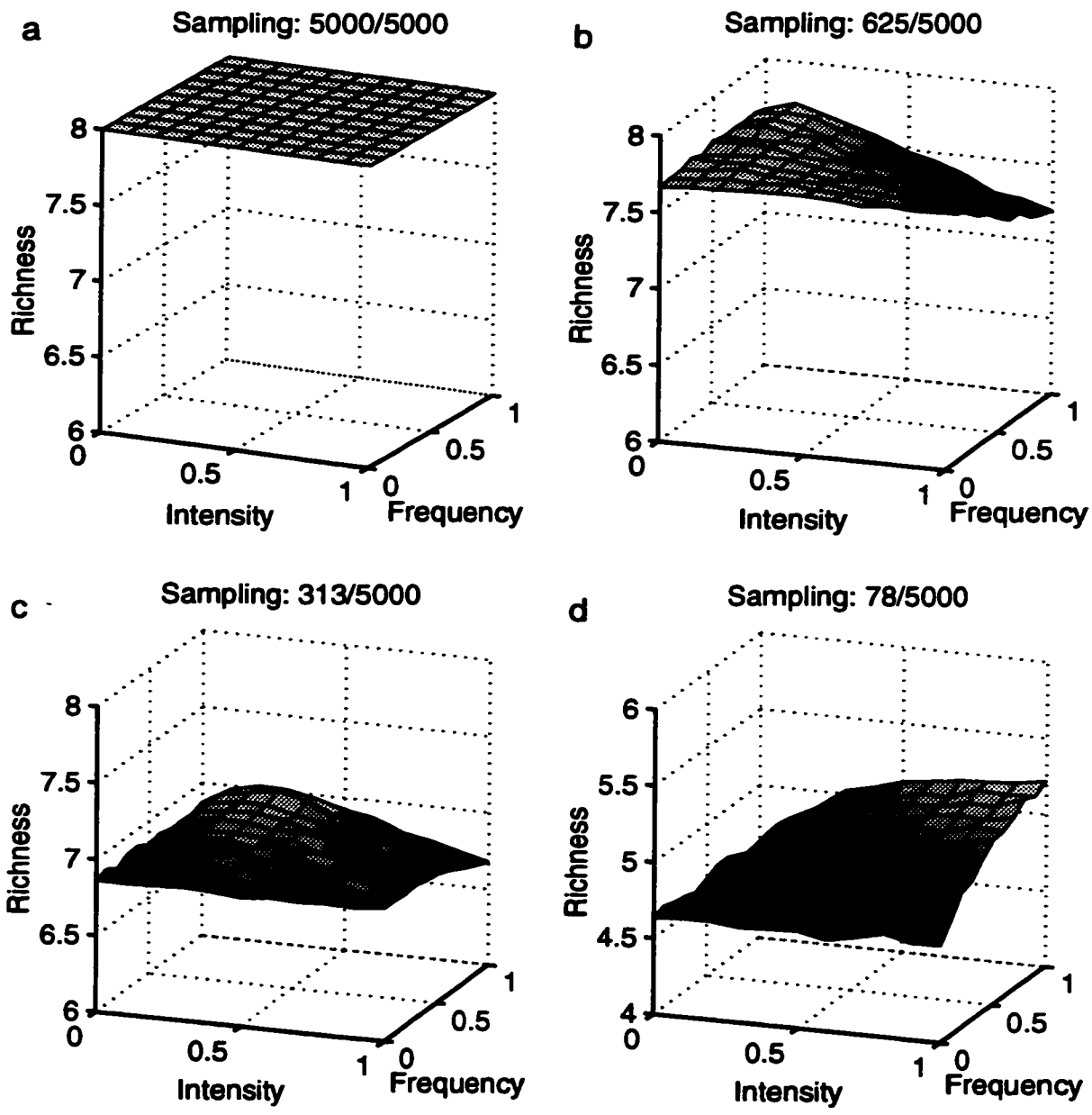
Sampling Intensity (%)

Figure 4: The shape of the species richness–disturbance relationship varied with sampling intensity in each community. In the heathland community, the model predicted (a) an independent relationship between species richness and disturbance when the sampling intensity (SI) was 5000 cells, or 100% of the community, (b) a negative monotonic relationship when SI = 625 or 12.5%, (c) a unimodal relationship when SI = 313 or 6.3%, and (d) a positive monotonic pattern when SI = 78 or 1.6%.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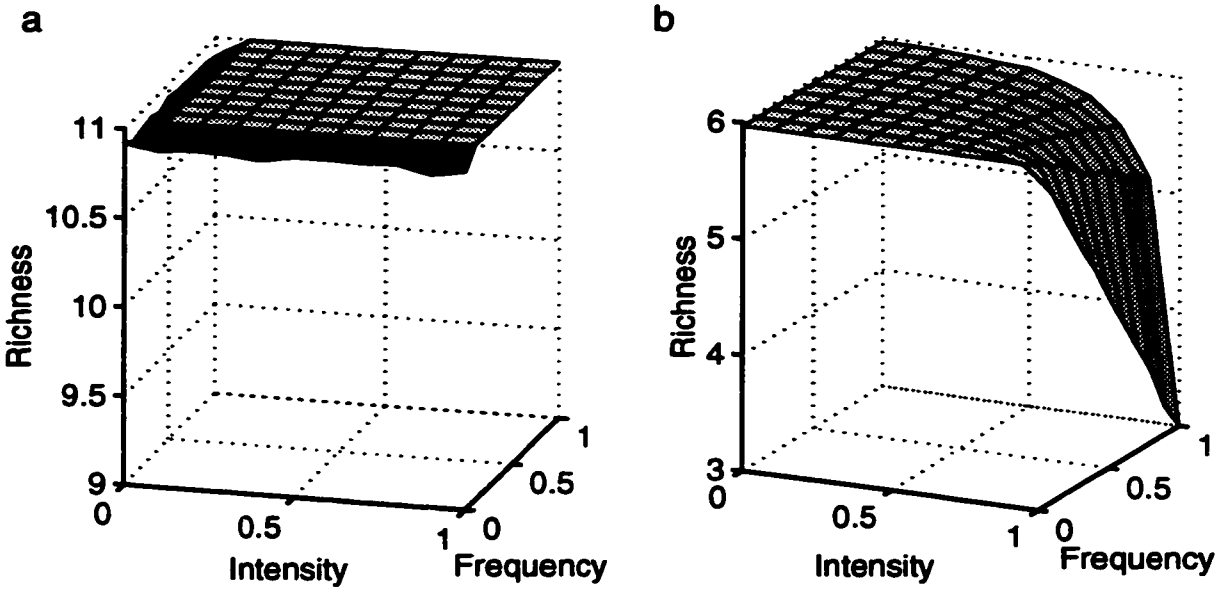
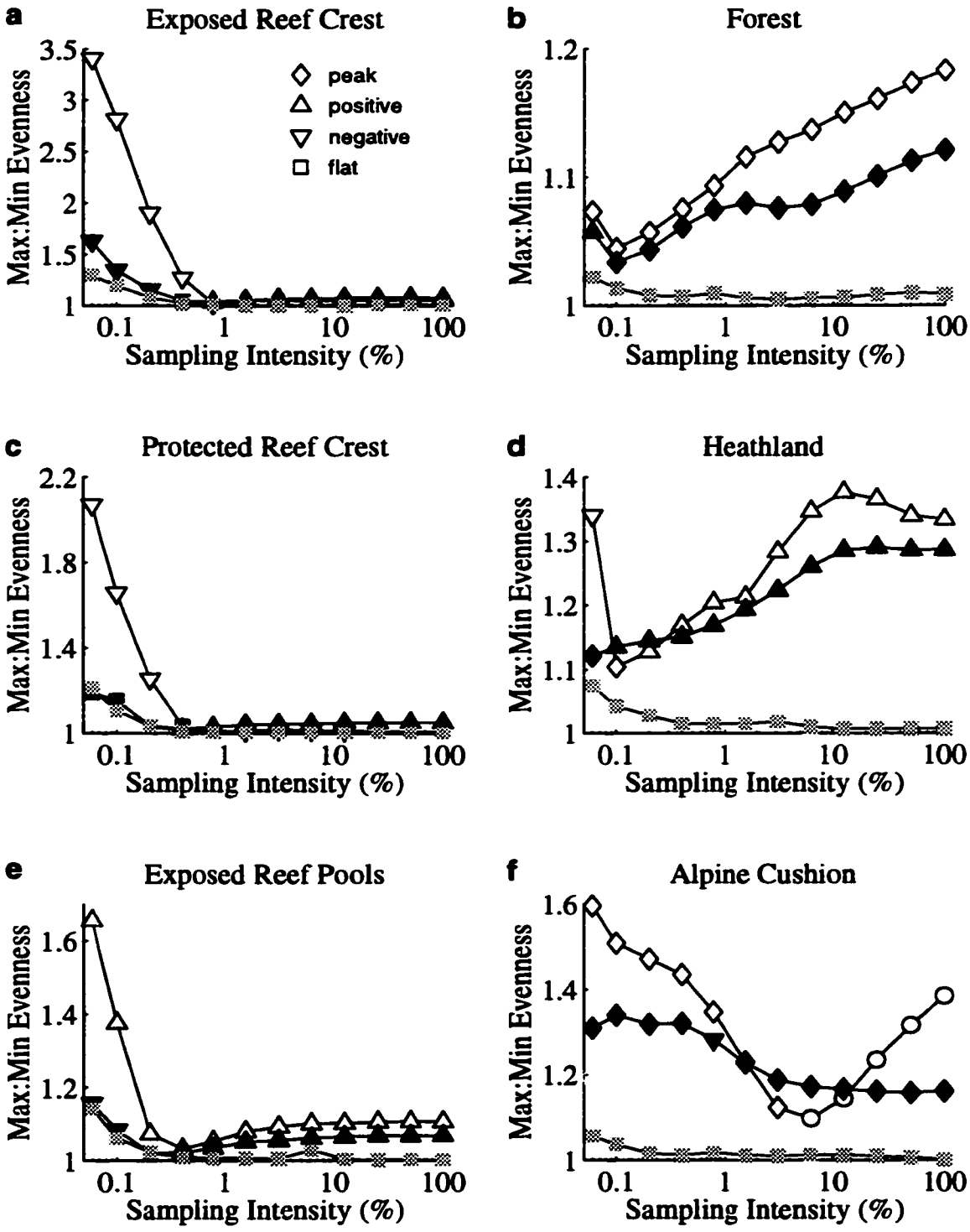


Figure 5: Species richness was predicted to be independent of disturbance at the highest sampling intensity (i.e. 5000 cells), except in the cases of: (a) forest community for non-selective (shown here) and dominant-selective disturbances, and (b) alpine cushion when the disturbances were non-selective.

Figure 6: Summary plots of the predicted range of species evenness over the complete gradient of disturbance frequency (0% probability of occurrence per time interval, to 100%). Other details are explained in the caption of Fig. 3., expressed as the ratio of the highest observed species richness to the lowest (Max:Min). The different symbols indicate the shape of the pattern. Sampling intensity is the number of individuals censused out of a total model community of 5000. Data are presented for non-selective disturbance (open symbols), and for selective disturbance that targets the numerically most dominant species (black symbols), and the numerically least dominant species (gray symbols). Panel a): exposed coral reef crest with a maximum of 8 taxa; b) forest community, 11 species; c) protected coral reef crest, 8 taxa; d) heathland, 8 species; e) exposed coral reef pools, 8 taxa; f) alpine cushion, 6 taxa. The results from the disturbance intensity gradients are very similar to those indicated here and are therefore not presented. In alpine cushion at high sampling intensity, relationships were peaked with an increase at the highest level of disturbance frequency or intensity (o). Note: at high sampling intensities, overlapping points sometimes give the appearance of missing data.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Max:Min Evenness
Sampling Intensity (%)
c
Protected Reef Crest
Max:Min Evenness
Sampling Intensity (%)
d
Heathland
Max:Min Evenness
Sampling Intensity (%)
e
Exposed Reef Pools
Max:Min Evenness
Sampling Intensity (%)
f
Alpine Cushion
Max:Min Evenness
Sampling Intensity (%)

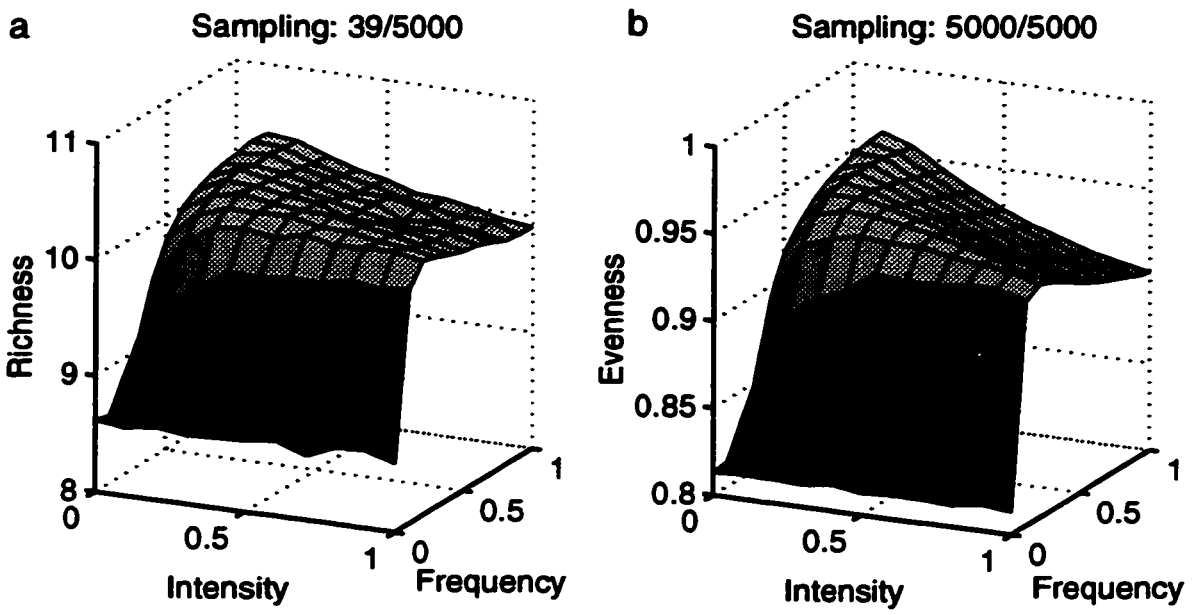


Figure 7: The species richness–disturbance relationships at low sampling intensities often reflect patterns of species evenness at the highest sampling intensity. a) Species richness of the forest community at a low sampling intensity of 39 cells, or 0.8% of the total community. b) Species evenness of the same forest community at a sampling intensity of 5000 cells, or 100%.

Chapter 2: The diversity–disturbance relationship: is it generally strong and peaked?

INTRODUCTION

Species diversity varies greatly through space and time. Many factors have been hypothesized to influence richness and other measures of species diversity (Palmer 1994); however, the evidence for many of these hypotheses is anecdotal and/or restricted to specific circumstances. Most authors postulate that only a small number of factors are responsible for the majority of the variation in richness in nature.

Disturbance is widely believed to be one of the main factors influencing variations in species diversity. According to Noss (1996), "One notable generalization of modern ecology is that moderate levels of disturbance maximize the diversity of habitats and species in a landscape". The ecological literature is virtually unanimous in postulating that species diversity is a peaked function of disturbance. The Intermediate Disturbance Hypothesis (IDH; Grime 1973a, Grime 1973b, Horn 1975, Connell 1978, Huston 1979, 1994) postulates that physical disturbance prevents or slows the rate of competitive exclusion of competitive subordinates in a community by competitively dominant species, and that there is a trade-off between species' ability to compete and their ability to tolerate disturbance. At low levels of disturbance, diversity is low because only the best competitors persist. When disturbances are very intense or frequent, few species can persist or repeatedly colonize after every disturbance. At intermediate intensities or frequencies of disturbance, there is a balance between competitive exclusion and loss of competitive dominants by disturbance; conditions favor the coexistence of competitive species and disturbance-tolerant species. Thus, a peak in diversity should occur at intermediate intensities and

frequencies of disturbance, as well as at intermediate times since the last disturbance.

A cursory examination of the disturbance literature reveals that diversity–disturbance relationships do not consistently show the peaked pattern predicted by the IDH. Positive monotonic, negative monotonic, and unimodal relationships all appear. Most surprising is the large number of non-significant diversity–disturbance relationships in the literature.

Equivocal published evidence regarding IDH indicates a need to determine why there is so much variation in the observed shape of species diversity–disturbance relationships and percent variance explained. Some authors suggest that peaked diversity–disturbance relationships may not be the rule. In communities where post-disturbance succession is not driven by competitive hierarchies, disturbance intensity and frequency may have little effect on species richness (Reice 1985, Chesson and Huntly 1999). Because in the absence of a competitive hierarchy community composition throughout succession will simply reflect colonization rates and mean longevities of species, there is no reason to expect that moderate levels of disturbance will promote the maintenance of high levels of species diversity. Productivity, rate of population growth, and rate of competitive exclusion may influence the shape of the diversity–disturbance relationship (Huston 1979, 1994): at low levels of each, Huston (1979, 1994) predicts that species diversity should decrease with increasing disturbance intensity or frequency; at high rates, species diversity is predicted to increase with disturbance; and, at intermediate levels of each, species diversity is predicted to be greatest at intermediate levels of disturbance. Unpredictable, severe, episodic disturbances may have greater effects on richness than do predictable, moderate events to which communities may adapt (Reice et al. 1990).

Wootton's (1998) models predict that, in multitrophic systems, IDH should hold for species competing for non-dynamic basal resources (e.g. sessile organisms competing for space), but not necessarily for mobile organisms at higher trophic levels. The effect of disturbance on mobile consumers may be altered by factors such as whether the disturbance causes mortality of only the consumers or of both the consumers and a limited resource being competed for (e.g. prey); how low the resource levels are driven by disturbance; and whether the disturbance is density–dependent, versus density–independent (Wootton 1998). Finally, Mackey and Currie (2000) suggest that significant and/or peaked richness–disturbance relationships are most likely to be observed when sampling intensity is low because species that are rare at low and high disturbance levels often will not be sampled.

This paper addresses the following questions about the importance of disturbance as a regulator of species diversity.

1) Is species diversity consistently related to measures of disturbance? How strong are the relationships (i.e., how much variation in species diversity is explained by disturbance)?

2) Does the amount of explained variation in species diversity depend upon the conditions under which the relationship was observed?

3) How frequently are diversity–disturbance relationships peaked?

4) Under what conditions are peaked diversity–disturbance relationships most likely to occur?

To answer these questions, I searched the published literature for studies examining effects of disturbance on species diversity. I considered several measures including richness (the number of different species that co-occur), evenness (how evenly distributed

the individuals of a community are among the different species present; e.g. Pielou's J), and measures that combined richness and evenness (e.g. Shannon-Weiner's H′, Simpson's D). I will use the term 'species diversity' when referring to the general concept of species diversity, and 'diversity' for the specific statistic that combines measures of richness and evenness. I tested the extent to which the strength (explained variation) and shape of observed relationships were related to characteristics of the community, the habitat, the disturbance, and the sampling design (Table 1). For this study, I defined disturbance as a temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass. By directly or indirectly changing the availability of substrate and/ or other resources, disturbance creates an opportunity for new individuals to become established (Sousa 1984, White and Pickett 1985). Disturbance, by this definition, includes abiotic processes such as fire, landslides, wave exposure, and floods, as well as the biotic processes of predation and grazing. It does not include prolonged stresses such as contamination by pollutants, invasion by exotics, or climate change.

METHODS

Data Collection

My literature search was as broad as possible, including all studies I could locate that related richness, diversity, or evenness to gradients of disturbance, whether or not those studies specifically tested IDH. I began by searching Biological Abstracts on CD-ROM (1990 - 1996, inclusive), using the following search strings with some minor variations: intermediate disturbance, disturbance, disturbance gradients, species richness, species diversity, species evenness, patterns in species richness (or diversity or evenness),

community dynamics, and community structure. Bibliographies of publications retrieved from the electronic search were searched for additional studies of diversity and disturbance. I then searched Biological Abstracts 1985 through 1990 in hardcopy format. Because disturbance is not a keyword in hardcopy volumes, the search was limited to the following strings: species composition, species diversity, species evenness, species richness, and succession. To prevent bias towards studies of particular types of disturbance, I did not use keywords such as fire, grazing, mining, logging, etc. I am confident that my search identified the majority of the disturbance literature published over at least 12 years and also many of the studies published prior to 1985.

Species diversity–disturbance relationships were retained in my analyses provided that:

1) Three or more disturbance levels were examined (at least three are required to detect a peaked relationship). Papers examining disturbance presence/absence are very abundant and frequently make conclusions about the IDH, but these could not be included in my analyses because such studies cannot identify the shape of the species diversity–disturbance relationship.

2) The disturbance gradient consisted of different levels of a single disturbance type (e.g. forest fire frequency, time since flooding, or intensity of sheep grazing) and was measured on either a continuous or an ordinal scale. Studies that used composite disturbance measures (combinations of disturbance types) were included only if their estimates of disturbance level could be confidently quantified or ranked.

3) The disturbance gradient was calculated from the actual disturbance frequency or intensity, or time passed since the last disturbance event, or some other physical

environmental attribute that was shown to be an indicator of disturbance. When gradients were inferred from a biological response to a supposed disturbance, I did not include them in my analyses.

4) The study examined species/taxonomic richness, evenness, and/or diversity.

5) Statistical results were reported, or sufficient data were included in the paper for me to perform statistical analyses. Studies reporting only qualitative relationships were excluded.

6) Potential explanatory variables could be determined (see below). Not all explanatory variables could be obtained from each study; therefore the sample sizes of my analyses varied. Studies failing to report methodology and descriptions of the community and/or disturbance were excluded.

A total of 1962 abstracts and papers were consulted. From these, 85 papers satisfying my criteria were found (Appendix 3), providing a total of 116 richness–disturbance relationships, 53 diversity–disturbance relationships, and 28 evenness–disturbance relationships from studies of many different types of disturbance (see Appendix 4 for list of disturbances and number of relationships associated with each).

I used two forms of meta-analysis to evaluate the form of the relationships between species diversity and disturbance and to summarize how much of the observed variation in species diversity can be related to disturbance. First, to determine the form of the species diversity–disturbance relationships, I used a vote-counting procedure based, in part, on statistical significance (i.e., I tallied the number of relationships of each possible shape, with shape based on statistical analyses (see below)). Vote-counting and other forms of meta-analysis based on statistical significance have been criticized (Gurevitch et al. 1992,

Osenberg et al. 1997). While a measure of effect strength would have been preferable (Osenberg et al. 1999), the diversity of studies in my data set made this impossible. Vote-counting provided an effective way to examine the conditions under which peaked relationships are detected in empirical studies. Second, I also extracted from each study the proportion of the variation in species diversity explained by disturbance (i.e. r^2) using a quadratic polynomial regression model or an analysis of variance. I then performed unweighted meta-analyses using r^2 from each study as the effect size. The three measures of species diversity (richness, diversity, and evenness) were analyzed separately because papers that contained relationships for two or three of these measures indicated that the form of the relationship for the three measures are frequently different.

Some of the relationships included in my data set are composed of data pooled from two or more relationships in a primary study. To avoid non-independence of multiple relationships retrieved from a single paper, I pooled data from studies in a single paper sharing a common sampling regime and examining the same taxa, disturbance, and measure of species diversity. Studies within a single paper that examined different taxa, different habitats, or different disturbances, or applied different sampling methods were all included in my data set because of my objective to determine whether any of these attributes are related to the form of species diversity–disturbance relationship observed in a study.

Each relationship was categorized as having one of five observed shapes: flat, positive monotonic, peaked, negative monotonic, or U-shaped. I performed the pattern analyses described below for 80 richness, 27 evenness, and 39 diversity relationships (see Appendix 5 for an example of pattern analysis). In further cases (36, 1, and 14 cases, for

richness, evenness, and diversity, respectively), I could not analyze the data myself, but the original authors had performed the analyses that I describe below. I accepted these analyses. Cases where I could not re-analyze the data were almost always studies of categorical disturbance gradients, and the authors provided only the mean species diversity values per category.

To characterize the shape of a relationship when the measure of disturbance was continuous, I used second-degree polynomial regressions. Statistically non-significant relationships ($P > 0.05$) were categorized as flat. When the linear regression term in a relationship was significant ($P \leq 0.05$) but the quadratic term was not, I categorized the relationship as monotonic positive or negative, according to the sign on the linear term. A relationship was categorized as peaked or U-shaped if: a) the linear and quadratic terms in the regression were significant, and b) the maximum or minimum of the curve fell within the observed range of disturbance values, as determined by an MOS test (Mitchell-Olds and Shaw 1987; see Appendix 5 for description). If the maximum fell outside the range of the data, the relationship was categorized as monotonic positive or negative. In a few cases where the distribution of the residuals violated the assumptions of least-squares regression, I used non-parametric correlation analysis to test the significance of monotonic relationships, after examining scatterplots of these few relationships for peaks.

When measures of disturbance were ordinal, I used ANOVA to test for significance. Multiple comparison tests were then done to determine which categorical levels of disturbance differed significantly. Relationships were classified as peaked if species diversity measures at both extremes of the disturbance gradient were significantly lower than at some intermediate level of disturbance.

The proportion of the variation in species diversity explained by disturbance in each relationship was obtained only from parametric analyses. When regressions were performed, explained variation was always obtained from models including both linear and quadratic terms. Parametric ANOVAs also yielded r^2 values, which I included in my analyses.

Variables that could potentially account for differences in total explained variation (i.e. strength) and shape of relationships are listed in Table 1. These variables are grouped into three categories: 1) organism and system attributes, 2) disturbance attributes, and 3) sampling and study design. Organism and system attributes include whether study organisms were animals or plants, terrestrial or aquatic/marine, and sessile or motile. Also, sessile producers were differentiated from motile consumers, based on Wootton's (1998) hypothesis that IDH should hold for species competing for nondynamic basal resources, but not for mobile species at higher trophic levels.

Measures of productivity were not provided in the original papers. However, Rosenzweig (1968) and Lieth (1975) showed that terrestrial productivity strongly correlates with actual evapotranspiration (AET). Therefore, by using the geographic locations provided in the papers, I estimated AET for terrestrial systems from the Atlas of World Water Balance (USSR National Committee for the International Hydrological Decade 1977), and used this as a surrogate for productivity. Productivity could not be estimated for aquatic systems because such studies rarely provided productivity or related data (e.g. chlorophyll, total phosphorus).

Disturbances were characterized as biotic (e.g. grazing) versus abiotic (e.g. fire), natural (e.g. windthrow) versus anthropogenic (e.g. cultivation), and chronic (e.g. grazing) versus episodic (e.g. landslides). To eliminate the anthropogenic factor from the abiotic

vs. biotic variable, I also examined abiotic vs. biotic for natural disturbances only. Each disturbance was classified as a gradient of either disturbance frequency or disturbance intensity at multiple sites (spatial gradient), or a gradient of time passed since the last disturbance occurred at single sites sampled several times (temporal gradients). Disturbances were also categorized as removing or damaging only the biomass of the community being examined, versus damaging the habitat of the community in question (or both). Although other aspects of disturbance might be associated with the strength and shape of species diversity–disturbance relationships (e.g. species-specific vs. non-specific disturbance, the size of the disturbance in relation to the area sampled, duration of disturbance events, etc.), data were not available for me to test these.

Other variables in my analyses describe sampling design (Table 1). I estimated sampling intensity with three variables: exhaustive sampling of the community versus incomplete or sub-sampling (e.g. point counts), the number of disturbance levels examined, and the total number of samples taken. I defined a 'sample' as yielding one datum; if authors pooled several samples to obtain a single estimate of species diversity, then I classified the sum of those pooled samples as one 'sample'. Two measures of sampling area were also examined: quadrat area and the total area sampled per level of disturbance. 'Quadrat area' is the area sampled to obtain a single data point. If a datum resulted from pooling sampled areas, then quadrat area is the sum of those areas. 'Total area of a disturbance level sampled' is defined as the sum of all areas sampled for each level of disturbance in the study (i.e. area per sample multiplied by number of samples per disturbance level). Another variable, single patch vs. mosaic, differentiates studies that measured species diversity within individual disturbed patches (e.g. recolonization of a gap created by a

windthrow) versus studies that measured species diversity in areas that contained small patches of disturbance (cf. Wilson 1994). In 'mosaic' studies (e.g. a forest stand containing uprooted trees) the disturbance level assigned to an area was the overall intensity or frequency of disturbed patches in the whole area (e.g. the frequency of tree uprooting within the stand). The duration of temporal gradients of studies examining patterns of species diversity over time was also included in my set of potential predictor variables. Finally, observational studies were compared with experimental or manipulative studies.

I located 119 species diversity–disturbance relationships examined along spatial gradients, and 78 examined on temporal gradients, either at replicate sites following a given disturbance, or at a series of sites differing in the time since the last disturbance (and assumed to be otherwise identical). Only four studies (Reice 1984, Armesto and Pickett 1985, Lake et al. 1989, Ambrose 1993; for a total of nine species diversity–disturbance relationships) examined temporal and spatial gradients simultaneously: a set of sites differing in disturbance intensity or frequency, followed through time (sometimes at just two times). Three of these four studies indicated that the observed relationship between species diversity and disturbance among sites changed temporally. Although time scale can be an important consideration in meta-analyses (Downing et al. 1999, Osenberg et al. 1999), there are insufficient data and few theoretical considerations to guide the selection of appropriate time-scales for these studies. Therefore, I restricted my analyses to the longest time scale available from each study that presented a time series.

The entire dataset is provided in Appendix 6.

Analyses

I used r^2 as the measure of the strength of species diversity–disturbance relationships. Some authors use regression slope as the measure of the strength of a relationship. Note that these two metrics are equivalent in my study. The standardized regression coefficient (i.e., the regression slope calculated on standardized data) is equal to r for bivariate linear relationships. It is practical in this study to use r (or rather, r^2) because it can also be used to describe bivariate non-linear relationships, which do not have a unique slope.

Logistic regressions were used to determine under what conditions the odds of observing the different shapes of disturbance - species relationship (flat, positive monotonic, negative monotonic, and unimodal) is greatest. The resulting statistical models take the form:

$$\log\hat{O} = \alpha + \beta_1(E_1) + \beta_2(E_2) + \ldots$$

where $\hat{O}$ is the estimated conditional odds of the relationship shape of interest, given the explanatory variables (E_i). Each β represents the change in log odds due to a unit increase in the value of the explanatory variable, controlling for all other predictors in the model. For binary explanatory variables, β is the change in log odds between group = 1 and group = 0. For continuous variables, β is the change in log odds per one-unit increment in the predictor. The interpretation of logistic regression results is more intuitive when expressed as the percentage change in odds (PCO) for a unit increment in the predictor:

$$PCO = 100[\exp(b_i) - 1],$$

where b_i is the sample estimate of β_i, and $\exp(b_i)$ is the estimated multiplicative change in the odds of observing the relationship shape of interest for a one-unit increment in the i th explanatory variable (DeMaris 1992).

Predictive efficacy of logistic models was measured with McFadden's Rho^2, which is analogous to r^2 and ranges between 0 and 1. This measure of efficacy generally underestimates the total variation explained by the model; therefore, the predictive efficacies I provide are conservative.

All statistical analyses were performed with SYSTAT 9.0.

RESULTS

Does species diversity have a consistent and significant relationship with disturbance?

Total Explained Variation in Species Diversity

The amount of variation in richness, diversity, and evenness statistically related to disturbance, using quadratic polynomial regression or ANOVA, varied enormously among studies, from 0.1% to 100% (Table 2). Not surprisingly, non-significant (i.e. flat) richness and evenness relationships generally explained less variation than significant relationships; however, this difference was not statistically significant for evenness relationships. Note that polynomial regressions always have r^2 values greater than 0, even when both variables are generated randomly. When the sample size is small, r^2 can be quite large simply by chance (Fig. 8). Among significant relationships, the different shapes of relationships (positive, peaked, negative, and U-shaped, as determined by quadratic polynomial regression, ANOVA, or non-parametric correlation) accounted for indistinguishable amounts of explained variation for any of the three measures of species diversity.

Frequency of Different Shapes of Relationship

RICHNESS

Flat (i.e., non-significant) relationships were observed more frequently than any other shape (H_0: uniform distribution; $\chi^2 = 33.5$, d.f. = 4, $P < 0.001$) (Table 2, Fig. 9). Among significant relationships, positive, negative and peaked relationships were observed equally frequently ($\chi^2 = 2.1$, d.f. = 2, $P > 0.25$), but U-shaped relationships were observed much less frequently than any other shape ($\chi^2 = 20.3$, d.f. = 3, $P < 0.001$).

DIVERSITY

There were no significant differences in the observed frequencies of non-significant, positive, peaked, and negative relationships ($\chi^2 = 3.9$, d.f. = 3, $P > 0.25$). As with richness, U-shaped relationships were observed much less frequently than any other shape of relationship ($\chi^2 = 12.6$, d.f. = 4, $P < 0.025$) (Table 2, Fig. 9).

EVENNESS

Flat relationships were again observed more frequently than any other shape ($\chi^2 = 23.8$, d.f. = 4, $P < 0.001$) (Table 2, Fig. 9). Among significant relationships, negative ones were observed most frequently ($\chi^2 = 6.1$, d.f. = 2, $P < 0.05$).

In sum, there is no evidence that a particular shape of species diversity–disturbance relationship is consistently detected.

Under what conditions are significant species diversity–disturbance relationships most likely to be observed?

RICHNESS

Only one of my predictors was significantly associated with the probability that a richness–disturbance relationship would be significant or non-significant. Odds of observing a significant relationship were 133% greater when the examined disturbance was natural rather than anthropogenic in origin (McFadden's $Rho^2 = 0.031$, $n = 116$, $P = 0.032$; Fig. 10).

DIVERSITY

Odds of observing a significant diversity–disturbance relationship were significantly related to three attributes of the disturbance and two attributes of the sampling design (Table 3). Studies examining chronic disturbances had odds 1209% greater than studies of episodic disturbance events. Odds of a significant relationship were 268% greater for studies of spatial gradients of disturbance vs. temporal gradients, and, more specifically, 653% greater when gradients of disturbance intensity vs. any other gradients were examined. The number of samples examined in a study had a great effect on the odds of observing a significant relationship: odds increased 6422% for each 10-fold increase in sample size. Finally, odds were 550% greater in studies examining communities in mosaics of patches, rather than in single patches. Many of these predictor variables were collinear: studies examining mosaics of patches, compared to single patches, more frequently involved chronic disturbances ($\chi^2 = 14.2$, d.f. = 1, $P = 0.0002$) and spatial gradients ($\chi^2 = 11.8$, d.f. = 1, $P = 0.0006$). Studies of both chronic, vs. episodic, disturbances and spatial, vs. temporal, gradients were also more likely to have greater samples sizes

(chronic: U=402, χ^2= 5.1, d.f. = 1, P = 0.02; spatial gradients: U=461, χ^2= 7.1, d.f. = 1, P = 0.008). The best multiple regression model for predicting whether a significant diversity–disturbance relationship will be observed included the number of samples examined and whether studies examined individual patches or mosaics of patches.

Evenness

None of my predictor variables were significantly associated with the odds of observing a significant evenness–disturbance relationship. This may be a result of the small number of studies in this group (n=28).

Does the amount of explained variation in species diversity depend upon the conditions under which the relationship was observed?

Richness

The amount of variation in richness explained by disturbance was significantly related to two attributes of the disturbances studied (Table 4). More variation in richness was related to disturbance when disturbances were biotic rather than abiotic, and when richness was measured along a gradient of time passed since the last disturbance rather than along spatial gradients of disturbance frequency or intensity.

Five attributes of sampling design were also related to the total explained variation. Relationships were stronger when sample sizes were small (Fig. 11a) and when the organisms within the samples were not enumerated exhaustively. Explained variation was also greater when low to moderate numbers of levels of disturbance were examined (i.e., a peak occurs at approximately 7 levels), and when the duration of temporal gradients was

moderate (~7 years) (Fig. 11).

Some of these significant relationships may reflect collinearities. Richness–disturbance relationships involving temporal gradients of disturbance were more likely to have greater numbers of disturbance levels (Mann-Whitney U-test: $U = 1121$, $\chi^2 = 7.1$, d.f = 1, $P = 0.008$) and lower sample sizes ($U = 2348$, $\chi^2 = 20.5$, d.f = 1, $P = 6 \times 10^{-6}$) than were relationships for spatial gradients. More levels of disturbance were also generally examined in studies of abiotic versus biotic disturbance ($U = 2293$, $\chi^2 = 11.7$, d.f = 1, $P = 0.006$). Relationships obtained from exhaustively searched samples included greater sample sizes than did cases where organisms were sub-sampled ($U = 1664$, $\chi^2 = 12.7$, d.f = 1, $P = 0.004$).

Multiple regression and multiple analysis of variance analyses indicate that the proportion of the variation in species richness that is statistically related to disturbance is best explained by a model including only the number of samples examined (NS; $2.06 - 1.53(\log_{10}NS) + 0.38(\log_{10}NS)^2$). An alternate model with slightly lower predictive efficacy is one that includes the following variables: animal vs. plant community, spatial vs. temporal gradient of disturbance, exhaustive sampling vs. subsampling, and the number of samples examined (Table 4).

DIVERSITY

A summary of the attributes that significantly affected the proportion of variation in diversity explained by disturbance is presented in Table 5. Variation in diversity explained by disturbance was greatest in studies that examined plants or, more specifically, sessile producers, as opposed to motile animals. Explained variation was also greatest when sample size was small and when low to moderate numbers (~7 - 8) of disturbance

levels were examined. The number of disturbance levels examined was greater in studies of plants, sessile organisms (producers or consumers), and, specifically, sessile producers ($U = 361$, $\chi^2 = 6.5$, d.f = 1, $P = 0.01$) than in studies of animals, all motile organisms, and motile consumers.

The proportion of the variation in diversity that is statistically related to disturbance is best explained by a model including linear, quadratic, and cubic terms of the number of disturbance levels examined in a study and the binary variable that separates studies of sessile producers from those of motile consumers (Table 5).

EVENNESS

The amount of explained variation in evenness was related to four explanatory variables (Table 6). Explained variation was greatest in studies of sessile producers (compared to motile consumers) and plants in general (includes sessile producers and non-attached phytoplankton). Relationships tended to be stronger when sample sizes were small and fewer levels of disturbance were examined. Sample size and number of disturbance levels examined were positively correlated for evenness–disturbance relationships ($r_s = 0.432$, $n = 28$, $P < 0.05$).

Multiple regression analyses indicate that the proportion of variation in species evenness is best explained by disturbance is best explained by models including the number of disturbance levels and the number of samples examined in a study, as well as the variable that differentiates studies of sessile producers from those of motile consumers (Table 6).

Under what conditions are peaked relationships most likely to be observed?

RICHNESS

Logistic regression analyses comparing peaked versus all other shapes of richness–disturbance relationships indicated that the odds of observing a peaked relationship were significantly associated with four explanatory variables (Table 7). Odds of a peaked richness–disturbance relationship were 371% greater for natural disturbances than for disturbances with anthropogenic causes (Fig. 10). Odds of a peaked relationship decreased 31% for each ten-fold increase in quadrat area and increased 535% for each ten-fold increase in the number of disturbance levels examined. Productivity in terrestrial systems, as estimated by actual evapotranspiration (AET), also affected the odds of observing a peaked relationship: odds decreased 97% for each 10-fold increase in AET. The number of disturbance levels examined was greater in studies of natural disturbance ($U=716$, $\chi^2= 29$, d.f $= 1$, $P < 10^{-7}$).

DIVERSITY AND EVENNESS

Analyses provided little insight into the conditions required to observe peaked evenness– or diversity–disturbance relationships. None of the explanatory variables were significant in analyses of evenness. For diversity–disturbance relationships, the only significant predictor was whether the organisms studies were sessile producers or motile consumers: odds of a peaked relationship were 540% greater for sessile producers than for motile consumers (McFadden's $Rho^2 = 0.103$, $n = 52$, $P = 0.040$; to deal with sparse data in one cell (peaked relationship, motile consumers), one case was added to each of the four cells in this analysis, increasing 'n' from the original 48 to 52).

DISCUSSION

The general opinion in the literature is that disturbance should have a strong effect on species diversity, and that the species diversity–disturbance relationship should peak at intermediate levels of disturbance. However, upon closer examination, data are actually equivocal on the subject. In 35%, 28% and 50% of published studies, no effect of disturbance on richness, diversity or evenness, respectively, was observed.

The high proportion of non-significant relationships indicates that peaked species diversity–disturbance relationships are actually not as prevalent as commonly believed. For two reason, my data set probably underestimates the proportion of non-significant relationships and overestimates the proportion of peaked relationships that are actually observed. First, non-significant relationships are more likely to remain unpublished than significant ones ("the file–drawer effect"; Gurevitch et al. 1992). Second, part of my search for papers involved searching bibliographies of retrieved publications for additional papers; this older literature (pre-1985) is represented by studies that first documented peaked species diversity–disturbance relationships and that continue to be cited in the recent literature, and, incidentally, contains a greater proportion of peaked relationships than does the more current literature (24%, versus 13%, of relationships).

Alternatively, the abundance of statistically non-significant relationships in my study could be a result of low statistical power (or low sample size) in the primary studies. Gurevitch et al. (1992) state that analyses like mine contain a strong bias towards finding no effect because many ecological studies have small sample sizes and relatively small effects, resulting in low statistical power. Gurevitch et al. (1992) and Osenberg et al. (1999) suggest that the number of significant, or non-significant, results one would expect

to find in a vote-counting analysis like mine is a function of both the sample sizes of the primary studies and the actual magnitude of the effect in question. My logistic regression analyses explicitly examined the effect of study sample size on the odds of observing a significant relationship. Sample size was not related to the odds of observing a significant richness– or evenness–disturbance relationship, but the odds did increase with sample size in the set of diversity–disturbance relationships. If low sample size were responsible for the abundant non-significant relationships in this study, I would have expected to find evidence of it in my analyses of richness– and evenness–disturbance relationships, as well.

Collinearities make it difficult to determine in which biological systems significant diversity–disturbance relationships are most likely to occur. In studies of richness, odds were higher for natural vs. anthropogenic disturbances. In the primary studies, natural disturbances more frequently caused the removal or damage of habitat, rather than affecting only the organisms being studied. Studies of natural disturbances were also more likely to examine plant or sessile communities. Together, these collinearities could explain the observed difference between natural and anthropogenic disturbances. Motile animal colonizers from communities surrounding a disturbed patch quickly re-establish the original species assemblage of the patch with little or no change in species diversity (Fuentes and Jaksic 1988). Plant communities, especially those recovering from disturbances that affected a primary resource (e.g., space), would likely have a much slower recovery than would motile animal communities, especially those recovering from less intense losses of individuals (Fuentes and Jaksic 1988, Wootton 1998).

Explained variation in species diversity–disturbance relationships is not consistently large. The median amount of variation explained by disturbance was 53% for

richness, 59% for diversity, and 60% for evenness. Again, because of the file-drawer effect, this is probably an overestimate. Even more importantly, these numbers are inflated because a regression always explains >0% of the variation in the dependent variable, especially when sample sizes are small (Fig. 8). If I consider only studies where $n \geq 10$, the median percent explained variation is 44% for richness, 48% for diversity, and 27% for evenness. Thus, while disturbance sometimes explains much of the observed variation in species diversity, it does not do so consistently. In contrast, Wright et al. (1993) found that studies of energy–related factors (which generally involve large sample sizes) explained a median 70% of the spatial variation in richness.

Further, the strength of species diversity–disturbance relationships appears to reflect sampling artifacts. The proportion of variation in richness, diversity, and evenness explained by disturbance significantly decreased as the number of samples examined in a study increased. Moreover, I found that explained variation was much greater for richness–disturbance relationships inferred from partial sampling (e.g., point counts; 62%) than for those derived from exhaustive sampling (36%). Mackey and Currie (2000) argue that with less intense sampling, one is less likely to detect rarer species; as sampling intensity increases, rarer species are detected and disturbance is predicted to have less effect on richness.

Disturbance appears to have a greater role in determining temporal than spatial patterns of species diversity. Temporal gradients of disturbance explained more variation in all three measures of species diversity than did spatial gradients, although this difference was significant only in the studies of species richness. This might be an artifact: temporal gradients typically involved fewer samples than did spatial gradients (see

discussion above). However, Collins and Glenn (1997) suggest that spatial and temporal responses of a community to disturbance are affected by different mechanisms and that the two responses may be very different. Also, data from Reice (1984), Armesto and Pickett (1985), and Lake et al. (1989) indicate that the observed shape of relationships between diversity and spatial gradients of disturbance changes over time. The spatial variation in diversity explained by disturbance may therefore be sensitive to how soon after disturbance communities along a spatial gradient are sampled, and whether each community in a study is given the same time to recover. If this is the case, inconsistencies in sampling time along a spatial gradient may alter the apparent r^2 of the relationship.

Explained variation in species diversity is also greater for studies of plants, or, more specifically, sessile producers, than for animals, or motile ones in particular. Plant ecologists have often been proponents of the important role of disturbance in patterns in species diversity (e.g. Grime 1973a, White 1979, Collins 1992, Collins et al. 1995), while ecologists studying freshwater invertebrates often fail to detect significant species diversity–disturbance relationships and are more skeptical of the role disturbance has in determining patterns in species diversity (e.g. Reice 1985, Resh et al. 1988, Lake et al. 1989). Fuentes and Jaksic (1988) discuss why peaked or strong species diversity–disturbance relationships are not frequently found among terrestrial vertebrates: their mobility and ability to diffuse into and out of disturbed patches, consumption of many different resources, and highly heterogeneous environments mean that many terrestrial animals do not meet the conditions required for disturbance to have a peaked or strong effect on species diversity. For the reasons that Fuentes and Jaksic (1988) suggest, I would expect explained variation in species diversity–disturbance relationships of plants to be greater

than in most studies of motile animals.

In addition to not being consistently strong (i.e. high explained variation), species diversity–disturbance relationships are also not generally peaked. With only 16%, 19%, and 11% of richness-, diversity–, and evenness–disturbance relationships, respectively, being significantly peaked, detectable intermediate disturbance responses are the exception rather than the rule. Even papers that are frequently cited as showing the classic peaked relationship do not consistently find peaks (e.g. Lubchenco 1978, Sousa 1979). For example, Sousa's (1979) study of intertidal boulder algal communities detected peaked richness–disturbance patterns 50% of the time. This may suggest that even when peaked relationships are the norm for a community, they may be detected in only 50% of studies. Even considering this possibility, my finding that 16% of richness–disturbance relationships are peaked is still low — too low for peaks to be considered the norm. Although I did identify some factors related to the probability of observing a peaked relationship, the consistently low values of McFadden's Rho^2 indicate that there are no predictable circumstances (that I could identify) under which species diversity–disturbance relationships are generally peaked.

Some authors have suggested that productivity influences the strength and shape of species diversity–disturbance relationships (Grime 1973a, 1973b; Huston 1979, 1994). Huston (1994, p.138) suggests that almost all studies supporting the IDH examined systems with high rates of population growth (or high levels of productivity), such as the intertidal zone, coral reef crests or weedy plant communities. Yet, this evidence is anecdotal; there are no data showing that these communities are more productive than those where the species diversity–disturbance relationship was not peaked. Evidence from my

study does not support Huston's conjecture that communities supporting the IDH are those with high productivity. I found that the odds of observing a peaked richness–disturbance relationship decreased by 97% for each 10-fold increase in actual evapotranspiration (AET; a surrogate of terrestrial productivity). This result may have arisen from the high proportion of tree studies in sites with high AET; trees are not the typical fast–growing organisms that Huston (1979, 1994) associates with high productivity. Among studies of field vegetation (i.e., fast–growing weeds and grasses), the odds of peaked vs. non-peaked relationships were not greater when AET was higher (McFadden's Rho^2=0.06, n=12, P=0.40). Actual evapotranspiration is an imperfect surrogate for terrestrial productivity; a better measure might reveal a different relationship between productivity and the shape of the species diversity–disturbance relationship. However, the evidence at hand does not support the hypothesis that intermediate disturbance relationships are associated with high productivity systems.

The odds of observing a peaked vs. non-peaked relationship were negatively related to quadrat area (i.e., the total area sampled to collect one estimate of species diversity, or one data point). Mackey and Currie's (2000) models of richness–disturbance relationships predict that peaked relationships should be observed only when sampling intensity (number of organisms censused) is low, as a result of rare species being overlooked when few individuals are censused. The decreasing probability of observing a peaked relationship when quadrat area is larger may indicate that peaked relationships are an artifact of restricted sampling. Alternatively, the effect of quadrat area on the odds of observing a peaked relationship may indicate that peaked richness–disturbance relationships occur mainly at small spatial scales. In apparent disagreement with Mackey and Currie (2000),

the number of samples examined in a study was not a significant predictor of relationship shape, and peaked richness–disturbance relationships were more likely to be observed when higher numbers of levels of disturbance were examined. However, because neither of these variables are necessarily good indicators of the number of individuals censused, valid comparisons of these results with those of Mackey and Currie (2000) are not possible. It is apparent, though, that sampling methodology (number of individuals censused, number of disturbance levels examined, and/or quadrat area sampled) does appear to significantly influence the shape of relationship that will be observed.

There has been much confusion in the literature with respect to whether the IDH is a within–patch or among–patch phenomenon (e.g. Fuentes and Jaksic 1988, Wilson 1994, Rosenzweig 1995). Many of the studies in my data set examined community structure within individual disturbed patches (e.g. a patch of burned grassland, a forest gap resulting from a fallen tree, or an intertidal boulder). Because, as Wilson (1994) states, "A single patch does not have a frequency of disturbance, only a time since last disturbance ", it is difficult to understand how the concept of intermediate disturbance frequency can be applied to a single patch. I therefore hypothesized that studies examining mosaics of patches would have greater odds of observing peaked species diversity–disturbance relationships than would studies of single patches. However, whether a study utilized single patches or mosaics had no apparent effect on whether the observed relationship was peaked, indicating that the IDH may be equally applicable to both kinds of studies (cf. Collins and Glenn 1997).

The number of published diversity– and evenness–disturbance studies was relatively low. This created problems of sparse data in several of the logistic regression

analyses. I did not feel that it was wise to make conclusions from either of these data sets.

In conclusion, the published literature provides evidence that disturbance plays some role in determining spatial and temporal patterns of species diversity, but species diversity–disturbance relationships are neither consistently strong nor consistently peaked. There is evidence that observed species diversity–disturbance relationships may often reflect sampling artifacts. I suggest that, of the factors that have been proposed to affect species diversity in nature, disturbance is probably not among the most important ones.

Table 1 : A list of the predictor variables used in the analyses. These variables encompass traits of the biological system, the disturbance, and the sampling design of the study. The range of each continuous variable is included in parentheses for each of richness–, diversity–, and evenness–disturbance relationships, respectively.

Predictor Variables
Organism and System Attributes
Animal vs. Plant
Terrestrial vs. Aquatic
Sessile vs. Motile
Sessile producers vs. Motile consumers
Actual Evapotranspiration (mm) [1] (100–1250, 220–1250, 275–1250)
Disturbance Attributes
Abiotic vs. Biotic [2]
Gradient of Frequency vs. Intensity vs. Time passed since last disturbance
Spatial vs. Temporal gradients
Anthropogenic vs. Natural
Chronic vs. Episodic
Disturbance removed Biomass of community studied vs. Habitat
Sampling and Study Design
Exhaustive or Subsampled species counts within samples
Quadrat Area (m^2; $2x10^{-4}$ - $3.28x10^7$, $3.96x10^{-3}$ - $3.28x10^7$, $3.96x10^{-3}$ - $3.28x10^7$)
Number of Disturbance Levels (3–125, 3–32, 3–32)
Number of Samples (4-640, 4-132, 4-132)
Total Area of Disturbance sampled (m^2; $8x10^{-4} - 3.28x10^7$, $1.19x10^{-2} - 3.28x10^7$, $1.19x10^{-2} - 3.28x10^7$)
Single Patch vs. Mosaic of patches
Time Span (range of temporal gradient, in years; 0.088-246, 0.088–246, 0.088-246)
Observation vs. Experimental

1 Actual Evapotranspiration values were estimated from USSR Committee for the International Hydrological Decade (1977) for terrestrial studies providing adequate site location information. A surrogate measure of terrestrial productivity.

2 Two variations of this predictor were examined: a) includes both natural and anthropogenic disturbances, with anthropogenic disturbances assigned to the category they best represent or were stated to simulate, and b) only natural disturbances were included.

Table 2 : The proportion of variation in species richness, diversity, or evenness statistically related to disturbance in a compilation of published studies. Results are shown separately for relationships that are non-significant (—), positive monotonic (/), peaked (⌒), negative monotonic (\), U-shaped (⌣), and for all studies combined. 'n' includes the studies that provided either r^2 values or sufficient data to calculate r^2. In parentheses is the number of additional studies found that observed the same shape of relationship but did not provide a value for r^2. The very high, but non-significant, r^2 values came from studies with very small sample sizes (generally $n = 4$).

Diversity Measure	—	/	⌒	\	⌣	All Studies
Species Richness						
n	25 (16)	25 (4)	16 (3)	18 (6)	3 (0)	87 (29)
Median	0.179 [a]	0.665 [b]	0.524 [a,b]	0.514 [a,b]	0.710 [b]	0.534
Skewness	+0.590	-0.206	-0.025	-0.239	+0.243	-0.156
Range	0.001-0.855	0.250-0.994	0.080-0.973	0.096-0.900	0.538-0.970	0.001-0.994
Species Diversity						
n	11 (4)	12 (0)	6 (4)	12 (3)	1 (0)	42 (11)
Median	0.707 [a]	0.516 [a]	0.678 [a]	0.594 [a]	0.611 [a]	0.605
Skewness	-0.561	-0.354	+0.350	-0.179	--	-0.392
Range	0.036-0.952	0.113-0.769	0.501-0.978	0.171-0.940	0.611	0.036-0.978
Species Evenness						
n	11 (3)	2 (0)	3 (0)	7 (2)	0 (0)	23 (5)
Median	0.266 [a]	0.723 [a]	0.993 [a]	0.794 [a]	--	0.601
Skewness	+0.381	--	-0.707	-0.463	--	-0.137
Range	0.025-0.855	0.663-0.782	0.423-1.000	0.147-0.999	--	0.025-1.000

a,b Medians in the same row identified by the same superscript are not statistically different from one another (Kruskal-Wallis; P>0.05).

Table 3 : Significant relationships observed in logistic regression analyses comparing the odds of significant (peaked, positive monotonic and negative monotonic) versus non-significant diversity - disturbance relationships. See Table 1 and related text for description of explanatory variables.

Explanatory Variable	*n*	P [1]	McFadden's Rho^2	Group with Highest Odds	% Change in Odds of Significant Relationship [2]
Simple Regressions					
Frequency vs. Intensity vs. Frequency*Intensity vs. Time	53	0.008	0.186	Intensity	+653 [3]
Spatial vs. Temporal	53	0.037	0.069	Spatial	+268
Chronic vs. Episodic	57 [4]	0.002	0.143	Chronic	+1209
Number of Samples	52	0.0003	0.206	High number	+6422/ 10-fold increase
Single Patch vs. Mosaic	53	0.010	0.106	Mosaic	+550
Multiple Regression					
Number of Samples	52	0.00009	0.298	High number	+5936/ 10-fold increase
Single Patch vs. Mosaic				Mosaic	+590

(1) Probability from Likelihood Ratio Chi-square.

(2) For binary predictors, the percentage change in odds of a peaked relationship is reported in terms of the change predicted for the group with the highest odds versus the group with the lowest odds. In the multiple regression, the change in odds was calculated while controlling for the other predictor in the model.

(3) % change in odds is given for Intensity vs. other 3 categories combined.

(4) Because of sparsity of cases in one cell (chronic disturbance and non-significant diversity–disturbance relationship), one case was added to each of the four cells for this analysis.

Table 4 : Does the proportion of the variation in species richness that is statistically related to disturbance (r^2) in published richness - disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors. Significant relationships ($P < 0.05$) are shown in bold. (Sheet 1 of 2)

Predictor Variable	Mean r^2 or Shape of Relationship [1]	n	Statistic [2]	P
Organism and System Attributes				
Animal vs. Plant	0.437, 0.540	28, 58	F=1.64, r^2=0.019	0.204
Terrestrial vs. Aquatic	0.529, 0.466	57, 30	F=0.65, r^2=0.008	0.424
Sessile vs. Motile	0.539, 0.407	62, 23	F=2.42, r^2=0.028	0.123
Sessile Producer vs. Motile Consumer	0.545, 0.420	57, 24	F=2.12, r^2=0.026	0.149
Actual Evapotranspiration		51	F=0.17, r^2=0.003	0.685
Disturbance Attributes				
Abiotic vs. Biotic	**0.427, 0.581**	**42, 45**	F=4.49, r^2=0.050	**0.037**
Abiotic vs. Biotic (natural disturbance only)	0.474, 0.529	36, 15	F=0.31, r^2=0.006	0.578
Frequency vs. Intensity vs. Frequency*Intensity vs.Time	**0.381, 0.466, 0.340, 0.611**	**11, 25, 10, 41**	H=12.16	**0.007**
Spatial vs. Temporal	**0.418, 0.611**	**46, 41**	U=563, χ^2=10.47	**0.001**
Anthropogenic vs. Natural	0.542, 0.482	37, 50	F=0.61, r^2=0.007	0.436
Chronic vs. Episodic	0.413, 0.552	28, 59	F=3.07, r^2=0.035	0.083
Biomass vs. Habitat vs. both	0.531, 0.380, 0.635	53, 22, 12	F=2.53, r^2=0.057	0.086

Table 4 : (Continued)Does the proportion of the variation in species richness that is statistically related to disturbance (r^2) in published richness - disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors. Significant relationships ($P < 0.05$) are shown in bold. (Sheet 2 of 2)

Predictor Variable	Mean r^2 or Shape of Relationship [1]	n	Statistic [2]	P
Sampling and Study Design				
Exhaustive or Subsampled sampling	**0.360, 0.624**	**30, 41**	**F=12.16, r^2=0.150**	**0.0009**
Log_{10} Quadrat Area (m^2)		68	F=0.16, r^2=0.002	0.690
Log_{10} Number of Disturbance Levels [3]	**unimodal**	**87**	F=7.75, r^2=0.219	**0.0001**
Log_{10} Number of Samples [3]	**negative monotonic**	**87**	F=29.02, r^2=0.409	**<1E-8**
Log_{10} Total Area of Disturbance sampled (m^2)		64	F=0.44, r^2=0.007	0.511
Single Patch vs. Mosaic	0.547, 0.426	58, 29	F=2.39, r^2=0.027	0.126
Log_{10} Time Span (years) [3, 4]	**unimodal**	**39**	**F=3.80, r^2=0.174**	**0.032**
Observed vs. Experimental	0.539, 0.432	61, 26	F=1.73, r^2=0.020	0.192
Multiple Regressions/MANOVA [5]				
Animal vs. Plant + Spat vs. Temp + Exh vs. Sub – Log_{10} NDL – (Spat vs. Temp)*Log_{10} NDL – (Exh vs. Sub)*Log_{10} NDL		71	**r^2=0.493**	

Footnotes are on the following page.

(1) Mean r^2: reported for categorical predictor variables. r2 values were arcsine-square root transformed to satisfy assumptions of residuals for parametric tests; values reported in table are back-transformed. Shape of Relationship: reported for significant continuous predictor variables.

(2) 'H' refers to Kruskal-Wallis non-parametric ANOVA; 'U' refers to Mann-Whitney non-parametric t-test.

(3) Relationships are non-linear. The statistics presented are from the following polynomial regression models:
$\log_{10}$ Number of Disturbance Levels ($\log_{10}$NDL), $-1.34 + 6.73(\log_{10}\text{NDL}) - 6.10(\log_{10}\text{NDL})^2 + 1.59(\log_{10}\text{NDL})^3$;
$\log_{10}$ Number of Samples ($\log_{10}$NS), $2.06 - 1.53(\log_{10}\text{NS}) + 0.38(\log_{10}\text{NS})^2$;
$\log_{10}$ Time Span ($\log_{10}$TS), $0.95 + 0.26(\log_{10}\text{TS}) - 0.15(\log_{10}\text{TS})^2$.

(4) Studies of temporal gradients of disturbance.

(5) In the best model obtained from multiple analysis of variance (MANOVA) and multiple regression analyses, the proportion of the variation in species richness that is statistically related to disturbance is greater for plant, vs. animal, communities; temporal, vs. spatial, gradients of disturbance; subsampling vs. exhaustive sampling, of samples; and low numbers of samples examined.

The full model is:

$$\arcsin\sqrt{r^2} = 1.27 + 0.10(\text{Animal vs. Plant}) + 0.38(\text{Spatial vs. Temporal}) + 0.32(\text{Exhaustive vs. Subsampling}) - 0.59(\text{Log}_{10}\text{ NDL}) - 0.29(\text{Spatial vs. Temporal})*\text{Log}_{10}\text{ NDL} - 0.26(\text{Exhaustive vs. Subsampling})*\text{Log}_{10}\text{ NDL}$$

Table 5 : Does the proportion of the variation in diversity (e.g. Shannon-Weiner's index, Simpson's *D*) that is statistically related to disturbance (r^2) in published diversity–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? The number of studies in each analysis (*n*) is reported per category for categorical predictors and as total for continuous predictors. Significant relationships ($P < 0.05$) are shown in bold (Sheet 1 of 2)

Predictor Variable	Mean r^2 or Shape of Relationship [1]	*n*	Statistic	P
Organism and System Attributes				
Animal vs. Plant	**0.366, 0.665**	**12, 30**	**F=12.01, r^2=0.231**	**0.001**
Terrestrial vs. Aquatic	0.589, 0.563	29, 13	F=0.07, r^2=0.002	0.789
Sessile vs. Motile	**0.641, 0.329**	**33, 8**	**F=9.16, r^2=0.190**	**0.004**
Sessile producer vs. Motile consumer	**0.671, 0.339**	**28, 10**	**F=12.20, r^2=0.253**	**0.001**
Actual Evapotranspiration		27	F=0.72, r^2=0.028	0.405
Disturbance Attributes				
Abiotic vs. Biotic	0.499, 0.636	17, 25	F=2.42, r^2=0.057	0.128
Abiotic vs. Biotic (natural disturbance only)	0.488, 0.640	14, 11	F=1.63, r^2=0.066	0.214
Frequency vs. Intensity vs. Frequency*Intensity vs. Time	0.412, 0.554, 0.508, 0.645	3, 13, 6, 20	F=0.843, r^2=0.062	0.479
Spatial vs. Temporal	0.523, 0.645	22, 20	F=1.99, r^2=0.047	0.166
Anthropogenic vs. Natural	0.619, 0.553	18, 24	F=0.56, r^2=0.014	0.461
Chronic vs. Episodic	0.555, 0.595	15, 27	F=0.19, r^2=0.005	0.670
Biomass vs. Habitat vs. both	0.623, 0.387, 0.641	28, 8, 6	F=2.46, r^2=0.112	0.098

Table 5 : (Continued)Does the proportion of the variation in diversity (e.g. Shannon-Weiner's index, Simpson's *D*) that is statistically related to disturbance (r^2) in published diversity–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? The number of studies in each analysis (*n*) is reported per category for categorical predictors and as total for continuous predictors. Significant relationships ($P < 0.05$) are shown in bold (Sheet 2 of 2)

Predictor Variable	Mean r^2 or Shape of Relationship [1]	*n*	Statistic	P
Sampling and Study Design				
Exhaustive or Subsampled sampling	0.561, 0.615	12, 26	F=0.32, r^2=0.009	0.578
Log_{10} Quadrat Area (m^2)		32	F=1.17, r^2=0.036	0.299
Log_{10} Number of Disturbance Levels [2]	**unimodal**	**42**	F=5.51, r^2=0.303	**0.003**
Log_{10} Number of Samples [2]	**negative monotonic**	**42**	F=9.07, r^2=0.318	**0.0006**
Log_{10} Total Area of Disturbance sampled (m^2)		30	F=0.43, r^2=0.015	0.517
Single Patch vs. Mosaic	0.599, 0.553	26, 16	F=0.25, r^2=0.006	0.622
Log_{10} Time Span (years) [3]		18	F=0.43, r^2=0.026	0.520
Observed vs. Experimental	0.558, 0.652	32, 10	F=0.84, r^2=0.021	0.364
Multiple Regression/MANOVA [4]				
Sessile producer vs. Motile consumer + Log_{10} NDL – $(Log_{10}$ NDL$)^2$ + $(Log_{10}$ NDL$)^3$		38	**r^2=0.545**	

Footnotes are on the following page.

(1) Mean r^2: reported for categorical predictor variables. r2 values were arcsine-square root transformed to satisfy assumptions of residuals for parametric tests; values reported in table are back-transformed. Shape of Relationship: reported for significant continuous predictor variables.

(2) Relationships are non-linear. The statistics presented are from the following polynomial regression models:
$\log_{10}$ Number of Disturbance Levels ($\log_{10}$NDL), $-2.92 + 12.91(\log_{10}\text{NDL}) - 13.30(\log_{10}\text{NDL})^2 + 4.23(\log_{10}\text{NDL})^3$;
$\log_{10}$ Number of Samples ($\log_{10}$NS), $2.05 - 1.55(\log_{10}\text{NS}) + 0.43(\log_{10}\text{NS})^2$.

(3) Studies of temporal gradients of disturbance.

(4) In the best model obtained from multiple analysis of variance (MANOVA) and multiple regression analyses, the proportion of the variation in species richness that is statistically related to disturbance is greater for communities of sessile produces, vs. motile consumers, and is a polynomial function of the number of disturbance levels examined in a study.

The full model is:

$$\arcsin\sqrt{r^2} = -1.91 + 0.18(\text{Sessile producer vs. Motile consumer}) + 9.74(\text{Log10 NDL}) - 10.27(\text{Log10 NDL})^2 + 3.24(\text{Log10 NDL})^3$$

Table 6 : Does the proportion of the variation in species evenness that is statistically related to disturbance (r^2) in published evenness–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? Mean explained variation is reported for each category of the categorical predictors. The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors. Significant relationships ($P < 0.05$) are shown in bold. (Sheet 1 of 2)

Predictor Variable	Mean r^2 or Shape of Relationship [1]	n	Statistic	P
Organism and System Attributes				
Animal vs. Plant	**0.232, 0.680**	**5, 18**	**F=5.71, r^2=0.214**	**0.026**
Terrestrial vs. Aquatic	0.627, 0.494	15, 8	F=0.52, r^2=0.024	0.479
Sessile vs. Motile	0.646, 0.170	20, 3	F=4.27, r^2=0.169	0.051
Sessile Producer vs. Motile Consumer	**0.683, 0.170**	**17, 3**	**F=4.50, r^2=0.200**	**0.048**
Actual Evapotranspiration		13	F=0.54, r^2=0.047	0.479
Disturbance Attributes				
Abiotic vs. Biotic	0.522, 0.636	11, 12	F=0.42, r^2=0.019	0.527
Abiotic vs. Biotic (natural disturbance only)	0.542, 0.441	9, 6	F=0.19, r^2=0.014	0.674
Frequency vs. Intensity vs. Frequency*Intensity vs. Time	0.467, 0.381, 0.423, 0.692	2, 6, 1, 14	F=0.87, r^2=0.121	0.474
Spatial vs. Temporal	0.404, 0.692	9, 14	F=2.80, r^2=0.118	0.109
Anthropogenic vs. Natural	0.724, 0.502	8, 15	F=1.584, r^2=0.070	0.222
Chronic vs. Episodic	0.569, 0.585	5, 18	F=0.01, r^2=0.000	0.943
Biomass vs. Habitat vs. both	0.578, 0.169, 0.858	18, 2, 3	F=2.11, r^2=0.174	0.147

Table 6 : (Continued)Does the proportion of the variation in species evenness that is statistically related to disturbance (r^2) in published evenness–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? Mean explained variation is reported for each category of the categorical predictors. The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors. Significant relationships ($P < 0.05$) are shown in bold.

Predictor Variable	Mean r^2 or Shape of Relationship [1]	n	Statistic	P
Sampling and Study Design				
Exhaustive or Subsampled sampling	0.506, 0.731	8, 12	F=1.62, r^2=0.082	0.220
Log_{10} Quadrat Area (m^2)		17	F=2.65, r^2=0.150	0.125
Log_{10} Number of Disturbance Levels	**negative monotonic**	**23**	F=12.69, r^2=0.377	**0.0002**
Log_{10} Number of Samples [2]	**negative monotonic**	**23**	F=24.05, r^2=0.706	**5E-6**
Log_{10} Total Area of Disturbance sampled (m^2)		17	F=1.64, r^2=0.099	0.219
Single Patch vs. Mosaic	0.645, 0.434	16, 7	F=1.23, r^2=0.055	0.280
Log_{10} Time Span (years) [3]		13	F=1.19, r^2=0.097	0.299
Observed vs. Experimental	0.593, 0.547	17, 6	F=0.05, r^2=0.002	0.822
Multiple regression/MANOVA [4]				
2.25 + Sessile producer – 1.01(Log_{10} NDL) – 0.53(Log_{10} NS)		20	r^2=0.842	

Footnotes are on the following page.

(1) Mean r^2: reported for categorical predictor variables. r^2 values were arcsine-square root transformed to satisfy assumptions of residuals for parametric tests; values reported in table are back-transformed. Shape of Relationship: reported for significant continuous predictor variables.

(2) Relationship is non-linear. The statistics presented are from the following polynomial regression model: $3.22 - 3.19(\log_{10}$ Number of Samples$) + 0.86(\log_{10}$ Number of Samples$)^2$.

(3) Studies of temporal gradients of disturbance.

(4) In the best model obtained from multiple analysis of variance (MANOVA) and multiple regression analyses, the proportion of variation in species evenness explained by disturbance is greater for studies of sessile producers, vs. motile consumers, and is a negative function of the number of disturbance levels and number of samples examined in a study.

The full model is:

$$\arcsin\sqrt{r^2} = 2.25 + 0.22(\text{Sessile producer vs. Motile consumer}) - 1.01(\text{Log}_{10}\text{ NDL}) - 0.53(\text{Log}_{10}\text{ NS})$$

Table 7 : Significant relationships observed in logistic regression analyses comparing the odds of peaked versus all other shapes (non-significant, positive or negative monotonic) of species richness - disturbance relationships. See Table 1 and related text for description of explanatory variables. Multiple regression models consistently dropped all variables except the one comparing disturbances of Anthropogenic vs. Natural origin

Explanatory Variable	*n*	P [1]	McFadden's Rho^2	Group with Highest Odds	% Change in Odds of Peaked Relationship [2]
Actual Evapotranspiration (AET)	69	0.030	0.078	Low AET	-97/ 10-fold increase
Anthropogenic vs. Natural	116	0.005	0.078	Natural	+371
Quadrat Area	88	0.021	0.064	Low quadrat area	-31/ 10-fold increase
Number of Disturbance Levels (NDL)	116	0.017	0.055	High NDL	+535/ 10-fold increase

(1) Probability from Likelihood Ratio Chi-square.

(2) For binary predictors, the percentage change in odds of a peaked relationship is reported in terms of the change predicted for the group with the highest odds versus the group with the lowest odds.

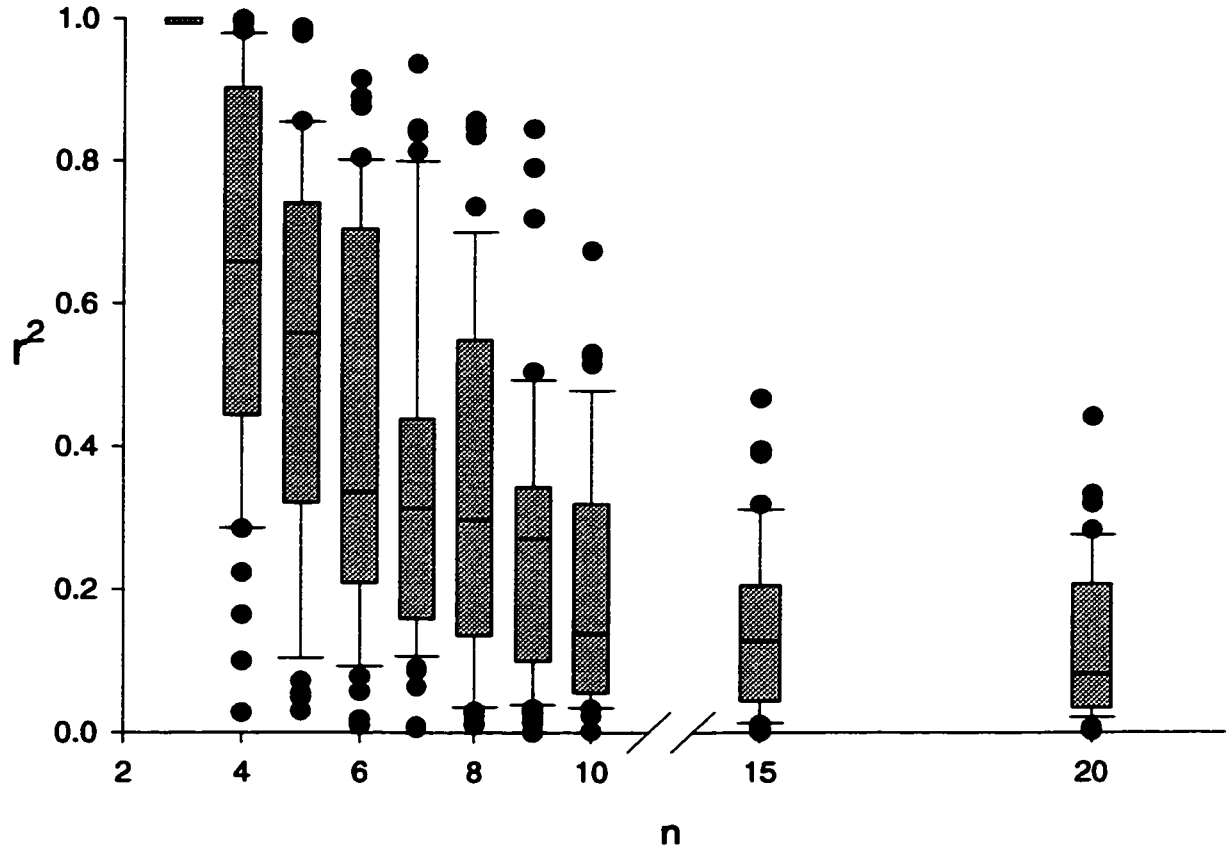


Figure 8: Box plots showing the coefficients of determination (r^2) estimated from second degree polynomial regressions between pairs of randomly generated, uncorrelated variables, each uniformly distributed on the interval 0 to 1. The number of points in each regression (*n*) was varied from 3 to 20. The horizontal lines in the boxes represent the 25th, 50th, and 75th percentiles in the distribution of ordered r^2 values obtained from 50 simulations for a given *n*. The whiskers above and below the boxes represent the 10th and 90th percentiles. Dots are observations falling outside those intervals. Note that, for small *n*, the percent explained variation is quite high, even though the two variables have no relationship to one another.

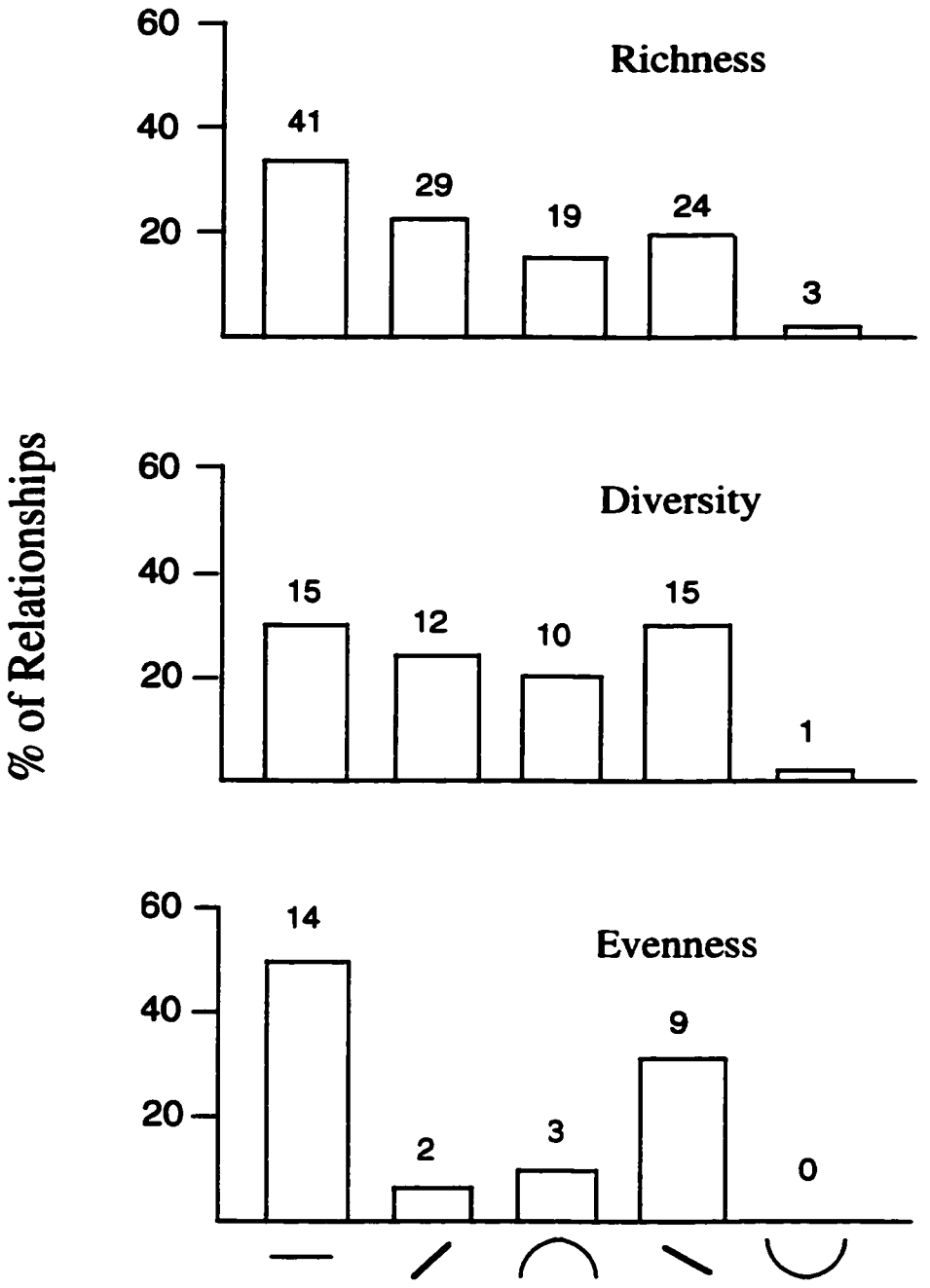


Figure 9: The percentage of species richness–, diversity–, and evenness–disturbance relationships exhibiting each of the five observed patterns (non-significant, positive monotonic, peaked, negative monotonic, and U-shaped). The number of observations in each category is indicated above each box.

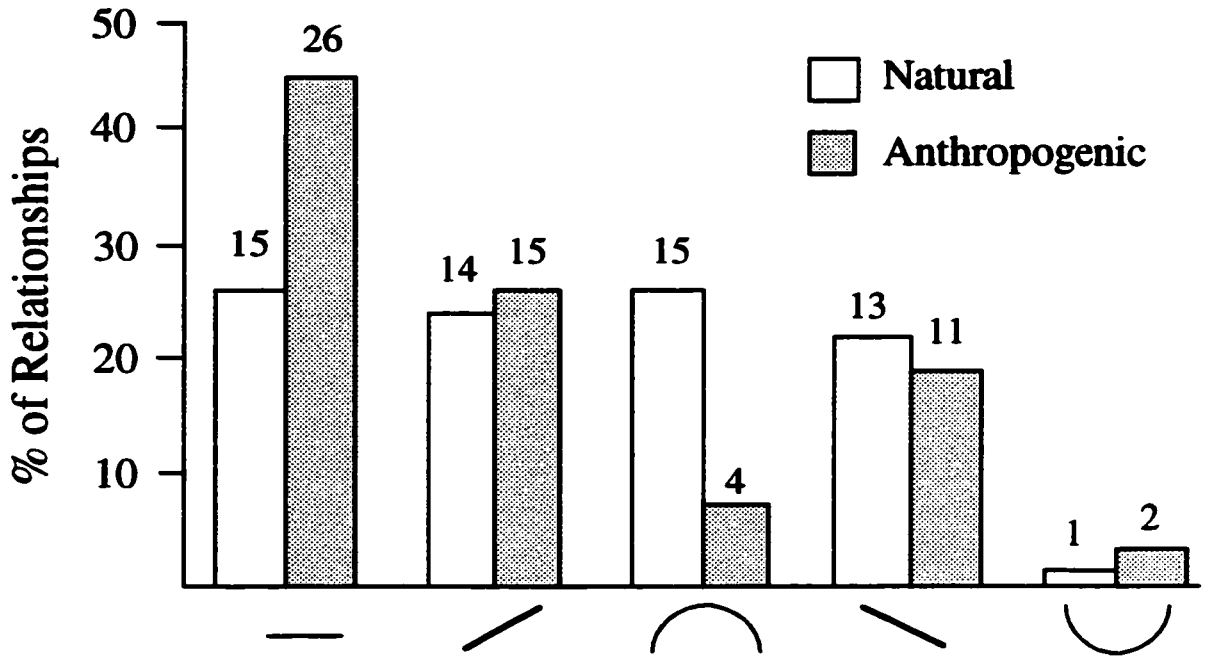
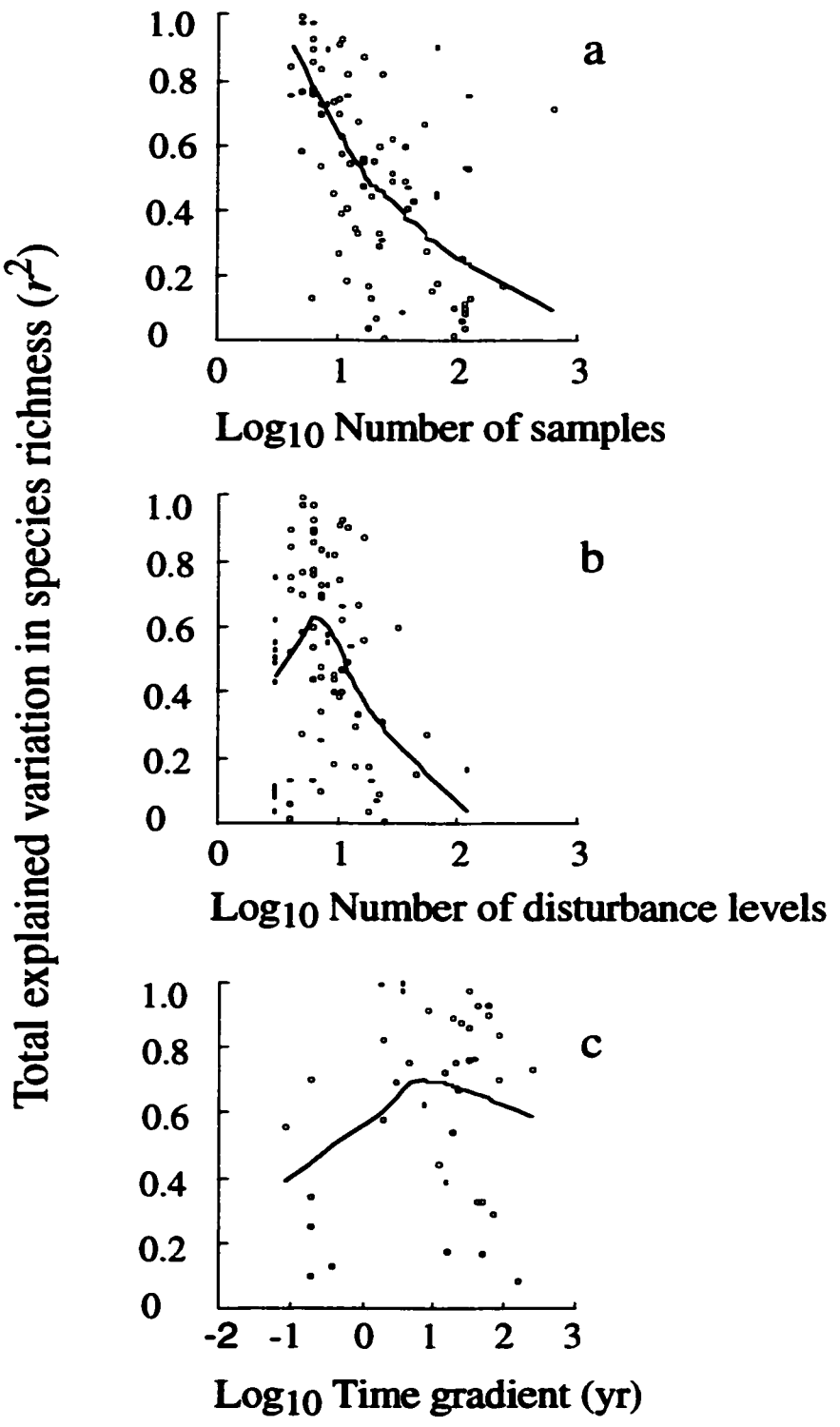


Figure 10: Natural (n = 58) vs. anthropogenic (n = 58) causes of disturbance. The percentage of richness–disturbance relationships exhibiting each of the five observed patterns (non-significant, positive monotonic, peaked, negative monotonic, and U-shaped). The number of observations is indicated above each bar.

Figure 11: The total proportion of variation in species richness explained by disturbance (r^2) is a) negatively related to the number of samples examined, b) a unimodal function of the number of levels of disturbance examined, and c) a unimodal function of the duration of a temporal disturbance gradient. The solid lines represent LOWESS lines of best fit. The relationship between r^2 and number of samples is similar for diversity– and evenness–disturbance relationships. Explained variation has a similar unimodal relationship with the number of disturbance levels examined in diversity–disturbance relationships, but the relationship is negative for evenness–disturbance relationships.


Total explained variation in species richness (r^2)
1.0
0.8
0.6
0.4
0.2
0
a
0
1
2
3
Log10 Number of samples
b
Log10 Number of disturbance levels
c
-2
-1
Log10 Time gradient (yr)

Chapter 3: Human Landuse and Losses of Imperiled Species in Canada

INTRODUCTION

There is little disagreement that humanity is contributing to the current global wave of species extinctions. Anthropogenic factors considered to be detrimental to biodiversity include habitat loss due to agriculture, urbanization, and deforestation; agricultural, industrial and residential pollution; the introduction of exotic species and diseases; and overharvesting (e.g. Soulé 1991, Wilson 1992, Flather et al. 1998, Wilcove et al. 1998, Chapin et al. 2000).

There is growing consensus in the conservation biology literature that habitat loss due to human activity is the most important cause of recent species extinctions and the primary threat to endangered species (e.g. Wilson 1989, Soulé 1991, Wilson 1992, Wilcove et al. 1998, Chapin et al. 2000). Two kinds of evidence have been cited to support this generalization. Case studies of individual endangered species virtually always conclude that some aspect of anthropogenic habitat loss is a threat to the species in question. At the global scale, Primack (1995) suggests that habitat loss is the primary threat to 68% of mammal species currently facing extinction, 58% of endangered birds, 77% of endangered amphibians, and 78% of endangered fishes. In a review of threats to imperiled species in the United States, Wilcove et al. (1998) concluded that habitat loss and degradation is the most prevalent threat to species diversity, contributing to the endangerment of 85% of all taxa, 92% of vertebrate species, 87% of invertebrates, and 81% of plants.

Broad-scale, multi-species approaches have also suggested that species endangerment is related to habitat loss. Several recent studies have examined hot spots of

biodiversity or endangered species (Prendergast et al. 1993, Sisk et al. 1994, Dobson et al. 1997, Flather et al. 1998, Ricketts et al. 1999, Myers et al. 2000). These studies identify areas of high species richness, areas where diversity hot spots of different taxa overlap, correlates of density of endangered species, and/or general landscape attributes of diversity hot spots.

Studies showing that hot spots of endangered species are associated with particular environmental characteristics could be interpreted two very different ways. First, some factor(s) in these regions may be causing species to undergo losses that lead to species extirpations. Alternatively, hot spots of endangered species may represent areas in which many endangered species persist, having been lost elsewhere. If the first scenario is true, then the characteristics of hotspots are undesirable, presumably contributing to species' endangered status. Conversely, if the second scenario is true, then environments with high numbers of endangered species presumably have desirable characteristics that promote persistence of rare species. To distinguish between the two possibilities, one must know where species have been lost, versus where they remain.

The objectives of this study are to determine where in Canada imperiled species have suffered reductions in their range in recent history, and what the differences are between areas where threatened/endangered species were historically found but have subsequently been lost versus areas where they currently persist. Are there hot spots of species losses? Are species losses correlated with habitat loss, or with other anthropogenic attributes of the landscape? By determining the spatial patterns of species losses that have occurred in Canada over the past 100 - 175 years and comparing them with human population, human land use, and landscape attribute data, this study will be the first, to my

knowledge, that both quantitatively examines the spatial distribution of species losses and statistically examines correlates of species losses.

METHODS

Species Distribution Data

Species distribution data were obtained from reports prepared for the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the body that officially designates the conservation status (e.g., threatened, endangered) of species in Canada. To determine where species have been lost, both historic and current distribution data are required. Unfortunately, the historic, and sometimes the current, distributions of most COSEWIC-listed plants and aquatic taxa are unknown. This study was therefore limited to terrestrial mammals, birds (breeding distribution only), amphibians and reptiles whose historic and current range distributions have been confidently described or mapped. The most recently reported distribution of a species in the COSEWIC reports was defined as the current distribution, and it was generally dated between the 1980s and the late 1990s. The historic distribution of a species was acquired from the earliest known or recorded range distribution and dated anywhere from the early 1800s to the early 1900s.

Within the four major taxa examined, those species listed as extinct, extirpated, endangered, threatened, or vulnerable/rare were included in this study. Several of COSEWIC's listings are for subspecies or specific populations of species. These were not included in my analysis unless only one subspecies or population of a species had ever existed in Canada, or if Canadian distributional data for the remainder of the species were included in the subspecies or population report. Refer to Appendix 7 for a list of species

included in this study.

I determined historic and current ranges of COSEWIC–listed species in the 217 terrestrial ecoregions that occur in Canada. Ecoregions, which are subunits of coarser eco-zones, delineate areas of distinctive climate, vegetation and fauna, physiography, soil, and water (Ecological Stratification Working Group 1995) (Fig. 12).

Although the ecoregion spatial scale is relatively coarse (ecoregions range in area from 183 to 2.35×10^6 km^2), it corresponds to the resolution of the coarsest-scale COSEWIC distribution maps. For each species, the historic and current presence/absence and the loss status (lost from the entire ecoregion, lost from part of the ecoregion, or no loss detected) of each species was recorded. Although errors are surely present in distribution maps and may be compounded in the calculated loss maps, I am confident that presence/absence and loss data at the ecoregion scale is accurate. For each ecoregion, I tallied the number of COSEWIC-listed species historically present, the number of species lost, and the total number of species still present. The number of species still present was tallied in two different ways: 1) the number still found anywhere in the ecoregion and 2) only those that had suffered no range loss in that ecoregion.

Ecoregion Attributes and Landuse Data

Ecoregion attributes and landuse/coverage data were obtained from several sources. Geographic, climatic, natural and human landcover, and human population data for each ecoregion were compiled from a number of published sources by Parks Canada (Rivard et al. 2000). Agricultural landcover, insecticide and herbicide use, fertilizer use, and additional population data for each ecoregion were obtained from E-Stat 1999

(Statistics Canada 1999). Predictor variables examined are those included in Table 8, as well as the following: human population (1991), human population density (1991; number of persons/km^2), human population growth (1871–1991), agricultural pesticides ($ purchased in 1991), cropland (1991), change in cropland area (1861–1991), farmland (cropland + rangeland, 1991), proportion of cropland treated with agricultural herbicides (and insecticides, 1991), proportion builtup landcover (proportion of ecoregion dominated by urban development, rural communities, industrial buildings, etc.), proportion cropland, proportion farmland, proportion rangeland, proportion human–dominated area, forest landcover, length of road and railway (km), Largest Patch Index (percentage of ecoregion area covered by the largest single patch of a particular habitat type) for both natural and human–dominated habitat types, mean annual temperature, and ecoregion area. Unfortunately, I could not obtain any useful data for extent or intensity of forestry in each ecoregion. The full dataset is provided in Appendix 8.

The landscape data used here are recent (1990s), and they therefore do not directly measure historic landscape characteristics. Historic (1871) human population data were obtained for most of the landmass that is now Canada (National Atlas Information Service 1991). European settlement of Canada began in the early 17th century, and colonists numbered fewer than 10 000 by 1681 (Moore 1991) and less than 100 000 by 1760 (Wynn 1991). Because colonial settlement is recent in Canada, widescale human landuse is as well. Intense forest clearing for timber/wood export and agriculture started in the early to mid-1800s and was limited to the southern sections of Ontario and Quebec and relatively small regions of the Atlantic Maritime provinces that are still heavily agricultural (Wynn 1991). Actual historic data are rare. I therefore assume that the differences in current

landscape characteristics among ecoregions are proportional to those that existed while species' declines occurred (e.g. areas where agriculture is now intense have historically been agriculture-intensive relative to other areas).

Threats to COSEWIC–listed species

Authors of the status reports of COSEWIC–listed species indicate what types of threats imperil the survival of each species. These threats are often divided into two categories: 1) known or very probable threats, and 2) threats based on speculation without observation or evidence. Only those from the first category have been included in this study. Some known threats are no longer perceived as threats to some species (e.g. over-exploitation of bison, widespread persecution of grizzlies), but have been included in my summary because they do provide valuable information about mechanisms leading to the endangerment of species in Canada. As with the species distribution and loss data, threats data were compiled at the species level, and for species currently listed as extinct, extirpated, endangered, threatened, or vulnerable. Threats that played a role in the loss of extinct and extirpated species are included.

I have included threats data not just for the species included in the species' losses study, but for all the major taxa for which there are COSEWIC status reports. Consequently, it is possible to examine whether the species included in my analyses (those with available distribution data) are representative of all COSEWIC–listed species in terms of threats affecting them, and whether different taxa are affected by the same threats.

Statistical Analyses

To determine which human and landcover factors are most closely related to species losses, multiple regressions were performed relating the numbers of losses of bird species, mammals, amphibians, reptiles, and all four taxa combined to habitat characteristics. Regional species richness was used as a covariate in these models to control for the fact that more losses can occur where more species were present. Bird species richness per ecoregion compiled from feral distributions was provided by Parks Canada. Mammal, amphibian, and reptile species richness per mainland ecoregion were estimated from feral regional distribution data compiled by Currie (1991), and richness in island ecoregions was estimated from feral distributions in Banfield (1974, mammals) and Cook (1984, amphibians and reptiles). Controlling for species richness is similar to regressing the proportion of species reductions as a function of habitat characteristics. Predictor variables were transformed as necessary to make their distributions approximately normal. Numbers of species' losses were square root transformed to satisfy the assumptions of normality of residuals and homogeneity of variances.

Canada is a country in which human population, human activities, species richness, and losses of species are all concentrated in the south. Only 80 of the 217 ecoregions have agricultural land cover, and these also contain 99% of the human population (Statistics Canada 1999). Based on Advanced Very High Resolution Radiometry (AVHRR) data with a pixel size of 1.1 km^2, none of the 137 remaining more northern, non-agriculture ecoregions had detectable human-dominated landcover. Therefore, in addition to analyzing the entire set of 217 ecoregions, the set of 80 ecoregions with agricultural land was extracted and examined separately.

Several statistically indistinguishable models relating the number of species losses to landscape attributes are possible for each taxon. The ones we chose are those in which all predictors in the regression model are significant ($P<0.05$) and contribute $\geq 1\%$ to the total explained variation of the model, and for which different approaches (forward, backward, and stepwise regressions) yielded similar models. The range and median values of all significant predictor variables are provided in Table 8.

Species distribution data such as those used in this study may include some degree of spatial autocorrelation, which would affect the number of degrees of freedom used in most standard statistical procedures that assume independence of data (Legendre 1993). In most cases, species' distributions overlapped more than one ecoregion. That is, ecoregions do not necessarily accrue or lose species independently, and therefore they may not be independent data points. Moran's I (Sokal and Oden 1978) was calculated to test for the presence of spatial autocorrelation in the species loss data. The irregularity of both ecoregion shape and size meant that distance between cells (ecoregions) to identify neighbours in tests of spatial autocorrelation was unsatisfactory. Therefore, for the purposes of these tests, neighbours are defined as ecoregions that are contiguous (Sokal and Oden 1978). Because habitat loss, land use, human population, and landscape attribute variables examined in this study are spatially structured and assumed to be driving species losses, these effects were first removed and Moran's I was then calculated using the residuals from the regression analyses (Legendre 1993).

In both the complete dataset ($n=217$) and the agriculture-landcover data subset ($n=80$), significant ($P<0.05$) spatial autocorrelation was found for all taxa. Thus, the number of degrees of freedom used in the regression analyses of species losses may be less

than the number of ecoregions. The number of degrees of freedom at which each regression model and the individual terms in each model would become nonsignificant were determined from tables of critical values of the F distribution and the t distribution (Zar 1984). In all cases, regression models for species losses were still significant when the residual degrees of freedom were as low as three. Additionally, the number of degrees of freedom required for individual terms to become non-significant was very low (2 - 7).

RESULTS

Distributions and losses of COSEWIC–listed species

A total of 62 COSEWIC-listed (extinct, extirpated, endangered, threatened, and vulnerable) bird ($n = 37$), mammal ($n = 12$), amphibian ($n = 6$), and reptile ($n = 7$) species with known historic and current range distributions were identified for this study. These numbers represent approximately 60% of the species in these groups listed by COSEWIC. Birds are the best represented with over 80% of COSEWIC-listed species included in this dataset, and the amphibians are the least with approximately 40% of the listed species represented here. The geographic locations of hot and cold spots of species' losses, with several of their respective landcover and agriculture attributes are presented in Table 9.

All four taxa combined

Several high concentrations of COSEWIC–listed species (birds, mammals, amphibians and reptiles combined) are apparent in several southern ecoregions of Canada (Fig. 13). The most prominent hot spot of listed species is in the Mixedwood Plains ecozone and an adjacent ecoregion of the Boreal Shield ecozone. High numbers of imperiled

species are also found in the Prairies and Boreal Plains ecozones, in the southern portion of the Montane Cordillera, and in the far southwest corner of the Pacific Maritime ecozone.

The greatest number of losses of COSEWIC–listed species occurred in the two southernmost ecoregions of the Mixedwood Plains ecozone; 30 of the 62 species included in this study suffered detectable range losses in the southernmost ecoregion (Fig. 14). A much larger but less intense (up to 20 losses in a single ecoregion) hot spot of species' losses is located in the Prairies ecozone and bordering ecoregions of the Boreal Plains ecozone. Smaller hot spots are found in the southwest corner of the Pacific Maritime ecozone (which contains the city of Vancouver, 12 species losses;), and ecoregions of the Atlantic Maritime ecozone (generally 7 - 9 losses per ecoregion).

Equally interesting are the ecoregions containing many COSEWIC–listed species that have suffered no known or detectable range losses in those ecoregions (i.e., 'cold spots' of species' losses) (Fig. 15). The most notable cold spot is found in the southern Montane Cordillera ecozone. Another apparent cold spot, eastern Mixedwood Plains and adjacent ecoregion of the Boreal Shield, may be somewhat misleading: species' losses were high across much of this area (up to 15 species) (cf. Fig. 14 and Fig. 15).

Individual taxa

Patterns of COSEWIC–listed bird species richness and species' losses resemble those for all species combined (Fig. 16, Fig. 17, Fig. 18): species richness and species' losses are greatest in the Mixedwood Plains and Prairies ecozones. Richness of imperiled mammal species is greatest in a large area of mountainous and taiga habitat encompassing

much of northwestern mainland Canada (Fig. 19); this region is also a cold spot of losses for imperiled mammals (Fig. 20). Listed mammal species have experienced their greatest losses in the Prairies ecozone and bordering ecoregions of the Boreal Plains ecozone (Fig. 21). As with the listed–bird species, imperiled amphibians and reptiles are most speciose in the Mixedwood Plains (Fig. 22, Fig. 23). No intense hot spots of amphibian species' losses are obvious in my data set, but the southernmost Mixedwood Plains and a southwestern portion of the Pacific Maritime ecozone may be areas of concern (Fig. 24). A potential cold spot of amphibian losses may be in the eastern Mixedwood Plains and nearby ecoregions of the Atlantic Maritime ecozone (Fig. 25). Losses of listed reptiles is greatest in the southernmost Mixedwood Plains ecoregions (Fig. 26); no cold spots of losses of reptiles are obvious (Fig. 27).

Correlates of Losses of COSEWIC–Listed Species

All Terrestrial Ecoregions of Canada (n=217)

For each of the vertebrate classes individually, and for all classes combined, the number of losses is strongly related to regional species richness and several landscape attributes (Table 10, Table 12). In other words, the more species present in a region, the greater the number of losses. Except for amphibians and reptiles, after controlling for species richness, the number of losses is always highly significantly related to two variables: one dealing with rates of use of agricultural chemicals in the ecoregion, the other describing some aspect of human domination of the landscape (Table 12). The influence of chemicals is strongest for bird and total losses (Table 12). Correlation matrices are provided in Table 10 for all significant variables from Table 12, and in Appendix 9A for all

variables examined in the analyses.

Ecoregions with Human Landuse (n=80)

Species' losses in the ecoregions with human landcover were strongly related to many landscape attributes (Table 11, Table 13). Regional species richness, however, was a strong correlate of number of losses for only amphibians and reptiles. For all classes but reptiles, and for all classes combined, number of losses was again correlated with agricultural chemical use and/or some measure of human domination of the landscape (Table 13). Correlation matrices are provided in Table 11 for all significant variables from Table 13, and in Appendix 9B for all variables examined in the analyses.

Summary of perceived threats to COSEWIC–listed species

Several categories of threats and the number of COSEWIC–listed species whose survival is/was thought to be at risk from each category of threat (according to the authors of each COSEWIC–species status report) are summarized in Table 14. The predominant risk to the four taxa included in this study is thought to be land conversion for agricultural and/or urban development. Pollutants are thought to be another serious, but less common, threat to imperiled birds. Historic persecution and overexploitation of many mammals (e.g. grizzly bear, bison, blue whale, harbour porpoise), reptiles (e.g. Massasauga rattlesnake, racer, spotted turtle), and fish (e.g.Atlantic cod, Pacific sardine, northern brook lamprey) has led to the present imperiled status of many species in Canada. Vascular plants are most commonly thought to be threatened by land conversion for agricultural and/or urban development, outdoor recreation (e.g. beaches, skiing, hiking, off-road vehicles),

and, to a lesser extent, water development (e.g. dams, flood control, water diversion, wetland drainage).

DISCUSSION

Hot spots of losses of COSEWIC–listed bird, mammal, amphibian, and reptile species were identified in several southern regions of Canada. Hot spots of losses coincide especially with areas of chemically–intensive agriculture. Collectively, all hot spots contain 12% of Canada's landcover, 61% of the human population, 84% of farmland, 87% of human–dominated landcover, and 90% of each of insecticide and herbicide treated croplands. The southernmost ecoregions of the Mixedwood Plains ecozone form an intense hot spot of losses for bird species especially, but also for amphibians and reptiles. This area is very densely populated (112 persons/km^2) and 71% of the landscape is dominated by human landuse (mostly farmland). With more fruit, vegetable, and other horticultural crop operations than any other ecozone, agriculture is very chemically–intensive in the Mixedwood Plains ecozone (Agriculture and Agri-Food Canada 1998). The Prairies ecozone and southern ecoregions of the Boreal Plains comprise a geographically large hot spot of losses of mammals and bird species that is less intense than the southern Mixedwood Plains hot spot. This hot spot is dominated by human landcover, but has a low human population density (5.2 persons/km^2). A total of 63% of agricultural pesticide expenditures are from this area; pesticide use is widespread because of vast field crops in this region (e.g. wheat, canola, barley), but is less intense than in the Mixedwood Plains or other hot spots of losses.

In contrast, many ecoregions with large population centers (e.g. Montreal, Halifax) have relatively low rates of species loss. Similarly, many ecoregions (e.g., the northern Boreal Plains, southern Taiga Plains, central and southern Laurentian Mountains in the eastern Boreal Shield ecozone, and the Appalachians and Saint John River Valley of the Atlantic Maritime ecozone) having very extensive human alteration of the environment also have had relatively few species' losses (Fig. 28; Biodiversity Science Assessment Team 1994). Montreal, Halifax, and other nearby centers of population were among the first to be settled in the 1600s. It is possible that losses of some species may have gone unrecorded in such areas during the 17th and 18th centuries. If this is the case, then species' losses will have been underestimated in these regions. While accounts of historic bird distributions appear to be relatively thorough, those of mammals and, particularly, both amphibians and reptiles appear less so. This is reflected in the percentage of COSEWIC-listed species of each taxa included in my analyses (e.g., 80% of COSEWIC-listed birds could be included in my analyses, but only 40% of the reports for COSEWIC-listed amphibians contained suitable distribution data). Potential underestimates of losses in the eastern population centers may have a much greater effect on my analyses of amphibians and reptiles than on my analyses of mammals and birds.

Cold spots of losses of listed species were characterized by natural landcover, low proportions of cropland, and only localized use of agricultural pesticides (especially insecticides). Areas with relatively high richness of imperiled mammal species, but few losses, are typically found in mountainous and northern taiga habitats, where human population density is very low (<0.5 persons/km^2), human–dominated landcover is virtually non-existent, and agriculture is neither common (0.01% of landcover is cropland) nor chemically–

intensive. In comparison, cold spots of losses of birds and amphibians are located in southern regions with greater human population density and habitat loss; but where neither agriculture landuse (0.7-14.5% of landcover is cropland) nor agricultural pesticide coverage is extensive.

My results clearly associate losses of imperiled species with aspects of loss of natural habitat. The nature of the effect of habitat loss is not straightforward for some of the taxa included in this study. Increased amounts of human landcover is consistently associated with losses of imperiled species. Effects of habitat fragmentation or patchiness, in contrast, are less clear. These results are consistent with other recent work that suggests that habitat area has a stronger effect on biodiversity than does habitat fragmentation (Bender er al. 1998, Rivard et al. 2000).

Even stronger than the effects of habitat loss are the effects of agricultural chemicals. After controlling for land conversion due to agriculture, losses of imperiled species are greatest in regions where agriculture is chemically–intensive. Perhaps surprisingly, species' losses of birds and mammals are particularly associated with herbicide use. Herbicides are the largest component of agricultural pesticides in Canada (Agriculture and Agri-Food Canada 1998, Crop Protection Institute of Canada 2000). For example, in the Prairies ecozone, 83% of farms with crops reported herbicide use, while 36% used insecticides and 20% used fungicides (Agriculture and Agri-Food Canada 1998). Agricultural herbicides are used routinely and extensively on both field crops (e.g. oil seeds, soy beans, wheat, corn) and horticultural crops (e.g. potatoes, strawberries, grapes, tomatoes). Horticultural crops generally also receive intense and frequent applications of insecticides (Crop Protection Institute of Canada 2000).

Agricultural herbicides adversely affect vertebrate species primarily through indirect mechanisms (Pimental and Edwards 1982, Rands 1986, Tew et al. 1992, Best et al. 1995, Freemark 1995, Freemark and Boutin 1995, Wilson et al. 1999). The availability of agricultural pesticides has resulted in more extensive and intensive agricultural practices that have in turn changed habitat patterns and made agricultural landscapes more homogeneous (Best et al. 1995, Freemark 1995, Freemark and Boutin 1995), thereby adversely affecting many invertebrate and vertebrate taxa. The use of agricultural herbicides may simply be a measure of overall agricultural intensity. Herbicides, fertilizers (Geier and Best 1980, Tilman 1987, Kleijn and Van Der Voort 1997), and further reduction and isolation of non-crop habitats (e.g. wooded fencerows, grassy waterways, uncultivated field margins, and woodlands; Arnold 1983, Best et al. 1995, Freemark 1995, Freemark and Boutin 1995, Wilson et al. 1999) collectively reduce abundance and diversity of natural vegetation, availability of nesting sites and protective cover, and availability of seed foods and prey. Such croplands can not support the populations and species that persist in less intensely used landscapes. Herbicide use is just one component of intense agricultural practices, which have adverse effects on the persistence of imperiled species.

Variation in losses of bird species among ecoregions with agriculture is strongly associated with agricultural insecticide use. Agricultural insecticides are acutely toxic to many non-target taxa, having direct adverse effects on some species of birds (Matz et al. 1998, Brunet et al. 1997, McKay et al. 1999, Mineau et al. 1999), mammals (Stinson et al. 1994), fish (Schuytema et al. 1991, Gupta 1994), amphibians (Mullie et al. 1991, Schuytema et al. 1991), reptiles (Stinson et al. 1994), aquatic invertebrates (Mullie et al. 1991, Wan et al. 1995, Kleijn and Van Der Voort 1997, Dauberschmidt et al. 1996), and

non-target insects (George et al. 1992, Pimental and Edwards 1982). Although agricultural insecticides are not used as extensively as herbicides (Agriculture and Agri-Food Canada 1998, Crop Protection Institute of Canada 2000), their effects can be much more devastating because of mortality resulting from direct contamination and consumption of contaminated prey. Effects can be even more lethal when non-target species are exposed to combinations of insecticides: the toxicity of some synergistic mixtures is increased by up to 100-fold (Thompson 1996). Additional losses also result from significant reductions in food availability for insectivores (Wilson et al. 1999).

The low numbers of amphibian (n=6) and reptile (n=7) COSEWIC–listed species included in this study make it difficult to discuss correlates of species' losses for these taxa. Species' losses for both taxa appear to be related to habitat loss, but not to agricultural pesticides. Amphibians are generally thought to be threatened by habitat loss and water development (e.g. wetland drainage, diversion of agriculture and residential use, flood control) (e.g. Hecnar and M'Closkey 1996, Findlay and Houlahan 1997) (Table 14). COSEWIC–listed reptiles are thought to be most threatened by habitat loss for both urban and agricultural development, and, in the past, direct mortality through persecution and harvest (Table 14).

Time lags exist between occurrence of habitat fragmentation, or other causes of population losses, and extirpation of species (Tilman et al. 1994, Findlay and Bourdages 2000). The full effect of mechanisms for population declines and losses of species may not be known for decades or generations (Tilman et al. 1994, Findlay and Bourdages 2000). Therefore, the effects of past and current agricultural pesticide use, habitat loss, habitat fragmentation, and human population have likely been underestimated and may

take several more decades to come into full view.

This study indicates that hot spots of imperiled species richness can be composed of two classes of areas: areas where many imperiled species (e.g. birds) have suffered range losses (hot spots of species' losses) and areas where many imperiled species (e.g. mammals) persist with their historic ranges intact (cold spots of species' losses). If one examined only the current distribution of imperiled mammal species richness in Canada (Fig. 19), it may appear that, because relatively few imperiled mammals exist in the Prairies ecozone, the survival of mammals is generally not at risk in this region. And, it may appear that mammals are at great risk in the mountainous and taiga regions of western Canada because many imperiled mammals are found in these areas. In contrast, Fig. 21 clearly indicates that imperiled mammals have undergone extensive losses throughout the prairies, but have suffered little loss throughout the western mountain ranges and taiga. Identifying and examining hot and cold spots of losses of species, compared with studying only hot spots of imperiled species richness, provides a clearer picture of where species are most threatened and what factors pose a risk to the survival of imperiled species.

Table 8 : Range and median values for predictor variables found to have a significant effect on losses of COSEWIC–listed species in regression analyses of all 217 terrestrial ecoregions occurring in Canada and the subset of 80 ecoregions containing agricultural landcover.

	n=217		n=80	
Predictor Variable	Range	Median	Range	Median
$\log_{10}$ area treated with agricultural insecticides (ha)	0 – 5.82	0	0 – 5.82	2.95
$\log_{10}$ area treated with agricultural herbicides (ha)	0 – 6.82	0	0 – 6.82	3.71
$\log_{10}$ $commercial agriculture fertilizers; $1 = 0.003 tonnes	0 – 8.46	0	3.52 – 8.46	6.11
$\log_{10}$ human population – 1871	0 – 5.96	0	0 – 5.96	0
$\log_{10}$ human population density – 1871 (persons/km^2)	0 – 1.41	0	0 – 1.41	0
$\log_{10}$ builtup area (ha): residential, commercial, infrastructure, etc.	0 – 5.26	0	0 – 5.26	2.74
$\log_{10}$ cropland area, 1861 (ha)	0 – 6.25	0	0 – 6.25	0
$\log_{10}$ rangeland area (ha)	0 – 6.79	0	0 – 6.79	0
$\log_{10}$ human-dominated area – cropland + rangeland + builtup area (ha)	0 – 7.20	0	0 – 7.20	4.68
$\log_{10}$ human-dominated area – cropland + builtup area (ha)	0 – 7.12	0	0 – 7.12	4.52
$\log_{10}$ road and railway density (km/km^2)	0 – 0.10	0.004	0.002 – 0.10	0.04
number of patches (polygons) in ecoregion (1)	1 – 491	24	3 – 491	70.5
number of patches (polygons) per km^2 in ecoregion (1)	$4*10^{-5}$ – 0.063	0.001	0.002 – 0.063	0.004
$\log_{10}$ natural landcover (ha)	2.85 – 7.37	6.37	2.85 – 7.31	6.09
$\log_{10}$ freshwater area (ha)	0 – 6.27	4.27	0 – 6.27	4.27

(1) Patches refers to the total number of human-dominated and natural landcover–dominated polygons distinguished from AVHRR data (i.e., number of human–dominated polygons + number of natural landcover–dominated polygons). Different kinds of human (e.g. crop type) and natural landcover (e.g. forest type) are not distinguished and included in this sum of patches.

Table 9 : Location, landcover, and agricultural pesticide data for hot and cold spots of losses of COSEWIC–listed species'. Hot spots are areas where many imperiled species have suffered historic range losses. Cold spots of losses are areas where many imperiled species currently persist and have not experienced historic range losses. Data are from 1991 Statistics Canada census (Statistics Canada 1999).

Hot or ColdSpot	Location	Taxa	Area (10^3 km^2)	% Human Landuse	% Farmland_ Cropland	$Pesticides/ ha crop	% Landcover Treated with Herbicides_ Insecticides	Population Density (persons/km^2)
Hot	Mixedwood Plains (2 southern ecoregions)	Total Birds Reptiles	72.2	70.7	57.3_39.4	48.5	22.5_6.0	112.1
Hot	Mixedwood Plains (southern-most ecoregion)	Amphibians	25.1	89.9	64.2_52.0	67.6	35.4_10.2	236.6
Hot	Prairies/southern Boreal Plains	Total Mammals Birds	812.5	62.0	62.0_31.0	18.1	21.9_2.4	5.2
Hot	Atlantic Maritime	Total	201.1	12.0	10.6_3.7	32.2	0.9_0.4	12.5
Hot	Pacific Maritime (southwest-ern tip)	Total	4.4	38.8	19.7_11.1	143.9	3.9_2.5	406.9
Hot	Pacific Maritime (southern coast and ranges of mainland)	Amphibians	58.3	0.2	0.2_0.06	53.8	<0.01_<0.01	0.6
Cold	Montane Cordillera (southern)	Total Birds	129.4	5.0	4.7_0.7	61.9	0.2_0.09	3.3
Cold	Cordillera and Taiga of north-west Canada	Mammals	1352.9	0.05	0.04_0.01	6.7	<0.01_<0.01	0.05
Cold	Eastern Mixedwood Plains/ southern Boreal Shield	Total Birds	111.5	27.3	23.6_13.2	30.8	5.7_1.0	57.4
Cold	Eastern Mixedwood Plains/ western Atlantic Maritime	Amphibian	123.1	31.8	28.3_14.5	29.8	5.6_1.1	55.4

Table 10 : Matrix of Spearman rank correlations between species richness, number of losses of species, and landscape attributes included in the regression models presented in Table 12 (N=217 ecoregions). See Appendix 10 for descriptions of abbreviations. (Sheet 1 of 3)

	SR_T	SR_B	SR_M	SR_A	SR_R	SL_T	SL_B	SL_M
SR_T	1	0.985	0.927	0.877	0.868	0.821	0.741	0.780
SR_B	0.985	1	0.880	0.836	0.828	0.813	0.731	0.777
SR_M	0.927	0.880	1	0.801	0.779	0.703	0.635	0.681
SR_A	0.877	0.836	0.801	1	0.900	0.813	0.725	0.738
SR_R	0.868	0.828	0.779	0.900	1	0.782	0.716	0.728
SL_T	0.821	0.813	0.703	0.813	0.782	1	0.930	0.936
SL_B	0.741	0.731	0.635	0.725	0.716	0.930	1	0.776
SL_M	0.780	0.777	0.681	0.738	0.728	0.936	0.776	1
SL_A	0.382	0.413	0.281	0.340	0.332	0.392	0.337	0.365
SL_R	0.268	0.226	0.248	0.253	0.306	0.253	0.263	0.184
AIns	0.701	0.688	0.575	0.704	0.750	0.741	0.720	0.692
AHerb	0.733	0.724	0.600	0.716	0.765	0.759	0.736	0.711
Pop1871	0.426	0.402	0.297	0.537	0.520	0.460	0.466	0.341
ABuilt	0.534	0.520	0.424	0.595	0.563	0.572	0.561	0.482
% ABuilt	0.527	0.510	0.415	0.599	0.567	0.566	0.554	0.475
ACrop	0.749	0.742	0.614	0.730	0.777	0.751	0.718	0.712
ARange	0.412	0.386	0.432	0.321	0.428	0.415	0.386	0.451
AHD1	0.725	0.710	0.612	0.722	0.756	0.763	0.723	0.712
AHD2	0.690	0.679	0.565	0.699	0.721	0.750	0.724	0.680
RRD	0.761	0.743	0.631	0.740	0.734	0.721	0.686	0.665
PDens	0.551	0.546	0.389	0.580	0.579	0.559	0.519	0.511
AWater	0.008	0.044	-0.014	-0.028	-0.067	0.090	0.137	0.028
AForest	0.646	0.680	0.601	0.555	0.431	0.522	0.457	0.476
ANatural	-0.179	-0.143	-0.136	-0.217	-0.218	-0.203	-0.164	-0.222

Table 10: continued (Sheet 2 of 3)

	SL_A	SL_R	AIns	AHerb	Pop1871	ABuilt	% ABuilt	ACrop
SR_T	0.382	0.268	0.701	0.733	0.426	0.534	0.527	0.749
SR_B	0.413	0.226	0.688	0.724	0.402	0.520	0.510	0.742
SR_M	0.281	0.248	0.575	0.600	0.297	0.424	0.415	0.614
SR_A	0.340	0.253	0.704	0.716	0.537	0.595	0.599	0.730
SR_R	0.332	0.306	0.750	0.765	0.520	0.563	0.567	0.777
SL_T	0.392	0.253	0.741	0.759	0.460	0.572	0.566	0.751
SL_B	0.337	0.263	0.720	0.736	0.466	0.561	0.554	0.718
SL_M	0.365	0.184	0.692	0.711	0.341	0.482	0.475	0.712
SL_A	1	0.124	0.305	0.358	0.135	0.324	0.305	0.371
SL_R	0.124	1	0.285	0.277	0.249	0.282	0.262	0.279
AIns	0.305	0.285	1	0.966	0.585	0.682	0.681	0.953
AHerb	0.358	0.277	0.966	1	0.560	0.666	0.663	0.978
Pop1871	0.135	0.249	0.585	0.560	1	0.675	0.681	0.566
ABuilt	0.324	0.282	0.682	0.666	0.675	1	0.995	0.681
% ABuilt	0.305	0.262	0.681	0.663	0.681	0.995	1	0.675
ACrop	0.371	0.279	0.953	0.978	0.566	0.681	0.675	1
ARange	0.121	0.132	0.466	0.461	0.003	0.191	0.172	0.454
AHD1	0.348	0.288	0.903	0.896	0.552	0.771	0.763	0.894
AHD2	0.359	0.291	0.879	0.874	0.560	0.802	0.794	0.867
RRD	0.261	0.205	0.754	0.762	0.494	0.582	0.593	0.768
PDens	0.162	0.124	0.563	0.566	0.446	0.400	0.422	0.572
AWater	0.198	0.084	-0.024	-0.010	0.088	0.203	0.171	0.002
AForest	0.360	0.039	0.301	0.339	0.287	0.374	0.355	0.362
ANatural	0.149	-0.071	-0.244	-0.221	-0.051	-0.027	-0.058	-0.210

Table 10: continued (Sheet 3 of 3)

	ARange	AHD1	AHD2	RRD	PDens	AWater	AForest	ANatural
SR_T	0.412	0.725	0.690	0.761	0.551	0.008	0.646	-0.179
SR_B	0.386	0.710	0.679	0.743	0.546	0.044	0.680	-0.143
SR_M	0.432	0.612	0.565	0.631	0.389	-0.014	0.601	-0.136
SR_A	0.321	0.722	0.699	0.740	0.580	-0.028	0.555	-0.217
SR_R	0.428	0.756	0.721	0.734	0.579	-0.067	0.431	-0.218
SL_T	0.415	0.763	0.750	0.721	0.559	0.090	0.522	-0.203
SL_B	0.386	0.723	0.724	0.686	0.519	0.137	0.457	-0.164
SL_M	0.451	0.712	0.680	0.665	0.511	0.028	0.476	-0.222
SL_A	0.121	0.348	0.359	0.261	0.162	0.198	0.360	0.149
SL_R	0.132	0.288	0.291	0.205	0.124	0.084	0.039	-0.071
AIns	0.466	0.903	0.879	0.754	0.563	-0.024	0.301	-0.244
AHerb	0.461	0.896	0.874	0.762	0.566	-0.010	0.339	-0.221
Pop1871	0.003	0.552	0.560	0.494	0.446	0.088	0.287	-0.051
ABuilt	0.191	0.771	0.802	0.582	0.400	0.203	0.374	-0.027
% ABuilt	0.172	0.763	0.794	0.593	0.422	0.171	0.355	-0.058
ACrop	0.454	0.894	0.867	0.768	0.572	0.002	0.362	-0.210
ARange	1	0.526	0.412	0.376	0.189	-0.086	0.053	-0.217
AHD1	0.526	1	0.967	0.726	0.519	0.037	0.362	-0.175
AHD2	0.412	0.967	1	0.710	0.502	0.058	0.351	-0.171
RRD	0.376	0.726	0.710	1	0.753	-0.156	0.440	-0.381
PDens	0.189	0.519	0.502	0.753	1	-0.318	0.245	-0.531
AWater	-0.086	0.037	0.058	-0.156	-0.318	1	0.286	0.671
AForest	0.053	0.362	0.351	0.440	0.245	0.286	1	0.318
ANatural	-0.217	-0.175	-0.171	-0.381	-0.531	0.671	0.318	1

Table 11 : Matrix of Spearman rank correlations between species richness, number of losses of species, and landscape attributes included in the regression models presented in Table 13 (N=80 ecoregions with detected human–dominated landcover). See Appendix 10 for descriptions of abbreviations. Sheet 1.

	SR_T	SR_B	SR_M	SR_A	SR_R	SL_T	SL_B	SL_M	SL_A	SL_R
SR_T	1	0.859	0.833	0.602	0.730	0.448	0.428	0.332	0.207	0.385
SR_B	0.859	1	0.568	0.330	0.405	0.433	0.426	0.346	0.300	0.213
SR_M	0.833	0.568	1	0.440	0.661	0.231	0.188	0.270	0.064	0.306
SR_A	0.602	0.330	0.440	1	0.833	0.318	0.345	0.004	0.041	0.314
SR_R	0.730	0.405	0.661	0.833	1	0.341	0.342	0.120	-0.051	0.439
SL_T	0.448	0.433	0.231	0.318	0.341	1	0.936	0.818	0.241	0.320
SL_B	0.428	0.426	0.188	0.345	0.342	0.936	1	0.632	0.139	0.337
SL_M	0.332	0.346	0.270	0.004	0.120	0.818	0.632	1	0.227	0.090
SL_A	0.207	0.300	0.064	0.041	-0.051	0.241	0.139	0.227	1	0.071
SL_R	0.385	0.213	0.306	0.314	0.439	0.320	0.337	0.090	0.071	1
AIns	0.296	0.267	0.154	0.290	0.334	0.746	0.680	0.637	0.009	0.247
AHerb	0.315	0.325	0.177	0.185	0.246	0.789	0.683	0.720	0.111	0.234
%ACH	0.187	0.151	0.119	0.041	0.166	0.666	0.555	0.666	0.076	0.163
ABuilt	0.209	0.137	0.038	0.452	0.307	0.396	0.438	0.144	0.107	0.288
ACrop	-0.004	-0.110	-0.186	0.543	0.368	0.175	0.231	-0.157	-0.225	0.234
AHD1	0.380	0.331	0.261	0.301	0.357	0.712	0.628	0.638	0.085	0.276
# P	0.133	0.271	-0.144	0.206	0.045	0.251	0.305	0.061	0.314	0.157
AWater	0.200	0.410	-0.085	0.059	-0.070	0.242	0.274	0.105	0.356	0.154

Table 11: Sheet 2

	AIns	AHerb	%ACH	ABuilt	ACrop	AHD1	# P	AWater
SR_T	0.296	0.315	0.187	0.209	-0.004	0.380	0.133	0.200
SR_B	0.267	0.325	0.151	0.137	-0.110	0.331	0.271	0.410
SR_M	0.154	0.177	0.119	0.038	-0.186	0.261	-0.144	-0.085
SR_A	0.290	0.185	0.041	0.452	0.543	0.301	0.206	0.059
SR_R	0.334	0.246	0.166	0.307	0.368	0.357	0.045	-0.070
SL_T	0.746	0.789	0.666	0.396	0.175	0.712	0.251	0.242
SL_B	0.680	0.683	0.555	0.438	0.231	0.628	0.305	0.274
SL_M	0.637	0.720	0.666	0.144	-0.157	0.638	0.061	0.105
SL_A	0.009	0.111	0.076	0.107	-0.225	0.085	0.314	0.356
SL_R	0.247	0.234	0.163	0.288	0.234	0.276	0.157	0.154
AIns	1	0.931	0.774	0.463	0.307	0.862	0.240	0.122
AHerb	0.931	1	0.819	0.382	0.206	0.884	0.218	0.176
%ACH	0.774	0.819	1	0.112	-0.012	0.586	-0.098	-0.030
ABuilt	0.463	0.382	0.112	1	0.497	0.516	0.565	0.384
ACrop	0.307	0.206	-0.012	0.497	1	0.287	0.453	0.046
AHD1	0.862	0.884	0.586	0.516	0.287	1	0.318	0.165
# P	0.240	0.218	-0.098	0.565	0.453	0.318	1	0.630
AWater	0.122	0.176	-0.030	0.384	0.046	0.165	0.630	1

Table 12 : Standardized regression coefficients from multiple-regression analysis of losses of COSEWIC-listed species in all 217 Canadian terrestrial ecoregions. Effect of ecoregion area was tested and found to be non-significant (P>0.05).

Independent Variable	Total [a]	Birds	Mammals	Amphibians	Reptiles
Species richness	**+0.453** [b]	**+0.258**	+0.175 *	+0.239 *	**+0.431**
Area treated with agricultural herbicides (log_{10})			+0.254		
(Area treated with agricultural herbicides)^2 (log_{10})	+0.363 ***	**+0.522**			
Human population, 1871 (log_{10})			-0.143 *	-0.291 **	
Built up landcover (log_{10})					**-0.921**
(Built up landcover)^2 (log_{10})		+0.147 *			**+1.288**
% Builtup landcover (arcsin √)				+0.257 ***	
Cropland (log_{10})				**+0.383**	
Rangeland (log_{10})					-0.153 *
Human-dominated landcover (builtup + cropland + rangeland) (log_{10})			+0.328 *		
Human-dominated landcover (builtup + cropland)(log_{10})	+0.193				
Road and railroad density (log_{10})					-0.185
Landscape patch (polygon) density (log_{10})		+0.107			
Area covered by freshwater (log_{10})		+0.131 **	+0.134 *		
Forested landcover (log_{10})			+0.251 ***		
Natural landcover (log_{10})			-0.229 ***	**+0.304**	
Total explained variation (r^2)	**0.786**	**0.742**	**0.691**	**0.306**	**0.423**

a Total refers to all four taxa combined

b Significance of variables: **bold**, P≤0.00001; ***, P<0.0001; **, P<0.001; *, P<0.01; rest are P<0.040

Table 13 : Standardized regression coefficients from multiple-regression analysis of losses of COSEWIC-listed species in the 80 Canadian ecoregions with human landcover. Effect of ecoregion area was tested and found to be non-significant (P>0.05).

Independent Variable	Total [a]	Birds	Mammals	Amphibians	Reptiles
Species richness [b]	+0.164 [c]	+0.088 ns	+0.082 ns	+0.369	**0.524**
(Area treated with agricultural insecticides)^2 ($\log_{10}$)		**+0.713**			
(Area treated with agricultural herbicides)^2 ($\log_{10}$)	**+0.676**				
% of cropland treated with herbicides (arcsin √)			+0.350 **		
(Built up landcover)^2 ($\log_{10}$)	0.160				
Cropland, 1861($\log_{10}$)			-0.292 **	**-0.630**	
Human-dominated landcover (builtup + cropland + range-land)($\log_{10}$)			**+0.514**		
Number of landcover patches (polygons) ($\log_{10}$)				**+0.534**	
Area covered by freshwater ($\log_{10}$)		+0.165			
Total explained variation (r^2)	**0.703**	**0.630**	**0.656**	**0.341**	**0.274**

a Total refers to all four taxa combined

b Species richness was forced into the models when non-significant to ensure any variability in losses that may be due to species richness is accounted for.

c Significance of variables: **bold**, P<0.00001; ***, P<0.0001; **, P<0.001; *, P,0.01; ns, P>0.05; rest are P≤0.03

Table 14 : Past and present threats to COSEWIC–listed species' survival (according to the authors of the species' COSEWIC status reports) and the proportion of species menaced by each kind of threat (all COSEWIC–listed species_COSEWIC–listed species included in this study). The number of species (*n*) included in each taxon are indicated. Threat categories follow the approach taken by Wilcove et al. (1998).

Threat	Total (*n*=253)	Terrestrial Vertebrates (*n*=96_62)	Birds (*n*=44_37)	Terrestrial Mammals (*n*=23_12)	Amphi-bians (*n*=14_6)	Reptiles (*n*=14_7)	Fish (*n*=42)	Vascular Plants (*n*=94)
Agriculture – land conversion	0.42	0.64_0.63	0.66_0.59	0.61_0.77	0.73_0.83	0.50_0.43	0.07	0.45
Agriculture – pollutants	0.17	0.21_0.21	0.27_0.24	0.13_0.08	0.33_0.50	0_0	0.26	0.07
Pollutants – total	0.34	0.35_0.37	0.50_0.49	0.17_0.08	0.33_0.50	0.21_0.14	0.67	0.13
Land conversion – residential, commercial, industrial	0.46	0.50_0.51	0.48_0.41	0.52_0.77	0.40_0.50	0.64_0.57	0.12	0.63
Logging – land conversion and siltation	0.16	0.25_0.25	0.27_0.24	0.30_0.38	0.27_0.33	0.07_0	0	0.12
Infrastructure development	0.13	0.19_0.21	0.20_0.19	0.04_0.08	0.20_0.50	0.36_0.43	0	0.15
Oil, gas, mining	0.08	0.07_0.11	0.07_0.08	0.13_0.23	0_0	0.07_0.14	0.02	0.12
Water development	0.21	0.22_0.21	0.20_0.14	0.09_0.15	0.40_0.67	0.29_0.29	0.17	0.24
Outdoor recreation	0.26	0.20_0.24	0.25_0.27	0.13_0.15	0.13_0.17	0.21_0.29	0	0.45
Fire suppression	0.08	0.05_0.05	0.09_0.08	0.04_0.00	0_0	0_0	0	0.16
Harvest, exploitation	0.22	0.20_0.19	0.18_0.14	0.30_0.46	0_0	0.29_0.14	0.19	0.16
Persecution	0.07	0.16_0.19	0.14_0.11	0.22_0.38	0_0	0.29_0.43	0.05	0
Introduced species	0.13	0.15_0.19	0.14_0.16	0.17_0.31	0.27_0.33	0_0	0.05	0.16

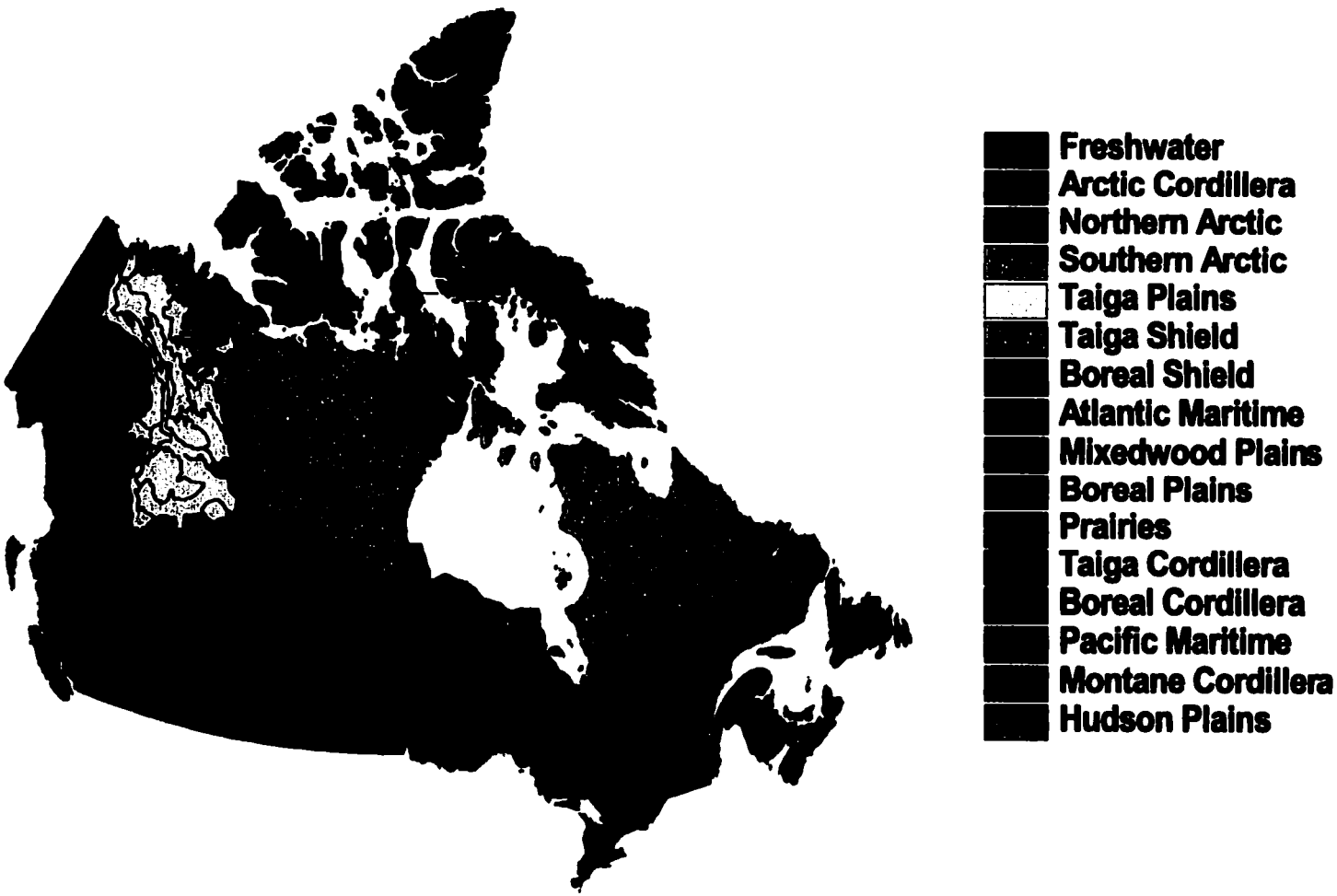


Figure 12: Map of the terrestrial ecozones (n=15) and ecoregions (n=217; delineated by black lines within ecozones) of Canada.

Figure 13: Map of combined current species richness per ecoregion for COSEWIC–listed birds, mammals, amphibians, and reptiles included in this study (n=62 species).

Figure 14: Map of species' losses per ecoregion for COSEWIC-listed birds, mammals, amphibians, and reptiles combined. Losses were determined through comparisons of historic and current range maps of each species (n=62 species).

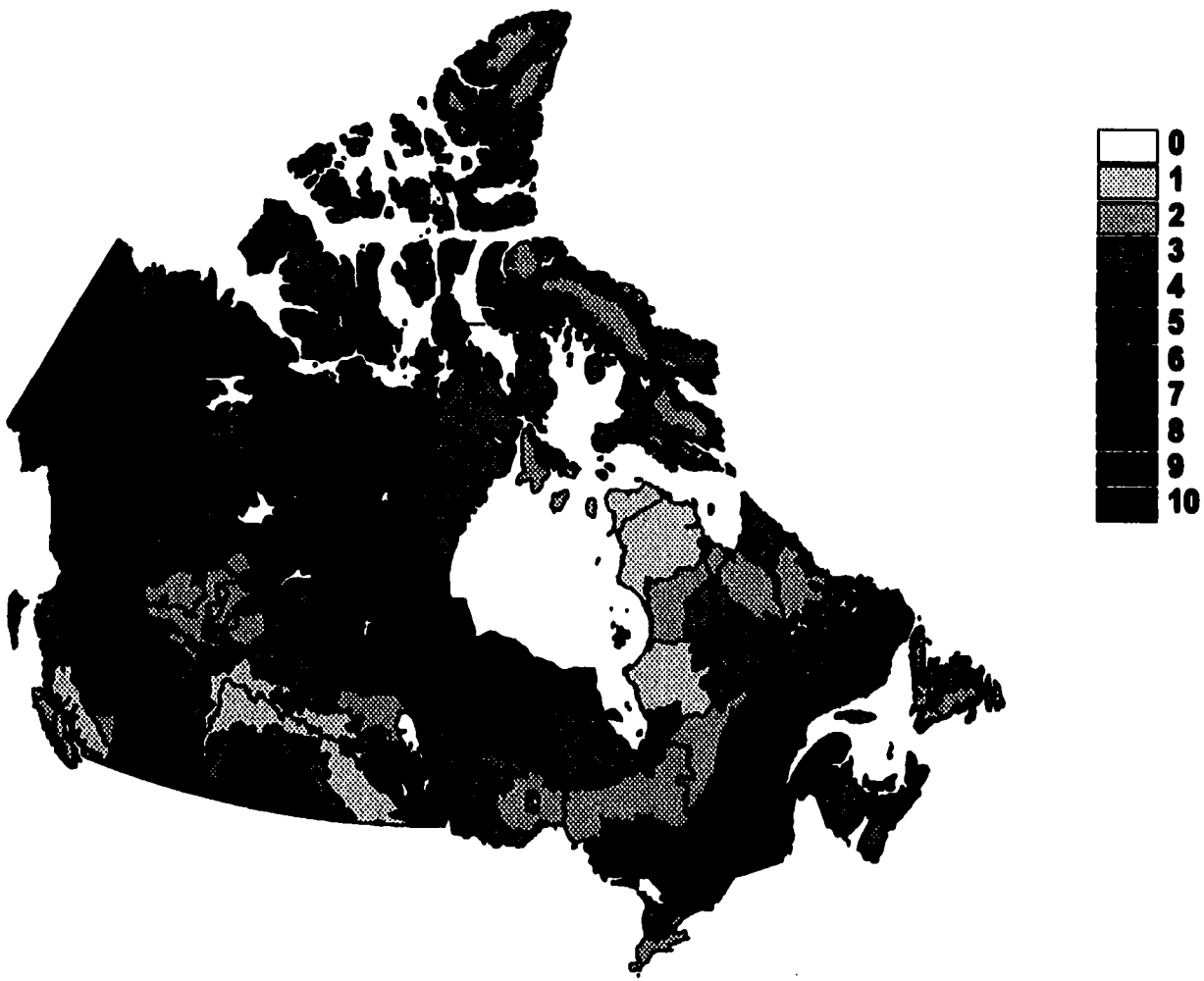


Figure 15: Map of COSEWIC–listed species richness per ecoregion for birds, mammals, amphibians, and reptiles combined, for only those species that have not suffered historic range losses in the ecoregion in question, but have undergone range losses in other ecoregions. This map depicts cold spots of COSEWIC–listed species' losses.

Figure 16: Map of current species richness per ecoregion for COSEWIC–listed birds (total N=37).

Figure 17: Map of species' losses per ecoregion for COSEWIC–listed birds. Losses were determined through comparisons of historic and current range maps of each species.

Figure 18: Map of species richness per ecoregion for COSEWIC–listed birds for only those species that have not suffered historic ranges losses in the ecoregion in question, but have undergone range losses in other ecoregions. This map depicts cold spots of COSEWIC–listed bird species' losses.

Figure 19: Map of current species richness per ecoregion for COSEWIC–listed mammals (total N=12).

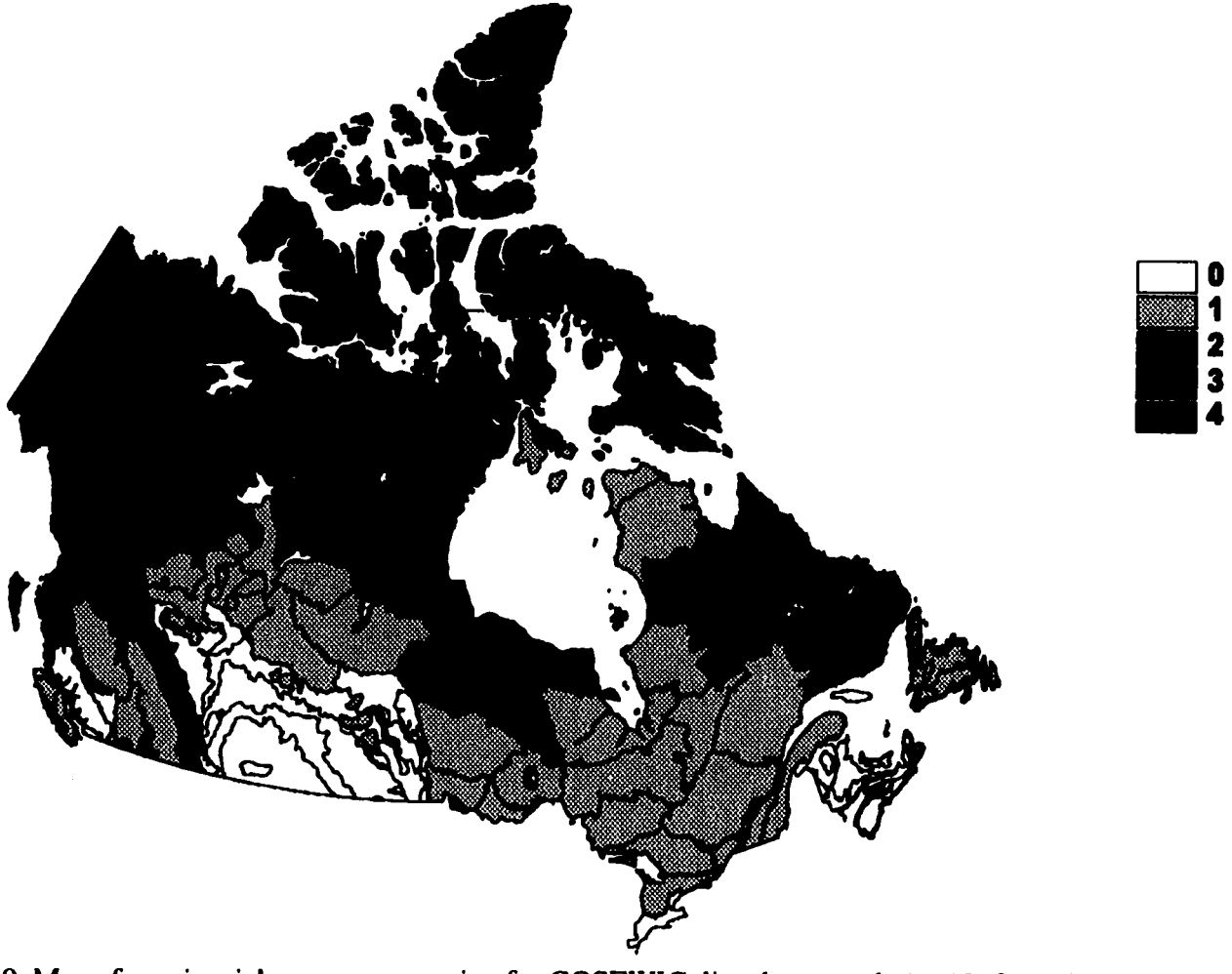


Figure 20: Map of species richness per ecoregion for COSEWIC–listed mammals (n=12) for only those species that have not suffered historic range losses in the ecoregion in question, but have undergone range losses in other ecoregions. This map depicts cold spots of COSEWIC–listed mammal species' losses.

Figure 21: Map of species' losses per ecoregion for COSEWIC–listed mammals. Losses were determined through comparisons of historic and current range maps of each species.

Figure 22: Map of current species richness per ecoregion for COSEWIC–listed amphibians (total N=6).

Figure 23: Map of current species richness per ecoregion for COSEWIC–listed reptiles (total N=7).

Figure 24: Map of species' losses per ecoregion for COSEWIC–listed amphibians. Losses were determined through comparisons of historic and current range maps of each species.

Figure 25: Map of species richness per ecoregion for COSEWIC–listed amphibians for only those species that have not suffered historic range losses in the ecoregion in question, but have undergone range losses in other ecoregions.

Figure 26: Map of species' losses per ecoregion for COSEWIC–listed reptiles. Losses were determined through comparisons of historic and current range maps of each species.

Figure 27: Map of species richness per ecoregion for COSEWIC–listed reptiles for only those species that have not suffered historic range losses in the ecoregion in question, but have undergone range losses in other ecoregions.

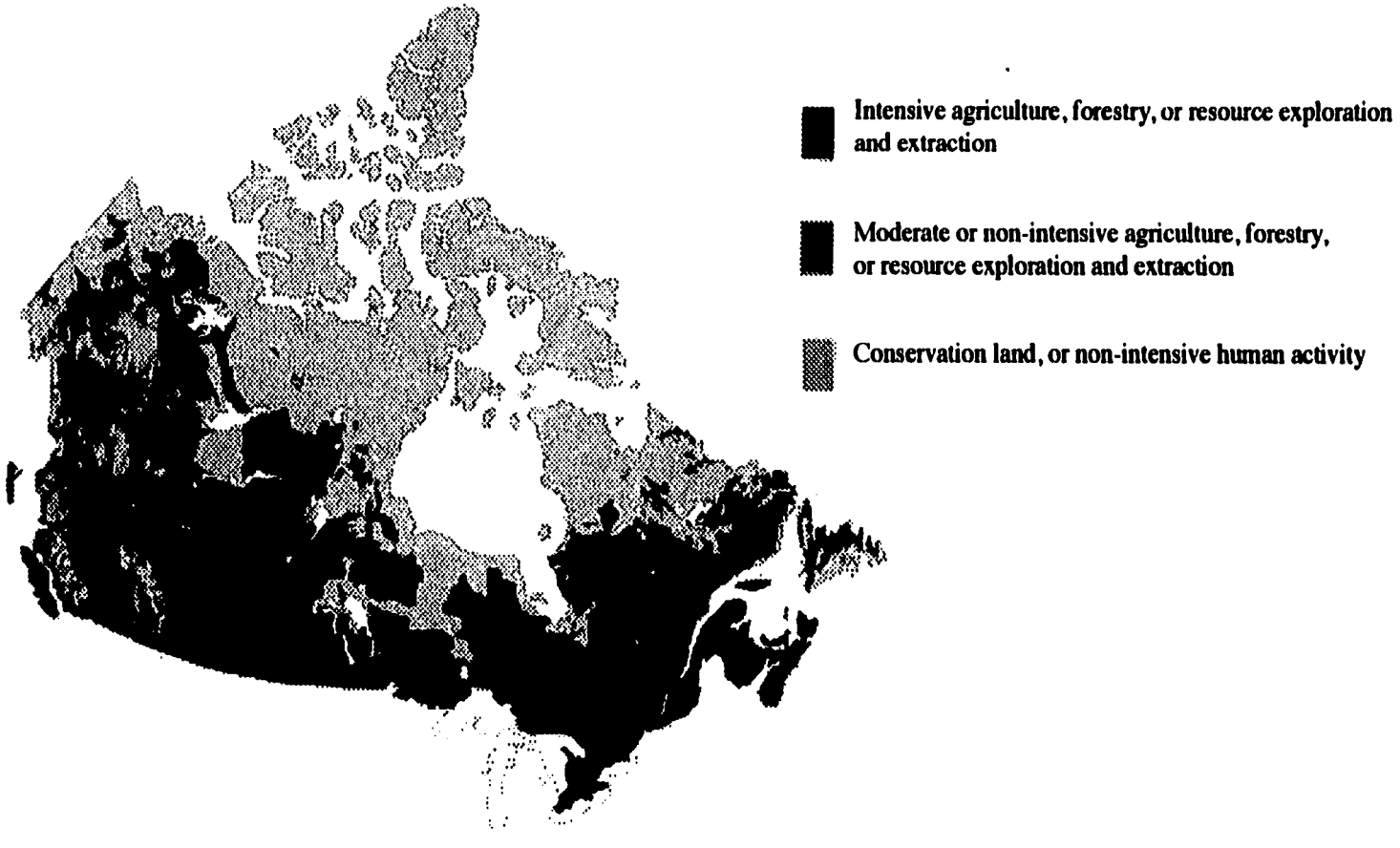


Figure 28: Map of human alteration to the landscape in Canada. Darker areas are characterized by more intensive landuse and habitat loss. (From Biodiversity Science Assessment Team 1994).

Conclusions

Species Diversity–Disturbance Relationships

The two quantitative studies of diversity–disturbance relationships were undertaken to clear up theoretical weaknesses and empirical ambiguities in the disturbance literature, and to determine what effects disturbance should be expected to have on species diversity. Contrary to general belief, species diversity is rarely observed to be greatest at an intermediate level of disturbance. Neither quantitative models of community dynamics in the face of disturbance nor a meta-analysis of published species diversity–disturbance relationships indicate that disturbance should be expected to have a consistently strong effect on diversity, although strong relationships are detected in some cases. Although I have identified some circumstances under which peaked and/or strong diversity–disturbance relationships may be observed, my work suggests that basic predictions of the Intermediate Disturbance Hypothesis and other qualitative models are not typically supported by either quantitative models or published species diversity–disturbance relationships. My modeling study and the meta-analysis suggest that the observed shape and strength of a species diversity–disturbance relationship are influenced by how thoroughly the community and the disturbance gradient are sampled. Thorough sampling is less likely to yield strong or peaked relationships, compared with studies applying less thorough sampling. This suggests that sampling artifacts may often be a strong element in observed species richness–disturbance relationships.

A major limitation of the IDH is that it is hard to falsify because it makes only qualitative predictions about changes in species diversity in response to disturbance

(Juhász-Nagy 1993). Because the IDH postulates a peaked relationship between species diversity and disturbance, virtually any shape of relationship (unimodal, positive monotonic, negative monotonic, and even non-significant) could be observed along a limited range of disturbance intensity or frequency. This may in turn be a limitation of the meta-analysis performed in Chapter 2. Because of this, it is not always possible to absolutely refute that monotonic or non-significant relationships observed in some of the primary studies may have resulted from examinations of relatively small sections of unimodal relationships. In some cases, it is possible that positive or negative monotonic relationships arose from sampling only the lower or higher part of the disturbance gradient, respectively. It can be difficult to determine *a priori* the range of disturbance that should be examined in order to detect the true nature of the relationship. However, when negative monotonic relationships are detected in studies that include a treatment of disturbance = 0, then one can confidently conclude that the relationship is indeed negative monotonic. When non-significant relationships are observed in studies that examine wide ranges of disturbance levels and sample many locations along the gradient, then one could confidently conclude that the relationship is truly non-significant.

Because it was not possible for me to determine the breadth of the examined disturbance gradient relative to the absolute for each primary study, I could not test the effect of this on the shape and strength of observed species diversity–disturbance relationships. It is possible that in some situations, only small fractions of the disturbance gradient were examined, and the observed relationships may, therefore, not depict the true nature of the relationship. Although a logistic regression model suggests that peaked species richness–disturbance relationships are more likely to be observed when greater numbers of

disturbance levels are examined (note that this variable does not necessarily correlate with the range of disturbance examined), the predictive efficacy of the model is very low (Table 7).

Much confusion regarding the relevancy of the IDH to small– and/or large–scale disturbances exists in the literature. The IDH does not explicitly make any assumptions about the scale of the disturbance relative to the size of the community. However, in his paper that popularized the IDH, Connell (1978) based his theory in part on anecdotal evidence from coral reefs that had undergone extensive damage from large-scale storms and from studies of tropical forests that examined community structure in single-age stands that had arisen from large–scale disturbance; this suggests that Connell believed that the IDH was relevant to large-scale disturbances and within–patch dynamics. Additionally, the work of others (e.g. Fuentes and Jaksic 1988) also suggests that the IDH is based on large-scale disturbances. And, those who study species diversity–disturbance relationships by examining species diversity in small areas located entirely within large disturbed patches inherently suggest that the IDH should be relevant to within–patch dynamics (e.g. Collins et al. 1995, Mehlman 1992, Wilson and Tilman 1991, Lake et al. 1989, Armesto and Pickett 1985, Sousa 1979). Conversely, discussions by authors such as Wilson (1994), and Abugov (1982), and the abundant studies that compare species diversity among communities that contain several small disturbed patches (e.g. Hiura 1995, McIntyre et al. 1995, Phillips et al. 1994, Shackleton et al. 1994, Sammarco 1982, Lubchenco 1978) suggest that the IDH is based on small-scale disturbances, or between–patch dynamics (i.e., the community is composed of several small patches in different stages of succession).

My Markov models assume that the scale of the disturbance is small relative to the

size of the community. Because transition probabilities rely, to varying extents, on sources of propagules both internal and external to the community, it would be logical to expect the probabilities to change if disturbances lead not only to mortality of much of the community in question, but also to large–scale mortality of surrounding individuals and sources of colonizing propagules. This assumption of small–scale disturbance inherently arises because the models assume that the transition probabilities do not change over time (i.e., the source of colonizing propagules remains unaffected by disturbance).

Because of the controversy of scale surrounding the IDH, those who support the idea that the IDH is relevant to only large-scale disturbance may argue that the small–scale assumption of my models renders them inadequate for making useful conclusions about the IDH. However, recent work by Collins and Glenn (1997) suggests that the IDH may be applied to both between– and within–patch scales, or, both small– and large–scale disturbances. Also, results from my meta-analysis indicate that whether a study examines between– or within–patch scales has no apparent effect on whether the observed species diversity–disturbance relationship is peaked, suggesting that the IDH is equally applicable (or equally irrelevant) to both small– and large–scale disturbances. Therefore, there is little evidence that the use of small–scale disturbances in my models to make quantitative predictions regarding the effect of disturbance on species diversity was problematic.

However, because the effect of large– vs. small–scale disturbances on species diversity is still debatable, the effects of large–scale disturbances should not be generalized from the predictions of my models. A discrepancy between the predictions of my models and the effects of large–scale disturbance on species richness is apparent in the results of Chapter 3. In Chapter 3, large–scale disturbances arising from extensive human

landuse and habitat loss, do appear to lead to losses of species (i.e., a significant negative relationship between species richness and disturbance).

A potentially more serious limitation of the modeling study is that some transition probability matrices were composed of functional groups, rather than species. The species information missing from these matrices is potentially very important. The modeling study suggests that matrix complexity (ratio of the number of non-zero transition probabilities : total number of possible transitions) is largely responsible for whether species declines will be observed along a disturbance gradient. Communities with high complexity (i.e., virtually any species can replace any other species and bare space in a short span of time) are unlikely to exhibit any loss of species, while communities with low complexity (i.e., transitions between species are more limited and few species can colonize bare space) are more likely to suffer extirpations. Thus, if a transition probability matrix that is composed of functional groups has a matrix complexity very different from the true complexity calculated from species' transition probabilities, then the model may not make accurate predictions.

Despite these limitations of the meta-analysis and the modeling study, my work provides a comprehensive examination of species diversity–disturbance relationships, and the results do allow one to make conclusions about the generality of the IDH. In the meta-analysis, non-significant relationships were, by far, the most common; and even if several of these were actually due to inadequate experimental design in the primary studies, the results would still indicate that peaked species diversity–disturbance relationships are not the norm. The results of the meta-analysis in conjunction with the predictions of my Markov models undoubtedly question the widely held beliefs that species diversity should

be greatest at intermediate levels of disturbance and that the relationship between species diversity and disturbance should be consistently strong.

To develop a very good experimental test of a species diversity–disturbance relationship, several items must be considered. Ideally, species diversity–disturbance relationships should illustrate the long term effect of disturbance history on a community, not the immediate effect. Therefore, the community must be composed of species with short generation times, so that the study can run long enough to ensure that the community is given sufficient time to recover from the initial mortality resulting from disturbance. Because sampling and study designs greatly influence the observed strength and shape of species diversity–disturbance relationships, one should conscientiously utilize sampling protocols that will yield results that reflect the true character of the relationship in question. Thorough sampling is a necessity, and it may take much preliminary effort to determine how many individuals, how much area, etc. will need to be sampled in order to obtain accurate measures of species diversity. More than one metric of diversity should be examined. Results from my work indicate that species richness and species evenness may respond differently to changes in disturbance, and that observations of evenness may be less sensitive to low sampling intensity than those of richness. Determining the disturbance gradient may be the most problematic. Although the minimum disturbance level is simple (no disturbance), it is difficult to know *a priori* what the natural maximum disturbance level is for any given community, what portion of the total range of disturbance needs to be examined to observe the true effect of disturbance on species diversity, and how many treatments (levels of disturbance) should be examined. Again, much preliminary work may be required to determine what kind of disturbance would be best to examine, and the

appropriate breadth of the disturbance gradient.

Even when the ideal experimental test of a species diversity–disturbance relationship is performed, my results indicate that the results from that one study should not be used to make generalizations about the effects of disturbance in other communities. Many well-designed studies are going to be required before we will know, with greater certainty than the results from my meta-analysis, under what circumstances peaked (or other shapes) of relationships are most likely to occur, and when these relationships are likely to be very strong or very weak.

Human Landuse and Losses of Imperiled Species

While recent studies in conservation biology have identified some hot spots of endangered species richness, quantitative studies of patterns of losses of imperiled species are absent from the literature. Hot spots of imperiled species are usually believed to indicate regions containing undesirable environmental attribute(s) that presumably contribute to the imperiled status of species. However, an alternative scenario is that regions containing high numbers of imperiled species have desirable environmental attributes that promote the persistence of these species. Studies of species' losses, vs. imperiled species richness, would be more informative about factors associated with species' extirpations and extinctions, and where the survival of imperiled species is currently at risk. Comparisons of hot spots of imperiled species richness and species' losses would indicate which hot spots of imperiled species richness coincide with high densities of losses, and which hot spots represent regions where imperiled species have been able to persist despite being lost elsewhere.

I quantitatively examined losses of COSEWIC–listed species in Canada to identify hot and cold spots of species' losses, and to determine what human landuse attributes are most closely associated with high frequencies of species' losses. Unlike many natural disturbances, the extensive, intensive, and chronic nature of human landuse has a significant long-term effect on species diversity. Several regions in southern Canada have lost many species that existed there historically. My work shows that, for imperiled bird species and mammals, these losses are associated with habitat loss and, more importantly, chemically–intensive agriculture. For imperiled amphibians and reptiles, the results are less clear, but still indicate that losses are associated with anthropogenic factors.

Although agricultural pesticides are clearly associated with losses of imperiled species, the nature of the relationship is unclear. The pesticides themselves could be directly responsible for the losses of many species in certain regions. Alternatively, the pesticide variables may be indicators of agricultural intensity, suggesting that agricultural that is both physically and chemically intense may pose the greatest risk to imperiled species.

My work suggests that both habitat loss and the ways in which human–dominated landscapes are used are related to losses of imperiled species. Continued loss and degradation of important habitats will be devastating, especially in many southern regions of Canada where landscapes are already dominated by intense human landuse (e.g. southernmost ecoregion of the Mixedwood Plains ecozone, 90% human landcover). Protection of critical habitat for imperiled species should be a minimum requisite for the conservation of imperiled species. Additionally, the kinds of intense landuse that are most detrimental to imperiled species will need to be limited and/or modified (e.g. reduction in pesticide use;

enrichment of croplands with non-crop habitats such as wooded fence rows, hedges, grassy waterways) to prevent further losses of imperiled species in Canada.

My comparisons of richness and losses of imperiled species indicated that hot spots of imperiled species richness in Canada represent two kinds of areas: 1) areas with undesirable environmental attributes that are clearly associated with losses of species (e.g. birds), and 2) areas with attributes that appear to promote the persistence of imperiled species that have been extensively lost elsewhere (mammals). Knowledge of where imperiled species are currently located, from where they have been lost, and detailed information about various environmental attributes are all necessary for understanding where species are the most threatened and what factors pose the greatest risk to the survival of imperiled species.

Results from the modeling study and the meta-analysis indicate that inadequate sampling can lead to false observations of patterns in species richness and, subsequently, losses of species. A sampling concern may arise from the use of COSEWIC-listed species for this study, and the inability to include every species that has suffered range reductions in Canada during the past 100-200 years. Obviously, because not all changes in species' distributions are known, not all species that have suffered range reductions in Canada are listed by COSEWIC. Additionally, not all listed species have well documented historic and/or current distributions, reducing the sample size of species even further. Because of the quality of data presented in the COSEWIC reports of species included in my analyses, and the variety of species included (e.g. hunted/persecuted vs. not, limited and extensive historic distributions, northern and southern species), I am confident that the qualitative conclusions from my analyses are applicable to Canadian birds and mammals in general,

despite the undersampling issue. The sample sizes for amphibians and reptiles in my analyses were too low for confident conclusions to be made, as noted in Chapter 3.

Losses of species may have been disproportionately underestimated in some heavily populated eastern regions (e.g. Montreal, Halifax), due to some losses potentially having gone unnoticed during colonial settlement in the 17th and 18th centuries. Losses may have occurred in some eastern population centers before the early settlers took inventories of the native species. With the data at hand, it is not possible to determine the extent of this temporal effect of colonization and what actual effect, if any, it has on my results. Because much of the landscape in these eastern regions is dominated by intensive agriculture and builtup urban centers, the most probable effect of the disproportionate underestimation of losses in these regions is that the effects of both habitat loss and agricultural pesticide use on species' losses have been underestimated by my analyses.

The results and conclusions from my analyses of species' losses need to be interpreted with some caution. In addition to potential problems from undersampling (see above), the collinearity (sometimes very strong) of many predictor variables may lead to erroneous conclusions about the effect of particular landuse attributes on losses of imperiled species. Correlation matrices of all examined variables are provided in Appendix 9, and should be consulted while reviewing the results presented in Chapter 3.

The analyses presented in Chapter 3 should not be used directly for conservation policy purposes, but, rather, should be considered a starting point for further research. Much more work is required to fully understand the effects of habitat loss on losses of different taxa and whether agricultural pesticides are direct causes of species' losses or rather are indicators of agricultural and landuse intensity. Additional human landuse variables to

consider in future work are: specific kinds of habitat loss (e.g. densely builtup cities vs. builtup regions with large areas of green space), different kinds of agricultural crops and practices, non-agricultural pesticides and fertilizers, and forestry (total, as well as different forestry practices). In my analyses, it was not possible to separate the effects of agricultural pesticides and fertilizers; doing so may be informative, especially in the case of amphibians, which may be more sensitive to fertilizers than are other taxa of terrestrial vertebrates. More complete datasets of COSEWIC-listed species, as well as non-listed species that have suffered range reductions in recent history, would provide a basis for more decisive conclusions about what factors pose the greatest risk to species in Canada.

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Appendices

Appendix 1: Transition Probability Matrices

The six transition probability matrices for communities modeled in Chapter 1 are outlined below. For further details consult the original sources. Columns represent starting species or species group (i.e., species at time t), and rows represent species or species group following transition (i.e., species at time t+1). Due to rounding, column sums may not equal 1.000.

Community: **Alpine cushion** (**CV**=*Cassinia vauvilliersii*, a shrub; **DL**=*Dracophyllum longifolium*, a shrub; **HO**=*Hebe odora*, a shrub; **Ch**=tussocks of the grass *Chionochloa rigida;* **Cu**=Cushion-forming species in discrete cushions, mainly *Donatia novae-zelandiae*, *Celmisia argentea*, and *Phyllachne colensoi;* **Tu**=Turf, or a mixture of mat-forming species, including *Pentachondra pumila*, *Cyathodes pumila*, and *Pernettya macrostigma;* **De**=Dead plant material (not included in species counts for estimates of species richness and evenness); **BS**=Bare space.

Source: Lough et al. (1987); Table 3.

Matrix complexity = 0.59 (38 non-zero transitions/64 possible transitions)

	CV	DL	HO	Ch	Cu	Tu	De	BS
CV	0.154	0	0.286	0.012	0.001	0.015	0	0
DL	0	0.250	0	0	0.001	0.001	0	0
HO	0.057	0	0.143	0	0.001	0.003	0	0
Ch	0.039	0	0.143	0.259	0.004	0.041	0	0.050
Cu	0.115	0.500	0	0.127	0.845	0.179	0.316	0.150
Tu	0.635	0.250	0.429	0.596	0.118	0.730	0	0.800
De	0	0	0	0	0.025	0.005	0.684	0
BS	0	0	0	0.006	0.005	0.026	0	0

Community: **Heathland** (**EN**=*Empetrum nigrum*, a dwarf shrub; **CV**=*Calluna vulgaris*, a dwarf shrub ; **ET**=*Erica tetralix*, a dwarf shrub; **MC**=*Molinia caerula*, a grass; **CP**=*Carex pilulifera*, a grass; **JP**=*Juncus squarrosus*, a grass; RA=*Rumex acetosella*; **OS**=other species; **BS**=bare space)

Source: Lippe et al. (1985); Table 2

Matrix complexity = 0.88 (71 non-zero transitions/ 81 possible transitions)

	EN	CV	ET	MC	CP	JS	RA	OS	BS
EN	0.808	0.232	0.321	0.358	0.426	0.280	0.154	0.390	0.270
CV	0.081	0.608	0.159	0.094	0.211	0.211	0.084	0.161	0.183
ET	0.038	0.037	0.358	0.057	0.088	0.123	0	0.169	0.078
MC	0.003	0.002	0.002	0.340	0.006	0.018	0	0	0.001
CP	0.006	0.011	0.011	0.019	0.135	0	0.021	0	0.012
JS	0.002	0.003	0.005	0.038	0.006	0.262	0.007	0.017	0.002
RA	0.001	0.002	0.002	0	0.006	0.018	0.182	0	0.018
OS	0.004	0.005	0.002	0	0.006	0	0	0.059	0.012
BS	0.056	0.100	0.141	0.094	0.117	0.088	0.552	0.203	0.425

Note: Probability values in the "other species" column differ from those reported in Lippe et al. (1985). Because the sum for the "other species" column in Lippe et al. (1985) is 1.18, I standardized the transition probabilities in this column so that the column sum equals the required value of 1.

Community: **Forest** (**BTA**=Big-toothed aspen, **GB**=Gray birch, **SF**=Sassafras, **BG**=Blackgum, **SG**=Sweetgum, **WO**=White Oak, **RO**=Red oak, **HI**=Hickory, **TT**=Tuliptree, **RM**=Red maple, **BE**=Beech, **BS**=Bare space)

Source: modified from Horn (1975) to compensate for longevities; see Chapter 1 Methods for details of modifications performed to make matrix appropriate for modeling. Original matrix is provided on next page.

Matrix complexity = 0.76 (110 non-zero transitions/ 144 possible transitions)

	BTA	GB	SF	BG	SG	WO	RO	HI	TT	RM	BE	BS [1]
BTA	0.903	0	0.002	0.0007	0	0	0	0	0	0	0	0.200
GB	0.005	0.933	0.0007	0.0007	0	0	0	0	0	0	0	0.200
SF	0.009	0.031	0.94	0.002	0.005	0.001	0.001	0.002	0.0009	0.013	0	0.200
BG	0.006	0.008	0.002	0.947	0	0.001	0.007	0.006	0.002	0.010	0.0005	0.050
SG	0.006	0.005	0.004	0.006	0.977	0.0007	0.005	0.002	0.002	0.009	0.0003	0.050
WO	0	0.001	0.002	0.0007	0	0.985	0.004	0.006	0	0.002	0.0003	0.050
RO	0.002	0.005	0.007	0.005	0.002	0.001	0.939	0.026	0.005	0.008	0.0003	0.050
HI	0.004	0	0.008	0.004	0.002	0.0005	0.005	0.808	0.003	0.019	0.0003	0.050
TT	0.002	0.002	0	0.007	0.002	0.002	0.005	0.018	0.960	0.003	0.002	0.050
RM	0.060	0.011	0.025	0.017	0.009	0.005	0.022	0.098	0.013	0.913	0.002	0.050
BE	0.003	0.002	0.010	0.011	0.002	0.003	0.011	0.034	0.015	0.023	0.995	0.050
BS [2]	0	0	0	0	0	0	0	0	0	0	0	0

1 Transitions from bare space were estimated based on whether species were pioneer species. Pioneers were assigned the highest transition probability, and others were assigned a lower probabiliy. A range of possible transition probabilities from bare space were examined; all of them yielded qualitatively similar model predictions.

2 In this model, transitions to bare space occur only when the community is disturbed. It is assumed that in the forest's undisturbed state, natural mortality of an individual is proceeded by the growth of sapling(s) already present in the understory.

Community: **Forest** (**BTA**=Big-toothed aspen, **GB**=Gray birch, **SF**=Sassafras, **BG**=Blackgum, **SG**=Sweetgum, **WO**=White Oak, **RO**=Red oak, **HI**=Hickory, **TT**=Tuliptree, **RM**=Red maple, **BE**=Beech)

Source: Horn (1975);

Note: in this original version, columns represent canopy species, and rows represent percentages of the total number of saplings found under each canopy species.

	BTA	GB	SF	BG	SG	WO	RO	HI	TT	RM	BE
BTA	3	0	3	1	0	0	0	0	0	0	0
GB	5	0	1	1	0	0	0	0	0	0	0
SF	9	47	10	3	16	6	2	1	2	13	0
BG	6	12	3	20	<0.5	7	11	3	4	10	2
SG	6	8	6	9	31	4	7	1	4	9	1
WO	0	2	3	1	<0.5	10	6	3	0	2	1
RO	2	8	10	7	7	7	8	13	11	8	1
HI	4	<0.5	12	6	7	3	8	4	7	19	1
TT	2	3	0	10	5	14	8	9	9	3	8
RM	60	17	37	25	27	32	33	49	29	13	6
BE	3	3	15	17	7	17	17	17	34	23	80

Community: **Corals** (**EA**=Encrusting Acroporid corals, **TA**=Tabular *Acropora*, **BA**=Bushy *Acropora*, **SA**=Staghorn *Acropora*, **SC**=Soft corals, **AL**=Algae, **MC**=Massive corals, **PC**=Pocilloporid corals, **BS**=Bare space)

Source: Tanner et al. (1994)

Matrix complexity = 0.91 (74 non-zero transitions/ 81 possible transitions; exposed crest) and 0.88 (exposed pools and protected crest)

	EA	TA	BA	SA	SC	AL	MC	PC	BS
Exposed Crest									
EA	0.623	0.005	0.014	0.013	0	0.049	0.036	0.037	0.022
TA	0.009	0.565	0.004	0.016	0.013	0.009	0.016	0.017	0.008
BA	0.036	0.012	0.586	0.023	0.053	0.067	0.088	0.044	0.047
SA	0.019	0.005	0.011	0.475	0.040	0.076	0.024	0.044	0.026
SC	0.001	0.007	0	0.001	0.267	0	0	0.002	0.004
AL	0.008	0.012	0.009	0.022	0.013	0.137	0.012	0.012	0.011
MC	0.001	0	0.004	0.002	0	0.012	0.424	0.005	0.006
PC	0.007	0	0.007	0.012	0.027	0.009	0.012	0.358	0.013
BS	0.297	0.395	0.365	0.436	0.587	0.640	0.388	0.480	0.863
Exposed Pools									
EA	0.257	0.002	0.003	0.004	0	0.008	0.029	0	0.006
TA	0.053	0.575	0.062	0.079	0.077	0.104	0.052	0.115	0.104
BA	0.150	0.039	0.391	0.005	0.128	0.102	0.029	0.071	0.067
SA	0.150	0.042	0.067	0.632	0	0.048	0.152	0.105	0.058
SC	0	0.002	0	0	0.128	0.005	0	0.003	0.003
AL	0.009	0.005	0.023	0	0.051	0.152	0.048	0.050	0.064
MC	0	0.001	0.006	0.011	0	0.025	0.224	0.003	0.018
PC	0.027	0.008	0.012	0.011	0.077	0.031	0.019	0.178	0.036
BS	0.354	0.326	0.437	0.258	0.538	0.526	0.448	0.476	0.644

Protected Crest	EA	TA	BA	SA	SC	AL	MC	PC	BS
EA	0.354	0.046	0.032	0.032	0	0.071	0.025	0.039	0.059
TA	0.021	0.314	0.005	0.004	0.003	0.014	0	0	0.014
BA	0.066	0.030	0.478	0.082	0.016	0.090	0.076	0.105	0.091
SA	0.049	0.016	0.038	0.439	0.009	0.057	0.031	0.053	0.039
SC	0.001	0.005	0.005	0.004	0.835	0.005	0.011	0	0.014
AL	0.009	0.036	0.007	0.004	0	0.033	0.015	0	0.007
MC	0.015	0.003	0.013	0.014	0.006	0.052	0.340	0	0.032
PC	0.002	0.005	0.001	0.001	0	0	0	0.224	0.004
BS	0.482	0.544	0.421	0.421	0.131	0.678	0.501	0.579	0.741

Appendix 2: Example of a Markov Model

My models consisted of three basic components: 1) a community vector composed of 5000 cells, each representing a single individual; 2) a transition probability matrix used to estimate changes in community composition over a given time interval; and 3) a generic disturbance (Fig. 29). Disturbance was applied to each community at varying levels of intensity (proportion of individuals killed), frequency (how often, on average, disturbance-induced mortality occurred), and species–selectivity; each of these was held constant for the duration of a run. Disturbance intensity ranged from 0 to 100% of individuals being killed, at 10% increments. Disturbance frequency ranged from 0 to 1 per transition time interval, at 0.1 increments. Cells that are determined to be affected by a disturbance are immediately converted to bare space.

Non-selective disturbances are those in which all species are treated equal in terms of mortality; if disturbance intensity is 50%, then 50% of all individuals, regardless of species, are killed and their cells are converted to bare space. Dominant-selective disturbances kill only the competitively most dominant species; if disturbance intensity is 50%, then 50% of individuals belonging to that dominant species are killed. Least dominant-selective disturbances kill only the competitively least dominant species. Species' dominance for the disturbance selectivity exercises was determined by running the models without any interference by disturbance. The dominant species is the one that numerically dominated the community when the community was allowed to reach equilibrium. The least dominant species is the one that was the first species to be eliminated by others, or, if no species was eliminated, the species that was numerically least dominant when the community was allowed to reach equilibrium.

The models were run for 100 transition time intervals, with disturbance intensity, frequency, and species selectivity held constant. Each of these time intervals was assigned a random number between 0 and 1 in order to randomly determine in which transition time intervals a disturbance would occur, based on the average disturbance frequency for that run. For example, if the assigned disturbance frequency was 0.30, then all time intervals with a random number ≤ 0.30 would have a disturbance event.

Fig. 29 is a schematic diagram illustrating the basic steps performed by the Markov models developed in Chapter 1. At the junction depicted by **A**, the community vector either passed directly to step **C** where it was multiplied by the transition probability matrix, or it underwent a disturbance event (**B**). Whether or not a disturbance event occurred depended upon the pre-assigned disturbance frequency, as well as the random number assigned to that particular time interval (see above). If a disturbance event did occur, each of the 5000 cells in the community vector was assigned a random number between 0 and 1. These random numbers were used to determine which individuals in the community would be affected by disturbance, and, therefore, which cells would be converted to bare space. If the pre-assigned disturbance selectivity was 70%, then all cells containing an individual (rather than bare space) and assigned a random number ≤ 0.70 were immediately converted to bare space. A post-disturbance community vector was then calculated: the contents of all undisturbed cells remained unchanged, and all disturbed cells then contained bare space.

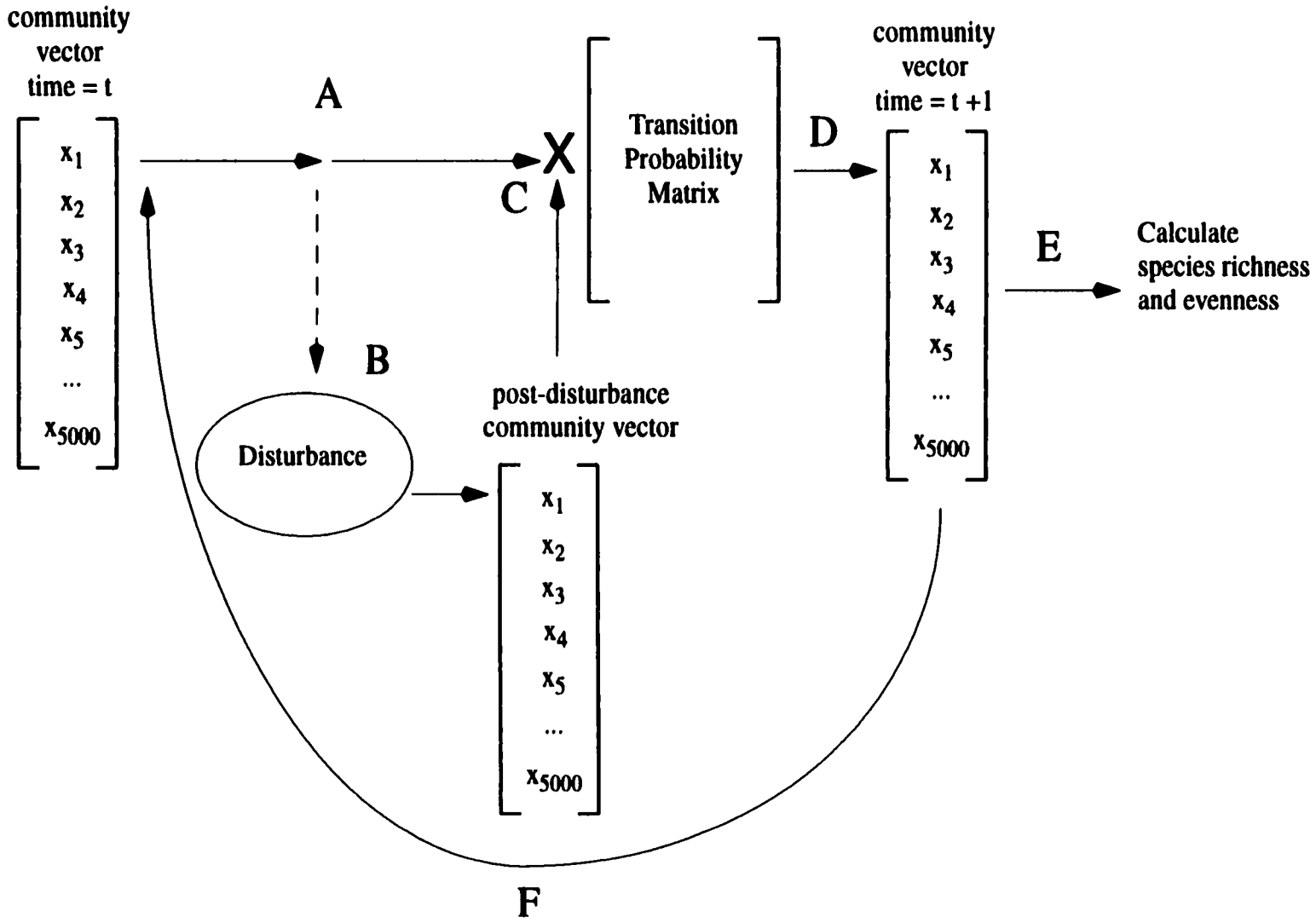
The post-disturbance community then passed to step **C** where it was multiplied by the transition probability matrix. At the beginning of step **C**, whether the community underwent disturbance or not, each cell was assigned a random number between 0 and 1.

These random numbers were used to determine which transitions each cell would undergo during the transition time interval. Remember that a transition probability matrix contains the probabilities associated with each possible transition from each species (or bare space) to each species (or bare space). If, for example, the probability of a transition from species 1 to species 1 is 0.5, then all cells containing individuals of species 1 and assigned a random number ≤ 0.5 will continue to contain species 1. If the transition probability from species 1 to species 2 is 0.15, from species 1 to species 3 is 0.05, from species 1 to species 4 is 0.1, and from species 1 to species 5 is 0.2, then use the following delimiters to determine which cells will undergo each transition: species 1 to 2, $0.5 <$ random number ≤ 0.65; species 1 to 3, $0.65 <$ random number ≤ 0.7; species 1 to 4, $0.7 <$ random number ≤ 0.8; and species 1 to 5, $0.8 <$ random number ≤ 1. This was repeated for each column (i.e., each species and bare space) in the transition probability matrix.

The community vector at time $t+1$ was calculated in step D. At this point, each cell in the community vector was assigned a random number ranging from 0 to 1. This time, random numbers were used to census the community. To determine whether sampling intensity affected the predictions made about a specific relationship, all 12 sampling intensities (5000, 2500, 1250, 625, 313, 156, 78, 39, 20, 10, 5, or 3 cells censused) were examined sequentially within the same model run. If only one sampling intensity was examined in each run, then it is possible that differences in model predictions from runs with different sampling intensities may actually be due to something other than sampling intensity. When sampling intensity was 3 cells (0.06%), then all cells with a random number ≤ 0.0006 were censused. As sampling intensity was increased, more cells were sequentially added to the census, until all cells were censused. Both species richness (the

number of species censused) and species evenness (Pielou's J; $J = -\sum p_i \log_2 p_i / \log_2(S)$, where p_i is the proportion of all individuals belonging to species i and S is the number of species) were calculated for each sampling intensity at this point. In step F, the community vector at $t+1$ became the starting point for the next transition time interval, and the whole procedure was repeated. A total of 100 transition time intervals were modeled in one run, and average species richness and evenness were calculated. This was repeated 20 times; average richness and evenness and standard errors of each are calculated at the end. For each community modeled, this process was repeated for each combination of disturbance frequency and intensity (11 frequencies x 11 intensities = 121 disturbance regimes), and each of the three disturbance selectivities.

Figure 29: A schematic diagram illustrating the basic steps of a Markov model modified by interfering disturbance events. The community composition at any given time *t* is represented by a community vector, with each of 5000 individuals noted by x_i.


community
vector
time = t
A
X
Transition
Probability
Matrix
C
D
community
vector
time = t +1
E
Calculate
species richness
and evenness
B
Disturbance
post-disturbance
community vector
F

Appendix 3: Data Sources for Meta-Analysis in Chapter 2

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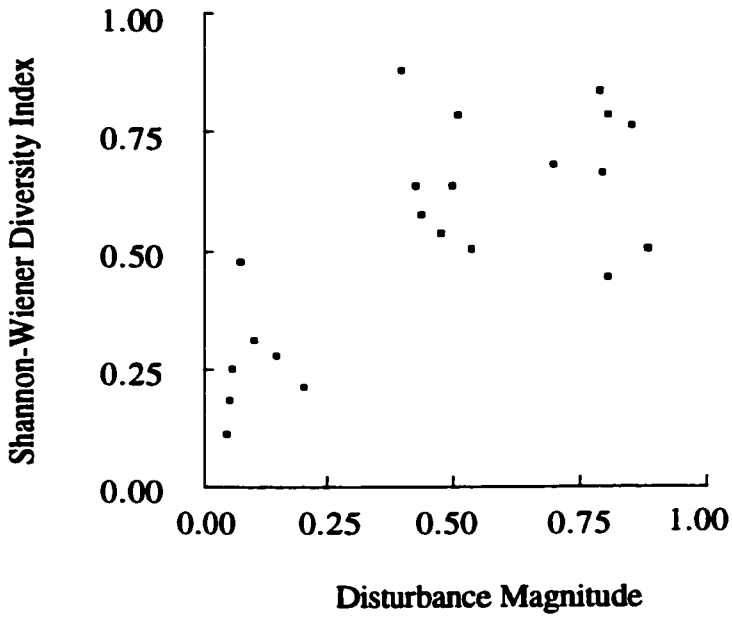
Appendix 4: Number of species diversity–disturbance relationships associated with different disturbances.

Disturbance	Richness	Diversity	Evenness
boulder movement	8	6	
bulldozing & soil deposition	1		
cattle/goat grazing			
clearcutting/deforestation	15	6	4
cultivation	8	4	3
currents/ wave action	9		1
dilution	1	2	1
dredging	1		
fire	17	6	3
flood/landslide	5	2	2
frost (soil)	3	4	
grazing	16	7	3
human landuse	1	1	1
immersion in formalin	4		
kicking/raking substratum	3	1	
mining	1		
pest infestation	1	1	1
pocket gopher/ porcupine soil disturbance	1	2	
predation	3	3	3
sedimentation	3	1	1
soil disturbance (miscellaneous)	4		
vegetation clipping	2		
volcanic eruption	1	1	
windthrow/ treefall	4	3	3
wrack mats in pond	1		
other	3	3	1

Appendix 5: Example of pattern analysis for the meta-analysis in Chapter 2

Pattern analysis of the primary species diversity–disturbance relationships obtained from published studies involved several steps, as outlined in the methods of Chapter 2. Below is one example, using data from: Martinsen, G.D., J. H. Cushman, and T.G. Whitham. 1990. Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. Oecologia 83: 132 - 138.

Step 1) Plot data for visual examination of pattern



Step 2a) Perform linear regression:

$$\text{diversity} = \text{constant} + \beta_1(\text{disturbance magnitude})$$

DEP VAR: H N: 21 MULTIPLE R: 0.718 SQUARED MULTIPLE R: 0.516
ADJUSTED SQUARED MULTIPLE R: 0.490 STANDARD ERROR OF ESTIMATE: 0.164919071

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	0.270004805	0.067143202	0.000000000	.	4.02133	0.00073
DISTURBANCE	0.556000137	0.123595258	0.718166562	.100E+01	4.49856	**0.00025**

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	0.550412055	1	0.550412055	.202370E+02	0.000246
RESIDUAL	0.516767697	19	0.027198300		

Step 2b) check residuals to ensure assumptions are satisfied (e.g. normality, homogeneity). If assumptions are not satisfied, use appropriate data transformations.

Step 2c) Is regression model significant? Yes (P = 0.00025).

Step 3a) Perform polynomial regression:

$$\text{diversity} = \text{constant} + \beta_1(\text{disturbance magnitude}) + \beta_2(\text{disturbance magnitude})^2$$

DEP VAR: H N: 21 MULTIPLE R: 0.809 SQUARED MULTIPLE R: 0.655
ADJUSTED SQUARED MULTIPLE R: 0.616 STANDARD ERROR OF ESTIMATE: 0.143054009

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	0.118128978	0.081072439	0.000000000	.	1.45708	0.16232
DISTURBANCE	1.722333464	0.446178152	2.224679851	0.0577358	3.86019	**0.00115**
DISTURBANCE^2	-1.297883583	0.481956338	-1.551981806	0.0577358	-2.69295	**0.01487**

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	0.698819659	2	0.349409830	.170740E+02	**0.0000696**
RESIDUAL	0.368360093	18	0.020464450		

Step 3b) check residuals to ensure assumptions are satisfied (e.g. normality, homogeneity)

Step 3c) Is regression model significant? Yes (P = 0.00007). Are both the linear and quadratic terms of the model significant? Yes (linear: 0.001; quadratic: 0.01).

Conclusion: both visual examination of the plotted data and the regression models indicate that the relationship may be either unimodal (i.e., maximum diversity occurs at some intermediate level of disturbance magnitude) or positive monotonic.

Note: If the model and only one term are significant, then the relationship would be classified as monotonic (positive monotonic if the sign of the significant slope is positive; negative monotonic if the slope is negative). If neither of the individual terms is significant, or if the model is not significant (i.e., if P>0.05), then the relationship would be classified as non-significant.

If the regression models indicate that the relationship may be unimodal, then proceed to Step 4. If regressions have indicated that the relationship is either non-significant or monotonic, then analyses are complete.

Step 4a) Calculate the position of the maximum value of diversity (z), as determined from the polynomial regression in Step 3a.

$$z = -\beta_1/(2 * \beta_2) = -1.722/(2*-1.298) = 0.663$$

Step 4b) Is the calculated maximum within the range of disturbance included in the dataset? Yes (maximum diversity is at a disturbance magnitude of 0.663, and disturbance ranges from 0.05185 to 0.88); proceed to Step 5.

If maximum diversity is calculated to occur outside the range of disturbance examined, then the relationship is classified as monotonic because it is not unimodal within the range of disturbance examined in the study, and analyses are complete.

Step 5) Perform Mitchell-Olds and Shaw test (Mitchell-Olds, T. and R.G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. Evolution 41: 1149 - 1161) to determine whether the position of the original maximum of diversity calculated to occur at some intermediate value along the examined disturbance gradient is statistically better than some other maximum of diversity constrained at the edge or outside of the range of disturbance examined in the study. That is, test the original model against new models in which the peak in diversity is forced to occur at the edge of or outside out of the range of disturbance examined in the study.

Step 5a) transform the values of disturbance magnitude:

$$x_{ti} = x_i^2 - 2(z_c)x_i,$$

where x_{ti} is the transformed value of disturbance magnitude, x_i is the untransformed value, and z_c is the value of disturbance at which the peak of the relationship will be constrained.

Because, in this case, the relationship is either peaked or positive monotonic, first constrain the maximum at the high end of the disturbance gradient (i.e., at disturbance magnitude = 0.88) to see if the position of the original maximum is better than a maximum at the highest level of disturbance examined. Thus, the transformation of disturbance magnitude is:

$$x_{ti} = x_i^2 - 2(0.88)x_i$$

Note: if the relationship was peaked or negative monotonic (rather than positive monotonic), then first constrain the maximum at the minimum value of disturbance. This will compare the original model with a model that forces the diversity maximum to occur at the lowest level of disturbance examined.

Step 5b) Perform a new regression with constrained transformed values of disturbance magnitude:

$$\text{diversity} = \text{constant} + \beta_2 x_{ti} + \beta_3 x_i$$

DEP VAR: H N: 21 MULTIPLE R: 0.809 SQUARED MULTIPLE R: 0.655
ADJUSTED SQUARED MULTIPLE R: 0.616 STANDARD ERROR OF ESTIMATE: 0.143054009

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	0.118128978	0.081072439	0.000000000	.	1.45708	0.16232
DISTURBANCE	-0.561941642	0.428756628	-0.725841002	0.0625231	-1.31063	**0.20646**
x_{ti}	-1.297883583	0.481956338	-1.491382942	0.0625231	-2.69295	0.01487

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	0.698819659	2	0.349409830	.170740E+02	0.0000696
RESIDUAL	0.368360093	18	0.020464450		

Step 5c) Is β_3 significant (i.e., $P<0.05$)? No; this indicates that the regression model with maximum diversity at the original intermediate level of disturbance (0.663) is statistically no different or better than the constrained model where maximum diversity was forced to occur at the highest level of disturbance examined in the study (0.88).

Step 5d) Repeat steps 5a, 5b, and 5c with a constrained maximum placed outside the range of disturbance (in this example, I use disturbance magnitude = 1.0).

DEP VAR: H N: 21 MULTIPLE R: 0.809 SQUARED MULTIPLE R: 0.655
ADJUSTED SQUARED MULTIPLE R: 0.616 STANDARD ERROR OF ESTIMATE: 0.143054009

VARIABLE	COEFFICIENT	STD ERROR	STD COEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	0.118128978	0.081072439	0.000000000	.	1.45708	0.16232
DISTURBANCE	-0.873433701	0.541524712	-1.128184755	0.0391945	-1.61292	**0.12416**
x_{ti}	-1.297883583	0.481956338	-1.883634365	0.0391945	-2.69295	0.01487

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	0.698819659	2	0.349409830	.170740E+02	0.0000696
RESIDUAL	0.368360093	18	0.020464450		

Is β_3 significant (i.e., $P<0.05$)? No. This indicates that the regression model with maximum diversity at the original intermediate level of disturbance (0.663) is statistically no different or better than the constrained model where maximum diversity was forced to occur at a level of disturbance greater than the maximum level examined in the study (0.88). Because β_3 from this model is more significant than β_3 from the model constrained at disturbance magnitude = 0.88, it appears that the true peak in diversity is indeed outside the range of disturbance examined in the study, rather than at some intermediate level of disturbance within the range examined. Further models with maximum diversity constrained at increasingly larger values of disturbance verify this; P values of β_3 get consistently smaller as z_c is increased.

Therefore, the peak in diversity originally thought to occur at an intermediate level of disturbance is, in fact, not a true "intermediate" peak. The relationship is classified as positive monotonic rather than unimodal (peaked).

Note: if β_3 was significant, then the original unconstrained model would be a statistically better model than the constrained model. Perform a few more constrained regressions (with z_c forced outside the range of disturbance examined in the study) to verify this conclusion. If β_3 remains significant, then the relationship should be classified as unimodal.

Appendix 6: Dataset for meta-analysis in Chapter 2

Listed below are brief explanations of the variable in each column of the data table that follows. For detailed explanations, consult the Methods section of Chapter 2.

Paper	Paper from which primary data were obtained
SD Metric	Measure of species diversity examined: species richness, species evenness, or diversity
r2	r^2 (from parametric regression and ANOVA); the proportion of the variation in species diversity explained by disturbance
Category	Shape assigned to species diversity–disturbance relationship. See Methods of Chapter 2 and Appendix 5 for details of pattern analysis.
Community	Organisms or community studied
Anim_Plant	Animal vs. Plant community
Terr_Aqua	Terrestrial vs. Aquatic system
Sess_Motile	Sessile (attached) vs. Motile/floating organisms
Sess_Motile_2	Sessile producers vs. Motile consumers
AET	Actual Evapotranspiration (mm water); an estimate of productivity for terrestrial systems
Disturbance	A brief description of the kind of disturbance examined
Abio_Bio	Abiotic (e.g. fire, flood) vs. Biotic (e.g. grazing, digging) disturbance
Abio_Bio_2	Abiotic vs. Biotic disturbance, for natural disturbances only (excludes anthropogenic disturbances)
Disturbance Gradient	Type of disturbance gradient examined: disturbance frequency, disturbance intensity, an interaction of frequency and intensity, or a gradient of time passes since the last disturbance event
Spat_Temp	Spatial vs. Temporal disturbance gradient. Gradients of disturbance frequency, disturbance intensity, or an interaction of the two are spatial gradients. Temporal gradients are those that involve gradients of time passed since the last disturbance.
Anth_Nat	Anthropogenic vs. Natural disturbance

Chron_Epi	Chronic (e.g. grazing) vs. Episodic (e.g. fire) disturbance.
Exh_Part	Exhaustive vs. Non-exhaustive censusing of samples
Quadrat Area	Area sampled to obtain one data point
NDL	Number of disturbance levels examined
NSamp	Number of samples (one datum is yielded from one sample)
Total Area	Total area of disturbance level sampled (# samples/treatment * quadrat area); if number of samples differed among treatments, then the average total area was used
SP_Mosaic	Single patch vs. mosaic of patches. Single patch: sample is from a homogeneously disturbed patch. Mosaic: sample is from an area containing small disturbed patches
Temp Grad	Duration of temporal gradient (yr.)
Obs_Exp/manip	Observational study vs. Experimental or manipulative
Biom_Hab	The disturbance directly affected or removed only biomass of the community studied vs. the habitat of the community vs. both

Sheet 1

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Abensperg-Traun et al 1996	richness	.	ns	earwigs	animal	terrestrial	motile
Abensperg-Traun et al 1996	richness	0.491	peaked	termites	animal	terrestrial	motile
Abensperg-Traun et al 1996	richness	.	ns	cockroaches	animal	terrestrial	motile
Abensperg-Traun et al 1996	richness	0.507	negative	scorpions	animal	terrestrial	motile
Abensperg-Traun et al 1996	richness	.	ns	ants	animal	terrestrial	motile
Abensperg-Traun et al 1996	richness	0.619	positive	beetles	animal	terrestrial	motile
Abensperg-Traun et al 1996	diversity	0.374	negative	termites	animal	terrestrial	motile
Abensperg-Traun et al 1996	diversity	0.391	positive	beetles	animal	terrestrial	motile
Abensperg-Traun et al 1996	diversity	0.354	positive	ants	animal	terrestrial	motile
Absalao 1991	diversity	0.177	negative	molluscs	animal	aquatic	sessile
Absalao 1991	evenness	.	ns	molluscs	animal	aquatic	sessile
Aide et al. 1995	richness	0.922	positive	forest	plant	terrestrial	sessile
Aide et al. 1995	richness	0.894	positive	forest	plant	terrestrial	sessile
Ambrose 1993	richness	.	ns	marine soft-bottom community	animal	aquatic	mixed
Ambrose 1993	diversity	.	negative	marine soft-bottom community	animal	aquatic	mixed
Ambrose 1993	evenness	.	ns	marine soft-bottom community	animal	aquatic	mixed
Anderson 1992	richness	0.904	positive	benthic invertebrates	animal	aquatic	motile
Armesto & Pickett 1985	richness	.	ns	field vegetation	plant	terrestrial	sessile
Armesto & Pickett 1985	richness	.	positive	field vegetation	plant	terrestrial	sessile
Aronson & Precht 1995	richness	0.128	ns	corals	animal	aquatic	sessile
Aronson & Precht 1995	diversity	0.599	peaked	corals	animal	aquatic	sessile
Aronson & Precht 1995	evenness	0.423	peaked	corals	animal	aquatic	sessile
Ayling 1981	richness	0.836	ns	encrusting species	animal	aquatic	sessile

Sheet 2

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Bailey 1988	richness	0.398	positive	fingernail clams	animal	aquatic	motile
Bailey 1988	richness	0.467	negative	macrophytes	plant	aquatic	sessile
Bestelmeyer & Wiens 1996	richness	0.52	negative	ants (ground foraging)	animal	terrestrial	motile
Bestelmeyer & Wiens 1996	richness	0.71	U	.	animal	terrestrial	.
Bestelmeyer & Wiens 1996	diversity	0.611	U	.	animal	terrestrial	.
Bunnell 1995	richness	0.45	positive	forest vertebrates	animal	terrestrial	motile
Carpenter 1981	richness	0.75	peaked	benthic algae	plant	aquatic	sessile
Cohen et al 1993	richness	.	ns	diatoms	plant	aquatic	motile
Cohen et al 1993	richness	.	negative	ostracods	animal	aquatic	motile
Cohen et al 1993	richness	.	ns	ostracods	animal	aquatic	motile
Cohen et al. 1995	richness	.	ns	fernland vegetation	plant	terrestrial	sessile
Cohen et al. 1995	diversity	.	peaked	fernland vegetation	plant	terrestrial	sessile
Collins 1992	diversity	0.42	negative	field vegetation	plant	terrestrial	sessile
Collins et al. 1995	richness	0.173	peaked	tallgrass prairie perennials	plant	terrestrial	sessile
Collins et al. 1995	richness	0.474	negative	tallgrass prairie perennials	plant	terrestrial	sessile
Collins et al. 1995	richness	0.44	negative	tallgrass prairie perennials	plant	terrestrial	sessile
Costello 1944	richness	0.855	ns	old field vegetation	plant	terrestrial	sessile
Costello 1944	richness	0.753	ns	old field vegetation	plant	terrestrial	sessile
Costello 1944	richness	0.973	peaked	old field vegetation	plant	terrestrial	sessile
Costello 1944	diversity	0.86	ns	old field vegetation	plant	terrestrial	sessile
Costello 1944	diversity	0.754	ns	old field vegetation	plant	terrestrial	sessile
Costello 1944	diversity	0.978	peaked	old field vegetation	plant	terrestrial	sessile
Costello 1944	evenness	0.799	ns	old field vegetation	plant	terrestrial	sessile

Sheet 3

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Costello 1944	evenness	0.855	ns	old field vegetation	plant	terrestrial	sessile
Costello 1944	evenness	0.993	peaked	old field vegetation	plant	terrestrial	sessile
Curtin 1995	richness	0.92	peaked	subalpine vegetation	plant	terrestrial	sessile
de las Heras et al. 1995	richness	0.691	positive	forest bryophytes	plant	terrestrial	sessile
de las Heras et al. 1995	diversity	0.769	positive	forest bryophytes	plant	terrestrial	sessile
de las Heras et al. 1995	evenness	0.782	positive	forest bryophytes	plant	terrestrial	sessile
de las Heras-Ibanez et al. 1992	richness	0.887	positive	forest bryophytes	plant	terrestrial	sessile
Dean & Connell 1987	richness	0.749	positive	marine invertebrates	animal	aquatic	motile
Dean & Connell 1987	diversity	0.377	positive	marine invertebrates	animal	aquatic	motile
Death & Winterbourn 1995	richness	0.659	negative	benthic invertebrates	animal	aquatic	motile
Doeg etal 1989	richness	0.692	positive	benthic invertebrates	animal	aquatic	motile
Dudgeon 1991	richness	0.013	ns	benthic invertebrates	animal	aquatic	motile
Dudgeon 1991	richness	0.095	ns	benthic invertebrates	animal	aquatic	motile
Dudgeon 1991	richness	0.055	ns	benthic invertebrates	animal	aquatic	motile
Dudgeon 1991	richness	0.25	positive	benthic invertebrates	animal	aquatic	motile
Elliott & Swank 1994	richness	0.748	ns	forest trees	plant	terrestrial	sessile
Elliott & Swank 1994	diversity	0.751	ns	forest trees	plant	terrestrial	sessile
Elliott & Swank 1994	evenness	0.999	negative	forest trees	plant	terrestrial	sessile
Fox 1981	richness	.	ns	arctic vegetation	plant	terrestrial	sessile
Fox 1981	diversity	.	peaked	arctic vegetation	plant	terrestrial	sessile
Fox 1985	richness	0.488	peaked	arctic vegetation	plant	terrestrial	sessile
Fox 1985	diversity	0.585	positive	arctic vegetation	plant	terrestrial	sessile
Fox 1992	richness	0.067	ns	arctic vegetation	plant	terrestrial	sessile

Sheet 4

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Fox 1992	diversity	0.31	positive	arctic vegetation	plant	terrestrial	sessile
Gaedeke & Sommer 1986	diversity	0.738	negative	phytoplankton	plant	aquatic	sessile
Gutterman et al. 1990	richness	0.152	peaked	desert vegetation	plant	terrestrial	sessile
Halpern & Spies 1995	richness	0.665	positive	forest vegetation	plant	terrestrial	sessile
Halpern & Spies 1995	richness	0.869	positive	forest vegetation	plant	terrestrial	sessile
Halpern & Spies 1995	diversity	0.501	peaked	forest vegetation	plant	terrestrial	sessile
Halpern & Spies 1995	diversity	0.691	peaked	forest vegetation	plant	terrestrial	sessile
Hiura 1995	richness	0.556	peaked	trees	plant	terrestrial	sessile
Hiura 1995	richness	0.036	ns	trees	plant	terrestrial	sessile
Hiura 1995	diversity	0.403	negative	trees	plant	terrestrial	sessile
Hiura 1995	diversity	0.036	ns	trees	plant	terrestrial	sessile
Hiura 1995	evenness	0.025	ns	trees	plant	terrestrial	sessile
Hiura 1995	evenness	0.334	negative	trees	plant	terrestrial	sessile
Huntly & Inouye 1987	richness	0.167	ns	small mammals	animal	terrestrial	motile
Inouye 1987	richness	0.326	positive	old field vegetation	plant	terrestrial	sessile
Jackson & Fox 1996	richness	.	ns	ants	animal	terrestrial	motile
Jackson & Fox 1996	richness	.	positive	ants	animal	terrestrial	motile
Jackson & Fox 1996	richness	.	peaked	ants	animal	terrestrial	motile
Jonsson & Esseen 1990	richness	0.087	ns	bryophytes	plant	terrestrial	sessile
Jonsson & Esseen 1990	diversity	0.171	negative	bryophytes	plant	terrestrial	sessile
Jonsson & Esseen 1990	evenness	0.147	negative	bryophytes	plant	terrestrial	sessile
Jullien & Thiollay 1996	richness	.	ns	rain forest raptors	animal	terrestrial	motile
Jullien & Thiollay 1996	diversity	.	ns	rain forest raptors	animal	terrestrial	motile

Sheet 5

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Jullien & Thiollay 1996	evenness	.	ns	rain forest raptors	animal	terrestrial	motile
Keddy 1983	richness	.	peaked	shore vegetation	plant	terrestrial	sessile
Keddy 1985	richness	.	positive	shore vegetation	plant	terrestrial	sessile
Keeley et al 1981	richness	0.723	negative	chaparral herb. flora	plant	terrestrial	sessile
Kitahara & Fujii 1994	richness	.	negative	butterflies	animal	terrestrial	motile
Kitahara & Fujii 1994	diversity	.	negative	butterflies	animal	terrestrial	motile
Kitahara & Fujii 1994	evenness	.	negative	butterflies	animal	terrestrial	motile
Kukert & Smith 1992	richness	0.57	positive	deep sea sediment community	animal	aquatic	mixed
Lake & Doeg 1985	richness	0.549	positive	stream macroinvertebrates	animal	aquatic	motile
Lake & Doeg 1985	diversity	0.498	positive	stream macroinvertebrates	animal	aquatic	motile
Lake & Doeg 1985	evenness	0.266	ns	stream macroinvertebrates	animal	aquatic	motile
Lake etal 1989	richness	.	ns	benthic macroinvertebrates	animal	aquatic	motile
Lake etal 1989	richness	0.337	ns	benthic macroinvertebrates	animal	aquatic	motile
Lake etal 1989	diversity	.	ns	benthic macroinvertebrates	animal	aquatic	motile
Lamberti et al. 1991	richness	0.819	peaked	benthic macroinvertebrates	animal	aquatic	motile
Lubchenco 1978	richness	0.723	peaked	tide pool algae	plant	aquatic	sessile
Lubchenco 1978	richness	0.773	negative	emergent substrata algae	plant	aquatic	sessile
Lubchenco 1978	diversity	0.626	ns	tide pool algae	plant	aquatic	sessile
Lubchenco 1978	diversity	0.94	negative	emergent substrata algae	plant	aquatic	sessile
Lubchenco 1978	evenness	0.51	ns	tide pool algae	plant	aquatic	sessile
Lubchenco 1978	evenness	0.968	negative	emergent substrata algae	plant	aquatic	sessile
Lubchenco & Menge 1978	richness	0.578	ns	intertidal invertebrates	animal	aquatic	sessile
Martinsen et al. 1990	diversity	0.665	peaked	shortgrass prairie	plant	terrestrial	sessile

Sheet 6

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Martinsen et al. 1990	diversity	0.655	positive	shortgrass prairie	plant	terrestrial	sessile
McIntyre & Lavorel 1994	richness	0.08	peaked	grassy vegetation	plant	terrestrial	sessile
McIntyre & Lavorel 1994	richness	0.114	negative	grassy vegetation	plant	terrestrial	sessile
McIntyre et al 1995	richness	0.032	ns	herbaceous vegetation	plant	terrestrial	sessile
McIntyre et al 1995	richness	0.036	ns	herbaceous vegetation	plant	terrestrial	sessile
McIntyre et al 1995	richness	0.53	negative	herbaceous vegetation	plant	terrestrial	sessile
McIntyre et al 1995	richness	0.096	negative	herbaceous vegetation	plant	terrestrial	sessile
Mehlman 1992	richness	0.446	positive	second growth pineland	plant	terrestrial	sessile
Mehlman 1992	richness	0.44	negative	second growth pineland	plant	terrestrial	sessile
Meier et al. 1981	richness	0.43	negative	forest herbs	plant	terrestrial	sessile
Mook 1981	richness	.	ns	fouling community	animal	aquatic	sessile
Mook 1981	diversity	.	negative	fouling community	animal	aquatic	sessile
Morgan & Freedman 1986	richness	0.291	positive	birds	animal	terrestrial	motile
Morgan & Freedman 1986	diversity	0.533	positive	birds	animal	terrestrial	motile
Morneau & Payette 1989	richness	0.728	peaked	lichen-spruce woodland	plant	terrestrial	sessile
Morneau & Payette 1989	diversity	0.889	peaked	lichen-spruce woodland	plant	terrestrial	sessile
Morneau & Payette 1989	evenness	0.886	negative	lichen-spruce woodland	plant	terrestrial	sessile
Muotka & Virtanen 1995	richness	0.001	ns	bryophytes	plant	aquatic	sessile
Nilsson 1987	richness	.	positive	stream edge vegetation	plant	terrestrial	sessile
Nilsson 1987	richness	0.273	peaked	stream edge vegetation	plant	aquatic	sessile
Paine & Levin 1981	richness	0.622	peaked	intertidal invertebrates	animal	aquatic	sessile
Paine & Levin 1981	diversity	0.417	ns	intertidal invertebrates	animal	aquatic	sessile
Paine & Levin 1981	evenness	0.252	ns	intertidal invertebrates	animal	aquatic	sessile

Sheet 7

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Pandey & Singh 1984/1985	richness	0.831	positive	forest herbs	plant	terrestrial	sessile
Pandey & Singh 1984/1985	richness	0.694	ns	forest shrubs	plant	terrestrial	sessile
Pandey & Singh 1984/1985	diversity	0.707	ns	forest herbs	plant	terrestrial	sessile
Pandey & Singh 1984/1985	diversity	0.952	ns	forest shrubs	plant	terrestrial	sessile
Pandey & Singh 1984/1985	evenness	0.736	ns	forest shrubs	plant	terrestrial	sessile
Pandey & Singh 1984/1985	evenness	1	peaked	forest shrubs	plant	terrestrial	sessile
Parker 1989	richness	0.386	ns	small mammals	animal	terrestrial	motile
Parker 1989	diversity	0.092	ns	small mammals	animal	terrestrial	motile
Parker 1989	evenness	0.192	ns	small mammals	animal	terrestrial	motile
Pearson & Jones 1975	richness	0.129	ns	stream benthos	animal	aquatic	motile
Phillips et al 1994	richness	0.306	positive	trees	plant	terrestrial	sessile
Raphael et al. 1987	richness	0.538	U	forest birds	animal	terrestrial	motile
Reice 1984	richness	.	ns	lotic invertebrates	animal	aquatic	motile
Reice 1984	diversity	.	ns	lotic invertebrates	animal	aquatic	motile
Rosser & Pearson 1995	richness	.	negative	benthic macroinvertebrates	animal	aquatic	motile
Rosser & Pearson 1995	richness	.	negative	benthic macroinvertebrates	animal	aquatic	motile
Roxburgh et al 1988	richness	0.97	U	alpine cushion field	plant	terrestrial	sessile
Sakai & Sulak 1985	richness	0.76	ns	forest vegetation	plant	terrestrial	sessile
Saldarriaga et al. 1988	richness	0.593	positive	tropical moist forest	plant	terrestrial	sessile
Saldarriaga et al. 1988	diversity	0.695	positive	tropical moist forest	plant	terrestrial	sessile
Saldarriaga et al. 1988	evenness	0.663	positive	tropical moist forest	plant	terrestrial	sessile
Sammarco 1982	richness	0.9	negative	algae	plant	aquatic	sessile
Sammarco 1982	diversity	0.901	negative	algae	plant	aquatic	sessile

Sheet 8

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Sammarco 1982	evenness	.	negative	algae	plant	aquatic	sessile
Shackleton etal 1994	richness	.	negative	vegetation	plant	terrestrial	sessile
Shafi & Yarranton 1973	richness	0.328	ns	forest vegetation	plant	terrestrial	sessile
Shafi & Yarranton 1973	diversity	0.457	ns	forest vegetation	plant	terrestrial	sessile
Shafi & Yarranton 1973	evenness	0.37	ns	forest vegetation	plant	terrestrial	sessile
Smith et al 1996	richness	.	ns	lizards	animal	terrestrial	motile
Sommer 1995	richness	0.267	ns	phytoplankton	plant	aquatic	sessile
Sommer 1995	diversity	0.414	ns	phytoplankton	plant	aquatic	sessile
Sommer 1995	evenness	0.601	ns	phytoplankton	plant	aquatic	sessile
Sousa 1979	richness	.	peaked	algal community	plant	aquatic	sessile
Sousa 1979	richness	.	negative	algal community	plant	aquatic	sessile
Sousa 1979	diversity	.	peaked	algal community	plant	aquatic	sessile
Sousa 1979	diversity	.	peaked	algal community	plant	aquatic	sessile
Steinman & Lamberti 1988	richness	0.548	negative	lotic algae	plant	aquatic	sessile
Steinman & Lamberti 1988	diversity	0.561	negative	lotic algae	plant	aquatic	sessile
Stone & Wolfe 1996	richness	0.592	positive	understory vegetation	plant	terrestrial	sessile
Stone & Wolfe 1996	diversity	0.55	positive	understory vegetation	plant	terrestrial	sessile
Stone & Wolfe 1996	evenness	0.068	ns	understory vegetation	plant	terrestrial	sessile
Swamikannu & Hoagland 1972	richness	0.739	negative	algae	plant	aquatic	sessile
Swamikannu & Hoagland 1972	diversity	0.841	negative	algae	plant	aquatic	sessile
Swamikannu & Hoagland 1972	evenness	0.794	negative	algae	plant	aquatic	sessile
Tester 1989	richness	0.179	ns	oak savanna	plant	terrestrial	sessile
Tester 1989	richness	0.818	positive	oak savanna	plant	terrestrial	sessile

Sheet 9

Paper	SD Metric	r2	Category	Community	Anim_Plant	Terr_Aqua	Sess_Motile
Tester 1989	richness	0.402	negative	oak savanna	plant	terrestrial	sessile
Thorp & Cothran 1984	richness	0.127	peaked	benthic invertebrates	animal	aquatic	motile
Thorp & Cothran 1984	diversity	0.113	positive	benthic invertebrates	animal	aquatic	motile
Thorp & Cothran 1984	evenness	0.076	ns	benthic invertebrates	animal	aquatic	motile
Uhl 1987	richness	0.994	positive	vegetation	plant	terrestrial	sessile
Uhl 1987	diversity	0.821	ns	vegetation	plant	terrestrial	sessile
Uhl et al 1981	richness	0.988	positive	vegetation	plant	terrestrial	sessile
Valiela & Rietsma 1995	richness	0.534	ns	salt marsh vegetation	plant	aquatic	sessile
Wilson & Keddy 1988	richness	0.16	peaked	shore vegetation	plant	terrestrial	sessile
Wilson & Shay 1990	richness	.	ns	mixed grass prairie	plant	terrestrial	sessile
Wilson & Shay 1990	diversity	.	ns	mixed grass prairie	plant	terrestrial	sessile
Wilson & Tilman 1991	richness	0.894	negative	old field vegetation	plant	terrestrial	sessile
Wilson & Tilman 1991	diversity	0.863	negative	old field vegetation	plant	terrestrial	sessile

Sheet 10

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
motile consumers	.	sedimentation	abiotic	abiotic	intensity	spatial	natural
motile consumers	.	sedimentation	abiotic	abiotic	intensity	spatial	natural
sessile producers	.	time since last cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	.	time since last cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
.	.	predation/substrate disturbance	biotic	biotic	intensity	spatial	natural
.	.	predation/substrate disturbance	biotic	biotic	intensity	spatial	natural
.	.	predation/substrate disturbance	biotic	biotic	intensity	spatial	natural
motile consumers	.	time since mud flow	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	820	vegetation clipping	biotic	.	intensity	spatial	anthropogenic
sessile producers	820	vegetation clipping	biotic	.	intensity	spatial	anthropogenic
.	.	topographic complexity	abiotic	abiotic	frequency*intensity	spatial	natural
.	.	topographic complexity	abiotic	abiotic	frequency*intensity	spatial	natural
.	.	topographic complexity	abiotic	abiotic	frequency*intensity	spatial	natural
.	.	% area disturbed annually	biotic	biotic	intensity	spatial	natural
motile consumers	.	wind/current induced exposure	abiotic	abiotic	intensity	spatial	natural

Sheet 11

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
sessile producers	.	wind/current induced exposure	abiotic	abiotic	intensity	spatial	natural
motile consumers	600	cattle/goat grazing	biotic	.	intensity	spatial	anthropogenic
motile consumers	600	cattle/goat grazing	biotic	.	intensity	spatial	anthropogenic
motile consumers	600	cattle/goat grazing	biotic	.	intensity	spatial	anthropogenic
motile consumers	.	fire frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	urchin grazing	biotic	biotic	intensity	spatial	natural
.	.	logging sedimentation	abiotic	.	intensity	spatial	anthropogenic
motile consumers	.	logging sedimentation	abiotic	.	intensity	spatial	anthropogenic
motile consumers	.	logging sedimentation	abiotic	.	intensity	spatial	anthropogenic
sessile producers	1250	soil disturbance	biotic	.	intensity	spatial	anthropogenic
sessile producers	1250	soil disturbance	biotic	.	intensity	spatial	anthropogenic
sessile producers	800	burn frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	800	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	800	fire frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	800	fire frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic

Sheet 12

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
sessile producers	340	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	275	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	.	time since boulder rolled	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	.	time since boulder rolled	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	.	stream stability	abiotic	abiotic	frequency*intensity	spatial	natural
motile consumers	.	kicking/raking substratum	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	immersion in formalin	abiotic	.	intensity	spatial	anthropogenic
motile consumers	.	immersion in formalin	abiotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	immersion in formalin	abiotic	.	intensity	spatial	anthropogenic
motile consumers	.	immersion in formalin	abiotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	930	time since clearcut	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	930	time since clearcut	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	930	time since clearcut	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	225	soil frost	abiotic	abiotic	intensity	spatial	natural
sessile producers	225	soil frost	abiotic	abiotic	intensity	spatial	natural
sessile producers	225	proportion soil disturbed	biotic	biotic	intensity	spatial	natural
sessile producers	225	proportion soil disturbed	biotic	biotic	frequency*intensity	spatial	natural
sessile producers	225	proportion soil disturbed	abiotic	abiotic	intensity	spatial	natural
sessile producers	225	proportion soil disturbed	abiotic	abiotic	intensity	spatial	natural

Sheet 13

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
.	.	dilution	abiotic	.	frequency*intensity	spatial	anthropogenic
sessile producers	100	time since porcupine digging	biotic	biotic	time since last disturbance	temporal	natural
sessile producers	400	harvest/burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	400	harvest/burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	400	harvest/burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	400	harvest/burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	.	windthrow	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	windthrow	abiotic	abiotic	intensity	spatial	natural
sessile producers	.	windthrow	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	windthrow	abiotic	abiotic	intensity	spatial	natural
sessile producers	.	windthrow	abiotic	abiotic	intensity	spatial	natural
sessile producers	.	windthrow	abiotic	abiotic	frequency	spatial	natural
motile consumers	675	time since last cultivated	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	650	time since cultivation	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	800	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	800	time since mining	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	800	time since clearing	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	375	uprooting patch age	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	375	uprooting patch age	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	375	uprooting patch age	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	1250	deforestation	biotic	.	intensity	spatial	anthropogenic
motile consumers	1250	deforestation	biotic	.	intensity	spatial	anthropogenic
motile consumers	1250	deforestation	biotic	.	intensity	spatial	anthropogenic

Sheet 14

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
sessile producers	600	wave exposure	abiotic	abiotic	frequency	spatial	natural
sessile producers	600	wave exposure	abiotic	abiotic	frequency	spatial	natural
sessile producers	250	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	850	degree of human disturbance	biotic	.	intensity	spatial	anthropogenic
motile consumers	850	degree of human disturbance	biotic	.	intensity	spatial	anthropogenic
motile consumers	850	degree of human disturbance	biotic	.	intensity	spatial	anthropogenic
.	.	sediment mounds	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	time since dist	abiotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	time since dist	abiotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	time since dist	abiotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	kicking/raking substratum	biotic	.	frequency	spatial	anthropogenic
motile consumers	.	kicking/raking substratum	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	kicking/raking substratum	biotic	.	frequency	spatial	anthropogenic
motile consumers	.	flood/landslide	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	.	snail density	biotic	biotic	intensity	spatial	natural
sessile producers	.	snail density	biotic	biotic	intensity	spatial	natural
sessile producers	.	snail density	biotic	biotic	intensity	spatial	natural
sessile producers	.	snail density	biotic	biotic	intensity	spatial	natural
sessile producers	.	snail density	biotic	biotic	intensity	spatial	natural
sessile producers	.	snail density	biotic	biotic	intensity	spatial	natural
.	.	wave exposure	abiotic	abiotic	intensity	spatial	natural
sessile producers	220	disturbance age	biotic	biotic	time since last disturbance	temporal	natural
sessile producers	220	gopher disturbance	biotic	biotic	intensity	spatial	natural

Sheet 15

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
sessile producers	525	grazing	biotic	.	intensity	spatial	anthropogenic
sessile producers	525	soil disturbance; vehicle use	biotic	.	intensity	spatial	anthropogenic
sessile producers	600	soil disturbance	biotic	.	frequency*intensity	spatial	anthropogenic
sessile producers	600	grazing	biotic	biotic	frequency*intensity	spatial	natural
sessile producers	600	soil disturbance	biotic	.	frequency*intensity	spatial	anthropogenic
sessile producers	600	grazing	biotic	biotic	frequency*intensity	spatial	natural
sessile producers	1000	fire frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	1000	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	920	logging intensity	biotic	.	intensity	spatial	anthropogenic
motile consumers	.	% cover removed	biotic	.	intensity	spatial	anthropogenic
motile consumers	.	% cover removed	biotic	.	intensity	spatial	anthropogenic
motile consumers	600	clearcutting	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	600	clearcutting	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	400	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	.	substrate instability	abiotic	abiotic	frequency	spatial	natural
sessile producers	360	current velocity	abiotic	abiotic	intensity	spatial	natural
sessile producers	.	current velocity	abiotic	abiotic	intensity	spatial	natural
.	.	time since patch formation	biotic	biotic	time since last disturbance	temporal	natural
.	.	time since disturbance	biotic	biotic	time since last disturbance	temporal	natural
.	.	time since disturbance	biotic	biotic	time since last disturbance	temporal	natural
sessile producers	.	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural

Sheet 16

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
sessile producers	.	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	.	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	.	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	.	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	.	time since landslide	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	600	time since clearcut/plantation	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	600	time since clearcut/plantation	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	600	time since clearcut/plantation	biotic	.	time since last disturbance	temporal	anthropogenic
motile consumers	.	time since dredging	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	.	tree mortality; turnover	abiotic	abiotic	frequency*intensity	spatial	natural
motile consumers	300	time since forest burn	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	.	rock tumbling frequency	abiotic	.	frequency	spatial	anthropogenic
motile consumers	.	rock tumbling frequency	abiotic	.	frequency	spatial	anthropogenic
motile consumers	.	substratum movement	abiotic	.	intensity	spatial	anthropogenic
motile consumers	.	substratum movement	abiotic	.	intensity	spatial	anthropogenic
sessile producers	700	bulldozing & soil deposition	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	700	time since burn/logging	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	1175	time since slash & burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	1175	time since slash & burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	1175	time since slash & burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	.	echinoid predation	biotic	biotic	intensity	spatial	natural
sessile producers	.	echinoid predation	biotic	biotic	intensity	spatial	natural
sessile producers	.	echinoid predation	biotic	biotic	intensity	spatial	natural

Sheet 17

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
sessile producers	600	logging/cutting	biotic	.	frequency*intensity	spatial	anthropogenic
sessile producers	490	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	490	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
sessile producers	490	time since fire	abiotic	abiotic	time since last disturbance	temporal	natural
motile consumers	350	livestock grazing	biotic	.	frequency*intensity	spatial	anthropogenic
.	.	dilution frequency	abiotic	.	frequency	spatial	anthropogenic
.	.	dilution frequency	abiotic	.	frequency	spatial	anthropogenic
.	.	dilution frequency	abiotic	.	frequency	spatial	anthropogenic
sessile producers	.	boulder movement	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	boulder movement	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	boulder movement	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	boulder movement	abiotic	abiotic	frequency	spatial	natural
sessile producers	.	volcanic eruption	abiotic	abiotic	intensity	spatial	natural
sessile producers	.	volcanic eruption	abiotic	abiotic	intensity	spatial	natural
sessile producers	275	mountain pine beetle	biotic	biotic	intensity	spatial	natural
sessile producers	275	mountain pine beetle	biotic	biotic	intensity	spatial	natural
sessile producers	275	mountain pine beetle	biotic	biotic	intensity	spatial	natural
sessile producers	.	grazing intensity	biotic	biotic	intensity	spatial	natural
sessile producers	.	grazing intensity	biotic	biotic	intensity	spatial	natural
sessile producers	.	grazing intensity	biotic	biotic	intensity	spatial	natural
sessile producers	650	fire frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	650	fire frequency	abiotic	abiotic	frequency	spatial	natural
sessile producers	650	fire frequency	abiotic	abiotic	frequency	spatial	natural

Sheet 18

Sess_Motile_2	AET	Disturbance	Abio_Bio	Abio_Bio_2	Disturbance gradient	Spat_Temp	Anth_Nat
motile consumers	.	dragonfly predation intensity	biotic	biotic	intensity	spatial	natural
motile consumers	.	dragonfly predation intensity	biotic	biotic	intensity	spatial	natural
motile consumers	.	dragonfly predation intensity	biotic	biotic	intensity	spatial	natural
sessile producers	1200	time since slash/burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	1200	time since slash/burn	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	700	time since cutting/burning	biotic	.	time since last disturbance	temporal	anthropogenic
sessile producers	.	damage by wrack mats	abiotic	abiotic	intensity	spatial	natural
sessile producers	600	exposure to wave action	abiotic	abiotic	frequency	spatial	natural
sessile producers	450	fire	abiotic	.	frequency	spatial	anthropogenic
sessile producers	450	fire	abiotic	.	frequency	spatial	anthropogenic
sessile producers	650	tillage	biotic	.	intensity	spatial	anthropogenic
sessile producers	650	tillage	biotic	.	intensity	spatial	anthropogenic

Sheet 19

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	2	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	2	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	100	3	29	mosaic	.	observational	habitat
chronic	non-exhaustive	.	3	44	single patch	.	observational	both
chronic	non-exhaustive	.	3	44	single patch	.	observational	both
episodic	non-exhaustive	367	6	6	single patch	60	observational	habitat
episodic	non-exhaustive	367	6	6	single patch	60	observational	habitat
episodic	exhaustive	0.00396	3	9	mosaic	.	experimental/manipulative	biomass
episodic	exhaustive	0.00396	3	9	mosaic	.	experimental/manipulative	biomass
episodic	exhaustive	0.00396	3	9	mosaic	.	experimental/manipulative	biomass
episodic	.	.	10	10	single patch	9	observational	both
episodic	exhaustive	0.25	5	50	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	0.25	5	50	single patch	.	experimental/manipulative	biomass
chronic	exhaustive	10	19	19	mosaic	.	observational	biomass
chronic	exhaustive	10	20	20	mosaic	.	observational	biomass
chronic	exhaustive	10	20	20	mosaic	.	observational	biomass

Sheet 20

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
chronic	.	2.5	4	4	mosaic	.	observational	biomass
chronic	.	.	11	41	single patch	.	observational	biomass
chronic	exhaustive	2.36	11	41	single patch	.	observational	biomass
chronic	non-exhaustive	.	4	128	mosaic	.	observational	habitat
chronic	non-exhaustive	.	4	640	mosaic	.	observational	habitat
chronic	non-exhaustive	.	4	128	mosaic	.	observational	habitat
episodic	non-exhaustive	.	9	9	mosaic	.	observational	habitat
chronic	.	0.0002	3	12	single patch	.	experimental/manipulative	biomass
chronic	non-exhaustive	.	3	30	single patch	.	observational	biomass
chronic	non-exhaustive	.	3	39	single patch	.	observational	biomass
chronic	non-exhaustive	.	3	20	single patch	.	observational	biomass
episodic	exhaustive	2.25	3	27	single patch	.	experimental/manipulative	habitat
episodic	exhaustive	2.25	3	27	single patch	.	experimental/manipulative	habitat
episodic	non-exhaustive	10	9	19	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	200	18	73	single patch	17	experimental/manipulative	biomass
episodic	non-exhaustive	250	7	16	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	200	9	19	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass

Sheet 21

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	non-exhaustive	9.29	6	6	single patch	35	observational	biomass
episodic	exhaustive	8	11	11	single patch	44	observational	both
episodic	non-exhaustive	10.25	7	7	single patch	3	observational	biomass
episodic	non-exhaustive	20.5	7	7	single patch	3	observational	biomass
episodic	non-exhaustive	20.5	7	7	single patch	3	observational	biomass
episodic	.	5	6	6	single patch	19	observational	biomass
episodic	exhaustive	0.01	3	126	single patch	5	observational	biomass
episodic	exhaustive	0.01	3	126	single patch	5	observational	biomass
chronic	exhaustive	.	11	55	mosaic	.	observational	biomass
episodic	subsample	0.25	5	10	single patch	0.192	experimental/manipulative	both
episodic	exhaustive	.	4	96	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	.	7	96	single patch	0.178	experimental/manipulative	biomass
episodic	exhaustive	0.13	4	112	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	0.13	7	112	single patch	0.178	experimental/manipulative	biomass
episodic	non-exhaustive	.	4	4	single patch	22	observational	biomass
episodic	non-exhaustive	.	4	4	single patch	22	observational	biomass
episodic	non-exhaustive	.	4	4	single patch	22	observational	biomass
chronic	non-exhaustive	.	17	.	mosaic	.	observational	biomass
chronic	non-exhaustive	.	17	.	mosaic	.	observational	biomass
chronic	exhaustive	0.1	12	37	single patch	.	observational	biomass
chronic	exhaustive	0.1	12	34	single patch	.	observational	biomass

Sheet 22

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
chronic	non-exhaustive	7.5	21	21	mosaic	.	observational	biomass
chronic	non-exhaustive	7.5	21	21	mosaic	.	observational	biomass
chronic	non-exhaustive	.	7	28	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	0.01	48	64	single patch	.	observational	both
episodic	non-exhaustive	516	15	15	mosaic	24	observational	biomass
episodic	non-exhaustive	236	17	17	mosaic	27	observational	biomass
episodic	exhaustive	516	15	15	mosaic	24	observational	biomass
episodic	exhaustive	236	17	17	mosaic	27	observational	biomass
episodic	point or all	.	16	16	mosaic	.	observational	biomass
episodic	point or all	.	18	18	mosaic	.	observational	biomass
episodic	point or all	.	16	16	mosaic	.	observational	biomass
episodic	point or all	.	18	18	mosaic	.	observational	biomass
episodic	point or all	.	18	18	mosaic	.	observational	biomass
episodic	point or all	.	16	16	mosaic	.	observational	biomass
episodic	non-exhaustive	3000	14	18	single patch	55	observational	both
episodic	exhaustive	50	15	22	single patch	55	experimental/manipulative	habitat
episodic	non-exhaustive	.	4	9	single patch	17	observational	habitat
episodic	non-exhaustive	.	4	10	single patch	17	observational	habitat
episodic	non-exhaustive	.	4	8	single patch	17	observational	habitat
episodic	exhaustive	0.24	23	36	single patch	173	observational	habitat
episodic	exhaustive	0.24	23	36	single patch	173	observational	habitat
episodic	exhaustive	0.24	23	36	single patch	173	observational	habitat
episodic	non-exhaustive	32800000	6	6	mosaic	.	observational	habitat

Sheet 23

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
episodic	non-exhaustive	32800000	6	6	mosaic	.	observational	habitat
episodic	non-exhaustive	32800000	6	6	mosaic	.	observational	habitat
chronic	exhaustive	20	25	25	?????	.	observational	biomass
chronic	exhaustive	0.25	25	75	single patch	.	observational	biomass
episodic	non-exhaustive	.	7	7	single patch	15	observational	biomass
chronic	non-exhaustive	10560	9	9	mosaic	.	observational	habitat
chronic	non-exhaustive	10560	9	9	mosaic	.	observational	habitat
chronic	non-exhaustive	10560	9	9	mosaic	.	observational	habitat
episodic	exhaustive	0.03	8	11	single patch	1.92	experimental/manipulative	both
episodic	exhaustive	.	8	16	single patch	0.088	experimental/manipulative	biomass
episodic	exhaustive	.	8	15	single patch	0.088	experimental/manipulative	biomass
episodic	exhaustive	.	8	15	single patch	0.088	experimental/manipulative	biomass
episodic	non-exhaustive	0.05	3	11	single patch	.	experimental/manipulative	both
episodic	non-exhaustive	0.25	7	14	single patch	0.192	experimental/manipulative	both
episodic	non-exhaustive	0.05	3	11	single patch	.	experimental/manipulative	both
episodic	non-exhaustive	0.765	8	24	single patch	2.041	observational	habitat
chronic	non-exhaustive	1	8	8	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	2.5	6	6	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	1	8	8	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	2.5	6	6	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	1	8	8	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	2.5	6	6	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	2.5	5	5	mosaic	.	observational	biomass

Sheet 24

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
episodic	non-exhaustive	4	3	21	single patch	.	observational	both
chronic	non-exhaustive	4	21	21	mosaic	.	observational	habitat
chronic	exhaustive	30	3	120	mosaic	.	observational	biomass
chronic	exhaustive	30	3	120	mosaic	.	observational	habitat
chronic	.	30	3	120	mosaic	.	observational	habitat
chronic	.	30	3	120	mosaic	.	observational	habitat
chronic	.	30	3	120	mosaic	.	observational	habitat
chronic	.	30	3	120	mosaic	.	observational	habitat
episodic	.	3000	7	70	single patch	.	experimental/manipulative	biomass
episodic	.	3000	6	70	single patch	13	experimental/manipulative	biomass
episodic	.	1	3	45	single patch	.	observational	habitat
episodic	.	0.0225	4	20	mosaic	.	experimental/manipulative	biomass
episodic	.	0.0225	4	20	mosaic	.	experimental/manipulative	biomass
episodic	non-exhaustive	47000	14	23	single patch	74	observational	habitat
episodic	non-exhaustive	47000	14	23	single patch	74	observational	habitat
episodic	non-exhaustive	1000	8	9	single patch	246	observational	biomass
episodic	non-exhaustive	1000	8	9	single patch	246	observational	biomass
episodic	non-exhaustive	1000	8	9	single patch	246	observational	biomass
episodic	exhaustive	2.34	25	25	mosaic	.	observational	habitat
chronic	exhaustive	.	58	58	single patch	.	observational	biomass
chronic	exhaustive	.	58	58	single patch	.	observational	biomass
episodic	?	1.8	11	11	single patch	8.12	observational	biomass
episodic	?	1.8	11	11	single patch	8.12	observational	biomass

Sheet 25

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
episodic	.	1.8	11	11	single patch	8.12	observational	biomass
episodic	non-exhaustive	45	7	7	single patch	90	observational	both
episodic	exhaustive	375	7	7	single patch	90	observational	both
episodic	non-exhaustive	45	7	7	single patch	90	observational	both
episodic	exhaustive	375	7	7	single patch	90	observational	both
episodic	exhaustive	375	7	7	single patch	90	observational	both
episodic	exhaustive	375	7	7	single patch	90	observational	both
episodic	non-exhaustive	1.55	10	11	single patch	16	observational	habitat
episodic	non-exhaustive	1.55	10	11	single patch	16	observational	habitat
episodic	non-exhaustive	1.55	10	11	single patch	16	observational	habitat
episodic	exhaustive	0.2	6	6	single patch	0.4	experimental/manipulative	habitat
chronic	exhaustive	.	24	24	mosaic	.	observational	biomass
episodic	non-exhaustive	85000	13	13	single patch	20	observational	habitat
episodic	exhaustive	.	3	12	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	.	3	12	single patch	.	experimental/manipulative	biomass
chronic	exhaustive	0.076	4	64	single patch	.	experimental/manipulative	biomass
chronic	exhaustive	0.076	4	64	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	.	5	5	single patch	4	observational	both
episodic	exhaustive	404.4	5	5	single patch	43	observational	biomass
episodic	non-exhaustive	2530	6	23	single patch	.	observational	both
episodic	non-exhaustive	2530	6	23	single patch	.	observational	both
episodic	non-exhaustive	2530	6	23	single patch	.	observational	both
chronic	.	0.129	12	68	mosaic	.	experimental/manipulative	biomass

Sheet 26

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
chronic	.	0.129	12	68	mosaic	.	experimental/manipulative	biomass
chronic	.	0.129	12	68	mosaic	.	experimental/manipulative	biomass
chronic	exhaustive	225	3	36	mosaic	.	observational	biomass
episodic	non-exhaustive	.	15	15	single patch	44	observational	biomass
episodic	non-exhaustive	.	15	15	single patch	44	observational	biomass
episodic	non-exhaustive	.	15	15	single patch	44	observational	biomass
chronic	non-exhaustive	9350	3	26	mosaic	.	observational	habitat
episodic	non-exhaustive	.	5	10	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	.	5	10	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	.	5	10	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	0.25	3	185	single patch	.	observational	biomass
episodic	non-exhaustive	0.25	3	193	single patch	.	observational	biomass
episodic	non-exhaustive	0.25	3	96	single patch	.	observational	biomass
episodic	non-exhaustive	0.25	3	92	single patch	.	observational	biomass
episodic	non-exhaustive	.	3	20	single patch	.	observational	both
episodic	non-exhaustive	.	3	20	single patch	.	observational	both
episodic	exhaustive	50	32	38	mosaic	.	observational	biomass
episodic	exhaustive	50	32	38	mosaic	.	observational	biomass
episodic	exhaustive	50	32	38	mosaic	.	observational	biomass
chronic	non-exhaustive	0.0224	10	10	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	0.0224	10	10	mosaic	.	experimental/manipulative	biomass
chronic	non-exhaustive	0.0224	10	10	mosaic	.	experimental/manipulative	biomass
episodic	non-exhaustive	3570	9	12	single patch	.	experimental/manipulative	biomass

Sheet 27

Chron_Epi	Exh_Part	Quadrat Area	NDL	NSamp	SP_Mosaic	Temp grad	Obs_Exp/manip	Biom_Hab
episodic	exhaustive	12	9	12	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	3570	9	12	single patch	.	experimental/manipulative	biomass
chronic	exhaustive	0.0296	4	132	single patch	.	experimental/manipulative	biomass
chronic	exhaustive	0.0296	4	132	single patch	.	experimental/manipulative	biomass
chronic	exhaustive	0.0296	4	132	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	1500	5	5	single patch	4	observational	biomass
episodic	non-exhaustive	1500	5	5	single patch	4	observational	biomass
episodic	non-exhaustive	40.5	5	5	single patch	1.833	observational	biomass
episodic	non-exhaustive	29000	6	7	mosaic	.	observational	biomass
chronic	exhaustive	0.25	125	243	single patch	.	observational	biomass
episodic	non-exhaustive	1.5	3	60	single patch	.	experimental/manipulative	biomass
episodic	non-exhaustive	1.5	3	60	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	0.5	4	8	single patch	.	experimental/manipulative	biomass
episodic	exhaustive	0.5	4	8	single patch	.	experimental/manipulative	biomass

Appendix 7: COSEWIC–listed species included in analyses for Chapter 3.

	Common Name	Scientific Name
Birds	Acadian flycatcher	*Empidonax virescens*
	American white pelican	*Pelecanus erythrorhynchus*
	Ancient murrelet	*Synthliboramphus antiquus*
	Bald eagle	*Haliaeetus leucocephalus*
	Bicknell's thrush	*Catharus bicknelli*
	Burrowing owl	*Speotyto cunicularia*
	Caspian tern	*Sterna caspia*
	Eskimo curlew	*Numenius borealis*
	Ferruginous hawk	*Buteo regalis*
	Forester's tern	*Sterna forsteri*
	Great auk	*Pinguinus impennis*
	Great blue heron	*Ardea herodias*
	Greater Prairie-chicken	*Tympanuchus cupido*
	Henslow's sparrow	*Ammodramus henslowii*
	Hooded warbler	*Wilsonia citrina*
	Ivory gull	*Pagophila eburnea*
	King rail	*Rallus elegans*
	Labrador duck	*Camptorhynchus labradorius*
	Least bittern	*Ixobrychus exilis*
	Lewis' woodpecker	*Melanerpes lewis*
	Loggerhead shrike	*Lanius ludovicianus*
	Long-billed curlew	*Numenius americanus*
	Louisiana waterthrush	*Seiurus motacilla*
	Northern bobwhite	*Colinus virginianus*
	Passenger pigeon	*Ectopistes migratorius*
	Peregrine falcon	*Falco peregrinus*
	Piping plover	*Charadrius melodus*
	Prairie warbler	*Dendroica discolor*
	Prothonotary warbler	*Prothonotaria citrea*
	Red-headed woodpecker	*Melanerpes erythrocephalus*
	Red-shouldered hawk	*Buteo lineatus*

	Common Name	Scientific Name
	Roseate tern	*Sterna dougallii*
	Sage grouse	*Centrocercus urophasianus*
	Sage thrasher	*Oreoscoptes montanus*
	Spotted owl	*Strix occidentalis*
	Sprague's pipit	*Anthus spragueii*
	Yellow-breasted chat	*Icteria virens*
Mammals	Bison	*Bison bison*
	Caribou	*Rangifer tarandus*
	Gray wolf	*Canis lupus*
	Grey fox	*Urocyon cinereoargenteus*
	Grizzly bear	*Ursus arctos*
	Mountain beaver	*Aplodontia rufa*
	Pacific water shrew	*Sorex bendirii*
	Southern flying squirrel	*Glaucomys volans*
	Swift fox	*Vulpes velox*
	Townsend's mole	*Scapanus townsendii*
	Vancouver Island marmot	*Marmota vancouverensis*
	Wolverine	*Gulo gulo*
Amphibians	Fowler's toad	*Bufo fowleri*
	Northern cricket frog	*Acris crepitans*
	Northern dusky salamander	*Desmognathus fuscus*
	Northern leopard frog	*Rana pipiens*
	Northern red-legged frog	*Rana aurora*
	Pacific giant salamander	*Dicamptodon tenebrosus*
Reptiles	Black rat snake	*Elaphe obsoleta obsoleta*
	Eastern hognose snake	*Heterodon platyrhinos*
	Eastern Massasauga rattlesnake	*Sistrurus catenatus catenatus*
	Five-lined skink	*Eumeces fasciatus*
	Queen snake	*Regina septemvittata*
	Racer	*Columber constrictor*
	Short-horned lizard	*Phrynosoma douglassii*

Appendix 8: Raw data from Chapter 3 analyses

For explanations of abbreviations used in the following tables, see Appendix 10.

Sheet 1

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
1	Arctic Cordillera	Ellesemere and Devon Island Icecaps	2	0	2	0	0	0	0	0	0	0	2
2	Arctic Cordillera	Ellesemere and Devon Island Icecaps	2	0	2	0	0	0	0	0	0	0	2
3	Arctic Cordillera	Ellesemere and Devon Island Icecaps	2	0	2	0	0	0	0	0	0	0	2
4	Arctic Cordillera	Ellesemere and Devon Island Icecaps	3	1	2	0	0	0	0	0	0	0	3
5	Arctic Cordillera	Baffin Mountains	3	1	2	0	0	0	0	0	0	0	3
6	Arctic Cordillera	Baffin Island Coastal Lowlands	2	0	2	0	0	0	0	0	0	0	2
7	Arctic Cordillera	Torngat Mountains	4	1	3	0	0	4	2	2	0	0	3
8	Northern Arctic	Ellesmere Mountains	3	0	3	0	0	0	0	0	0	0	3
9	Northern Arctic	Eureka Hills	3	0	3	0	0	0	0	0	0	0	3
10	Northern Arctic	Ellesmere Mountains	2	0	2	0	0	0	0	0	0	0	2
11	Northern Arctic	Sverdrup Islands Lowland	4	1	3	0	0	1	1	0	0	0	3
12	Northern Arctic	Parry Islands Plateau	4	1	3	0	0	1	0	1	0	0	3
13	Northern Arctic	Lancaster Plateau	4	1	3	0	0	0	0	0	0	0	4
14	Northern Arctic	Banks Island Coastal Plain	4	1	3	0	0	0	0	0	0	0	4
15	Northern Arctic	Banks Island Lowland	4	1	3	0	0	0	0	0	0	0	4
16	Northern Arctic	Amundsen Gulf Lowlands	5	1	4	0	0	0	0	0	0	0	5
17	Northern Arctic	Shaler Mountains	3	0	3	0	0	0	0	0	0	0	3
18	Northern Arctic	Victoria Island Lowlands	4	1	3	0	0	1	1	0	0	0	3
19	Northern Arctic	Prince of Wales Island Lowland	3	0	3	0	0	0	0	0	0	0	3
20	Northern Arctic	Boothia Peninsula Plateau	4	1	3	0	0	0	0	0	0	0	4
21	Northern Arctic	Gulf of Boothia Plain	3	0	3	0	0	0	0	0	0	0	3
22	Northern Arctic	Borden Peninsula Plateau	2	0	2	0	0	0	0	0	0	0	2
23	Northern Arctic	Melville Peninsula Plateau	3	1	2	0	0	0	0	0	0	0	3
24	Northern Arctic	Baffin Island Uplands	2	0	2	0	0	0	0	0	0	0	2
25	Northern Arctic	Foxe Basin Plain	3	1	2	0	0	0	0	0	0	0	3
26	Northern Arctic	Pangnirtung Upland	3	1	2	0	0	0	0	0	0	0	3
27	Northern Arctic	Hall Peninsula Upland	2	0	2	0	0	0	0	0	0	0	2
28	Northern Arctic	Meta Incognita Peninsula	3	1	2	0	0	0	0	0	0	0	3

Sheet 2

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
29	Northern Arctic	Baffin Upland	2	0	2	0	0	0	0	0	0	0	2
30	Northern Arctic	Wager Bay Plateau	4	1	3	0	0	0	0	0	0	0	3
31	Northern Arctic	Northern Ungava Peninsula	2	1	1	0	0	1	0	1	0	0	1
32	Southern Arctic	Yukon Coastal Plain	3	0	3	0	0	0	0	0	0	0	3
33	Southern Arctic	Tuktoyaktuk Coastal Plain	4	1	3	0	0	1	1	0	0	0	3
34	Southern Arctic	Anderson River Plain	5	2	3	0	0	1	1	0	0	0	4
35	Southern Arctic	Dease Arm Plain	6	2	4	0	0	1	1	0	0	0	5
36	Southern Arctic	Coronation Hills	4	1	3	0	0	0	0	0	0	0	4
37	Southern Arctic	Bluenose Lake Plain	4	1	3	0	0	0	0	0	0	0	4
38	Southern Arctic	Bathurst Hills	4	1	3	0	0	0	0	0	0	0	4
39	Southern Arctic	Queen Maud Gulf Lowland	4	1	3	0	0	0	0	0	0	0	4
40	Southern Arctic	Chantrey Inlet Lowland	4	1	3	0	0	0	0	0	0	0	4
41	Southern Arctic	Takijuq Lake Upland	4	1	3	0	0	1	1	0	0	0	4
42	Southern Arctic	Garry Lake Lowland	4	1	3	0	0	0	0	0	0	0	4
43	Southern Arctic	Back River Plain	4	1	3	0	0	0	0	0	0	0	4
44	Southern Arctic	Dubwant Lake Plain/Upland	4	1	3	0	0	0	0	0	0	0	4
45	Southern Arctic	Maguse River Upland	4	1	3	0	0	1	1	0	0	0	3
46	Southern Arctic	Southampton Island Plain	2	1	1	0	0	0	0	0	0	0	2
47	Southern Arctic	Central Ungava Peninsula	3	1	2	0	0	4	2	2	0	0	1
48	Southern Arctic	Ottawa Islands	0	0	0	0	0	1	0	1	0	0	0
49	Southern Arctic	Belcher Islands	2	1	1	0	0	1	0	1	0	0	2
50	Taiga Plains	Mackenzie Delta	5	2	3	0	0	1	1	0	0	0	3
51	Taiga Plains	Peel River Plateau	6	2	4	0	0	1	0	1	0	0	6
52	Taiga Plains	Great Bear Lake Plain	6	2	4	0	0	4	2	2	0	0	3
53	Taiga Plains	Fort McPherson Plain	6	2	4	0	0	2	1	1	0	0	5
54	Taiga Plains	Colville Hills	6	2	4	0	0	2	2	0	0	0	4
55	Taiga Plains	Norman Range	6	2	4	0	0	2	1	1	0	0	5

Sheet 3

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
56	Taiga Plains	Mackenzie River Plain	6	2	4	0	0	1	1	0	0	0	6
57	Taiga Plains	Grandin Plains	4	1	3	0	0	2	1	1	0	0	4
58	Taiga Plains	Franklin Mountains	6	2	4	0	0	1	1	0	0	0	6
59	Taiga Plains	Keller Lake Plain	5	2	3	0	0	4	2	2	0	0	3
60	Taiga Plains	Great Slave Lake Plain	6	3	3	0	0	4	1	3	0	0	5
61	Taiga Plains	Nahanni Plateau	5	1	4	0	0	1	1	0	0	0	5
62	Taiga Plains	Sibbeston lake Plain	6	1	5	0	0	2	1	1	0	0	5
63	Taiga Plains	Horn Plateau	6	1	5	0	0	3	1	2	0	0	5
64	Taiga Plains	Hay River Lowland	7	2	5	0	0	5	2	3	0	0	3
65	Taiga Plains	Northern Alberta Uplands	7	2	5	0	0	3	1	2	0	0	4
66	Taiga Plains	Muskwa Plateau	5	1	4	0	0	2	1	1	0	0	5
67	Taiga Plains	Northern Alberta Uplands	6	2	4	0	0	5	1	4	0	0	2
68	Taiga Shield	Coppermine River Upland	5	2	3	0	0	2	2	0	0	0	4
69	Taiga Shield	Tazin Lake Upland	8	2	5	1	0	6	3	2	0	0	4
70	Taiga Shield	Kazan River Upland	5	2	3	0	0	1	1	0	0	0	4
71	Taiga Shield	Selwyn Lake Upland	5	1	4	0	0	2	1	1	0	0	4
72	Taiga Shield	La Grande Hills	2	0	2	0	0	3	1	2	0	0	1
73	Taiga Shield	Southern Ungava Peninsula	3	1	2	0	0	3	1	2	0	0	2
74	Taiga Shield	New Quebec Central Plateau	4	2	2	0	0	2	1	1	0	0	3
75	Taiga Shield	Ungava Bay Basin	3	1	2	0	0	4	2	2	0	0	2
76	Taiga Shield	George Plateau	3	1	2	0	0	4	2	2	0	0	3
77	Taiga Shield	Kingurutik-Fraser Rivers	3	1	2	0	0	3	1	2	0	0	2
78	Taiga Shield	Smallwood Reservoir–Michikamau	3	1	2	0	0	2	1	1	0	0	3
79	Taiga Shield	Coastal Barrens	5	2	2	1	0	4	1	2	0	0	5
80	Taiga Shield	Mecatina River	3	1	2	0	0	2	1	1	0	0	2
81	Taiga Shield	Kingurutik-Fraser Rivers	4	1	2	1	0	3	1	1	0	0	3
82	Taiga Shield	Eagle Plateau	5	2	2	1	0	3	1	1	0	0	4

Sheet 4

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
83	Taiga Shield	Mecatina River	2	0	2	0	0	2	1	1	0	0	2
84	Taiga Shield	Winokapau Lake North	2	0	2	0	0	2	1	1	0	0	2
85	Taiga Shield	Goose River West	3	1	2	0	0	2	1	1	0	0	3
86	Taiga Shield	Mecatina River	4	1	2	1	0	3	1	1	0	0	4
87	Boreal Shield	Athabasca Plain	6	2	3	1	0	5	1	3	0	0	3
88	Boreal Shield	Churchill River Upland	6	2	3	1	0	5	1	3	1	0	3
89	Boreal Shield	Hayes River Upland	6	2	3	1	0	4	2	1	1	0	4
90	Boreal Shield	Lac Seul Upland	6	2	3	1	0	5	2	2	1	0	3
91	Boreal Shield	Lake of the Woods	9	6	2	1	0	13	7	5	1	0	4
92	Boreal Shield	Rainy River	5	2	2	1	0	7	4	2	0	0	8
93	Boreal Shield	Thunder Bay–Quetico	5	2	2	1	0	6	3	2	0	0	3
94	Boreal Shield	Lake Nipigon	7	2	4	1	0	7	4	2	1	0	2
95	Boreal Shield	Big Trout Lake	5	1	3	1	0	3	1	1	0	0	4
96	Boreal Shield	Abitibi Plains	4	1	2	1	0	5	2	2	1	0	2
97	Boreal Shield	Lake Temiscaming Lowland	8	5	1	1	1	8	4	2	1	1	4
98	Boreal Shield	Algonquin–Lake Nipissing	14	8	2	1	3	15	8	4	0	2	8
99	Boreal Shield	Southern Laurentians	9	4	3	2	0	7	4	2	0	0	4
100	Boreal Shield	Riviere Rupert Plateau	4	1	2	1	0	5	2	2	0	0	2
101	Boreal Shield	Central Laurentians	6	3	2	1	0	5	2	2	0	0	4
102	Boreal Shield	Anticosit Island	3	2	0	1	0	1	0	0	0	0	3
103	Boreal Shield	Mecatina Plateau	6	3	2	1	0	6	4	1	0	0	4
104	Boreal Shield	Paradise River	5	2	2	1	0	3	1	1	0	0	4
105	Boreal Shield	Lake Melville	5	2	2	1	0	2	0	1	0	0	4
106	Boreal Shield	Strait of Belle Isle	3	1	2	0	0	4	3	1	0	0	2
107	Boreal Shield	Northern Peninsula	4	1	3	0	0	4	2	2	0	0	2
108	Boreal Shield	Long Range Mountains	3	1	2	0	0	3	1	2	0	0	2
109	Boreal Shield	Southwestern Newfoundland	3	1	2	0	0	5	3	2	0	0	2

Sheet 5

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
110	Boreal Shield	Long Range Mountains	3	1	2	0	0	3	1	2	0	0	2
111	Boreal Shield	Long Range Mountains	3	1	2	0	0	3	1	2	0	0	2
112	Boreal Shield	Central Newfoundland	4	2	2	0	0	3	1	2	0	0	3
113	Boreal Shield	Northeastern Newfoundland	3	1	2	0	0	5	3	2	0	0	2
114	Boreal Shield	Maritime Barrens	2	1	1	0	0	3	1	2	0	0	2
115	Boreal Shield	Avalon Forest	2	1	1	0	0	4	2	2	0	0	2
116	Boreal Shield	South Avalon–Burin Oceanic Barrens	3	2	1	0	0	3	1	2	0	0	3
117	Atlantic Maritime	Appalachians	8	4	2	2	0	9	4	3	0	0	5
118	Atlantic Maritime	Northern New Brunswick Uplands	4	3	0	1	0	8	4	3	0	0	3
119	Atlantic Maritime	New Brunswick Highlands	3	2	0	1	0	7	3	3	0	0	3
120	Atlantic Maritime	Saint John River Valley	4	2	0	2	0	8	3	3	0	0	4
121	Atlantic Maritime	Southern New Brunswick Uplands	6	3	1	2	0	9	4	3	0	0	5
122	Atlantic Maritime	Maritime Lowlands	5	3	1	1	0	7	4	2	0	0	3
123	Atlantic Maritime	Fundy Coast	5	4	0	1	0	6	3	2	0	0	4
124	Atlantic Maritime	Southwest Nova Scotia Uplands	5	3	1	1	0	7	4	2	0	0	3
125	Atlantic Maritime	Atlantic Coast	6	4	1	1	0	7	4	2	0	0	2
126	Atlantic Maritime	Annapolis-Minas Lowlands	5	3	1	1	0	5	2	2	0	0	4
127	Atlantic Maritime	South-central Nova Scotia Uplands	5	3	1	1	0	7	4	2	0	0	3
128	Atlantic Maritime	Nova Scotia Highlands	5	3	1	1	0	5	2	2	0	0	4
129	Atlantic Maritime	Cape Breton Highlands	4	2	1	1	0	4	1	2	0	0	3
130	Atlantic Maritime	Prince Edward Island	6	4	1	1	0	3	1	1	0	0	4
131	Atlantic Maritime	Iles-de-la-Madeleine	2	1	0	1	0	2	1	0	0	0	2
132	Mixedwood Plains	St. Lawrence Lowlands	12	8	2	2	0	12	6	4	0	0	8
133	Mixedwood Plains	Frontenac Axis	9	6	1	1	1	5	2	2	0	0	10
134	Mixedwood Plains	Manitoulin–Lake Simcoe	21	14	1	1	5	25	16	3	0	5	3
135	Mixedwood Plains	Lake Erie Lowland	28	17	1	4	6	30	16	4	2	6	2
136	Boreal Plains	Slave River Lowland	7	3	3	1	0	6	1	4	0	0	4

Sheet 6

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
137	Boreal Plains	Clear Hills Upland	5	2	3	0	0	6	2	4	0	0	2
138	Boreal Plains	Peace Lowland	6	2	4	0	0	8	3	4	1	0	2
139	Boreal Plains	Mid-Boreal Uplands	3	2	1	0	0	5	2	3	0	0	2
140	Boreal Plains	Mid-Boreal Uplands	3	1	1	1	0	5	1	3	1	0	2
141	Boreal Plains	Mid-Boreal Uplands	4	1	2	1	0	6	1	4	0	0	3
142	Boreal Plains	Wabasca Lowland	7	3	3	1	0	7	2	4	1	0	2
143	Boreal Plains	Western Boreal	7	3	4	0	0	6	2	4	0	0	2
144	Boreal Plains	Mid-Boreal Uplands	7	5	1	1	0	9	3	5	1	0	3
145	Boreal Plains	Western Alberta Upland	10	6	3	1	0	11	5	5	1	0	3
146	Boreal Plains	Western Alberta Upland	7	6	1	0	0	8	3	5	0	0	6
147	Boreal Plains	Mid-Boreal Uplands	8	4	3	1	0	11	6	4	1	0	3
148	Boreal Plains	Mid-Boreal Uplands	9	4	4	1	0	13	7	5	1	0	2
149	Boreal Plains	Boreal Transition	12	9	2	1	0	17	11	5	1	0	1
150	Boreal Plains	Mid-Boreal Uplands	5	3	1	1	0	9	4	4	0	0	3
151	Boreal Plains	Mid-Boreal Uplands	5	3	1	1	0	8	3	4	0	0	4
152	Boreal Plains	Mid-Boreal Uplands	6	4	1	1	0	12	7	4	0	0	3
153	Boreal Plains	Mid-Boreal Uplands	7	5	1	1	0	8	4	3	0	0	5
154	Boreal Plains	Mid-Boreal Uplands	5	3	1	1	0	9	4	4	0	0	3
155	Boreal Plains	Interlake Plain	12	9	2	1	0	15	8	6	0	0	4
156	Prairies	Aspen Parkland	16	12	3	1	0	20	12	7	1	0	1
157	Prairies	Moist Mixed Grassland	13	10	2	1	0	17	10	6	0	0	3
158	Prairies	Fescue Grassland	9	7	1	1	0	11	4	6	0	0	5
159	Prairies	Mixed Grassland	18	13	2	1	2	18	10	6	0	1	5
160	Prairies	Cypress Upland	14	10	2	1	1	10	3	6	0	0	9
161	Prairies	Aspen Parkland	5	3	1	1	0	7	3	3	0	0	5
162	Prairies	Lake Manitoba Plain	10	7	2	1	0	16	10	5	0	0	4
163	Prairies	Boreal Transition	6	5	0	1	0	11	5	5	0	0	6

Sheet 7

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
164	Prairies	Boreal Transition	7	6	0	1	0	9	3	5	0	0	7
165	Taiga Cordillera	British–Richardson Mountains	5	2	3	0	0	1	1	0	0	0	4
166	Taiga Cordillera	Old Crow Basin	5	2	3	0	0	0	0	0	0	0	5
167	Taiga Cordillera	Old Crow Flats	5	2	3	0	0	0	0	0	0	0	5
168	Taiga Cordillera	North Ogilvie Mountains	5	2	3	0	0	0	0	0	0	0	5
169	Taiga Cordillera	Eagle Plains	5	2	3	0	0	1	0	1	0	0	5
170	Taiga Cordillera	Mackenzie Mountains	6	2	4	0	0	1	0	1	0	0	5
171	Taiga Cordillera	Selwyn Mountains	6	2	4	0	0	0	0	0	0	0	6
172	Boreal Cordillera	Klondike Plateau	7	2	5	0	0	1	0	1	0	0	6
173	Boreal Cordillera	St. Elias Mountains	6	2	4	0	0	1	0	1	0	0	5
174	Boreal Cordillera	Ruby Ranges	6	2	4	0	0	1	0	1	0	0	5
175	Boreal Cordillera	Yukon Plateau–Central	6	2	4	0	0	0	0	0	0	0	6
176	Boreal Cordillera	Yukon Plateau–North	6	2	4	0	0	1	0	1	0	0	5
177	Boreal Cordillera	Yukon Southern Lakes	6	2	4	0	0	2	1	1	0	0	4
178	Boreal Cordillera	Pelly Mountains	6	2	4	0	0	1	1	0	0	0	5
179	Boreal Cordillera	Yukon–Stikine Highlands	6	2	4	0	0	2	1	1	0	0	4
180	Boreal Cordillera	Boreal Mountains and Plateaus	5	1	4	0	0	1	1	0	0	0	5
181	Boreal Cordillera	Liard Basin	6	2	4	0	0	2	1	1	0	0	5
182	Boreal Cordillera	Hyland Highlands	6	1	5	0	0	2	1	1	0	0	5
183	Boreal Cordillera	Northern Canadian Rocky Mountains	6	1	5	0	0	2	1	1	0	0	5
184	Pacific Maritime	Mount Logan	5	2	3	0	0	1	0	1	0	0	5
185	Pacific Maritime	Northern Coastal Mountains	5	2	3	0	0	2	0	2	0	0	4
186	Pacific Maritime	Northern Coastal Mountains	6	2	4	0	0	2	1	1	0	0	4
187	Pacific Maritime	Nass Basin	4	1	3	0	0	3	2	1	0	0	4
188	Pacific Maritime	Queen Charlotte Ranges	5	4	1	0	0	1	1	0	0	0	3
189	Pacific Maritime	Queen Charlotte Lowland	5	4	1	0	0	1	1	0	0	0	3
190	Pacific Maritime	Nass Ranges	5	1	4	0	0	2	0	2	0	0	3

Sheet 8

ER	Ecozone	Ecoregion	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr	SNLt
191	Pacific Maritime	Coastal Gap	5	3	2	0	0	4	2	2	0	0	3
192	Pacific Maritime	Pacific Ranges	9	5	2	2	0	9	4	3	2	0	1
193	Pacific Maritime	Western Vancouver Island	6	3	2	1	0	5	2	2	1	0	2
194	Pacific Maritime	Eastern Vancouver Island	6	3	2	1	0	5	2	2	1	0	2
195	Pacific Maritime	Georgia–Puget Basin	3	3	0	0	0	1	1	0	0	0	2
196	Pacific Maritime	Lower Mainland	12	5	5	2	0	12	4	6	1	0	2
197	Pacific Maritime	Cascade Ranges	4	3	0	1	0	6	2	3	0	0	2
198	Montane Cordillera	Skeen Mountains	4	1	3	0	0	2	1	1	0	0	4
199	Montane Cordillera	Omineca Mountains	5	1	4	0	0	3	2	1	0	0	4
200	Montane Cordillera	Central Canadian Rocky Mountains	6	1	5	0	0	2	1	1	0	0	5
201	Montane Cordillera	Bulkley Ranges	5	1	4	0	0	2	1	1	0	0	4
202	Montane Cordillera	Fraser Plateau	6	3	3	0	0	5	2	3	0	0	4
203	Montane Cordillera	Fraser Basin	6	2	4	0	0	4	2	2	0	0	3
204	Montane Cordillera	Chilcotin Ranges	4	1	3	0	0	1	0	1	0	0	4
205	Montane Cordillera	Columbia Mountains and Highlands	11	5	4	1	1	6	2	3	0	0	7
206	Montane Cordillera	Western Continental Ranges	7	2	4	1	0	4	1	2	1	0	5
207	Montane Cordillera	Eastern Continental Ranges	6	2	4	0	0	4	2	2	0	0	5
208	Montane Cordillera	Interior Transition Ranges	6	3	3	0	0	3	0	3	0	0	2
209	Montane Cordillera	Thompson–Okanagan Plateau	10	5	4	0	1	7	4	3	0	0	7
210	Montane Cordillera	Okanagan Range	6	3	2	0	1	7	4	3	0	0	6
211	Montane Cordillera	Okanagan Highland	9	5	3	0	1	6	3	2	0	1	8
212	Montane Cordillera	Selkirk–Bitterroot Foothills	7	3	3	0	1	4	2	2	0	0	6
213	Montane Cordillera	Southern Rocky Mountain Trench	7	2	4	1	0	4	1	2	1	0	5
214	Montane Cordillera	Northern Continental Divide	10	5	4	1	0	6	2	3	1	0	6
215	Hudson Plains	Coastal Hudson Bay Lowland	5	1	3	1	0	3	1	1	0	0	4
216	Hudson Plains	Hudson Nay Lowland	5	1	3	1	0	2	1	0	0	0	6
217	Hudson Plains	James Bay Lowland	5	1	3	1	0	5	2	2	1	0	3

Sheet 9

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
1	0	2	0	0	26	17	9	0	0	33588	0	0	0	0
2	0	2	0	0	30	21	9	0	0	24746	0	0	0	0
3	0	2	0	0	26	17	9	0	0	12934	0	0	0	0
4	1	2	0	0	44	35	9	0	0	45960	0	0	0	0
5	1	2	0	0	46	36	10	0	0	80734	0	0	0	0
6	0	2	0	0	36	27	9	0	0	8325	0	0	0	0
7	0	3	0	0	73	50	23	0	0	29418	0	0	0	0
8	0	3	0	0	31	22	9	0	0	40078	0	0	0	0
9	0	3	0	0	34	25	9	0	0	78073	0	0	0	0
10	0	2	0	0	30	21	9	0	0	11768	0	0	0	0
11	0	3	0	0	36	27	9	0	0	62606	0	0	0	0
12	1	2	0	0	42	33	9	0	0	56321	0	0	0	0
13	1	3	0	0	48	36	12	0	0	98598	0	0	0	0
14	1	3	0	0	50	39	11	0	0	9903	0	0	0	0
15	1	3	0	0	53	42	11	0	0	47402	0	0	0	0
16	1	4	0	0	69	60	9	0	0	82333	0	0	0	0
17	0	3	0	0	45	36	9	0	0	21551	0	0	0	0
18	0	3	0	0	55	45	10	0	0	172849	0	0	0	0
19	0	3	0	0	44	34	10	0	0	15893	0	0	0	0
20	1	3	0	0	46	36	10	0	0	32457	0	0	0	0
21	0	3	0	0	46	35	11	0	0	23146	0	0	0	0
22	0	2	0	0	45	36	9	0	0	29366	0	0	0	0
23	1	2	0	0	47	36	11	0	0	104543	0	0	0	0
24	0	2	0	0	41	31	10	0	0	75178	0	0	0	0
25	1	2	0	0	49	39	10	0	0	48679	0	0	0	0
26	1	2	0	0	45	36	9	0	0	29275	0	0	0	0
27	0	2	0	0	46	36	10	0	0	33040	0	0	0	0
28	1	2	0	0	53	43	10	0	0	68485	0	0	0	0

Sheet 10

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
29	0	2	0	0	49	39	10	0	0	15037	0	0	0	0
30	0	3	0	0	59	45	14	0	0	235494	0	0	0	0
31	0	1	0	0	47	36	11	0	0	33722	0	0	0	0
32	0	3	0	0	109	84	25	0	0	5421	0	0	0	0
33	0	3	0	0	113	90	23	0	0	18379	0	0	0	0
34	1	3	0	0	95	72	23	0	0	14851	0	0	0	0
35	2	3	0	0	107	84	23	0	0	53754	0	0	0	0
36	1	3	0	0	81	59	22	0	0	53478	0	0	0	0
37	1	3	0	0	84	62	22	0	0	21736	0	0	0	0
38	1	3	0	0	63	50	13	0	0	8245	0	0	0	0
39	1	3	0	0	59	47	12	0	0	61010	0	0	0	0
40	1	3	0	0	50	38	12	0	0	18849	0	0	0	0
41	1	3	0	0	79	59	20	0	0	109996	0	0	0	0
42	1	3	0	0	62	50	12	0	0	79528	0	0	0	0
43	1	3	0	0	64	46	18	0	0	35967	0	0	0	0
44	1	3	0	0	64	46	18	0	0	47156	0	0	0	0
45	0	3	0	0	123	98	24	1	0	72844	0	0	0	0
46	1	1	0	0	100	94	6	0	0	35218	0	0	0	0
47	0	1	0	0	71	42	29	0	0	143499	0	0	0	0
48	0	0	0	0	.	35	.	0	0	183	0	0	0	0
49	1	1	0	0	67	61	6	0	0	2509	0	0	0	0
50	1	2	0	0	115	92	23	0	0	8367	0	0	0	0
51	2	4	0	0	157	121	35	1	0	57115	0	0	0	0
52	1	2	0	0	128	101	27	0	0	74428	0	0	0	0
53	2	3	0	0	120	89	31	0	0	28421	0	0	0	0
54	1	3	0	0	115	84	31	0	0	18756	0	0	0	0
55	2	3	0	0	147	116	31	0	0	39418	0	0	0	0

Sheet 11

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
56	2	4	0	0	151	118	31	2	0	15254	0	0	0	0
57	1	3	0	0	87	65	22	0	0	6943	0	0	0	0
58	2	4	0	0	144	115	29	0	0	6052	0	0	0	0
59	1	2	0	0	134	105	27	2	0	25213	0	0	0	0
60	3	2	0	0	177	135	37	4	1	35463	0	0	0	0
61	1	4	0	0	167	126	40	1	0	11538	0	0	0	0
62	1	4	0	0	170	129	39	2	0	12815	0	0	0	0
63	2	3	0	0	158	129	29	0	0	23247	0	0	0	0
64	1	2	0	0	188	144	39	4	1	115673	0	0	0	0
65	1	3	0	0	182	138	39	4	1	58250	0	0	0	0
66	1	4	0	0	179	136	39	3	1	22853	0	0	0	0
67	1	1	0	0	187	148	34	4	1	12327	0	0	0	0
68	1	3	0	0	121	95	26	0	0	125817	0	0	0	0
69	1	2	1	0	190	148	37	4	1	95591	4	0	0	0
70	1	3	0	0	123	92	30	1	0	167771	0	0	0	0
71	1	3	0	0	148	107	39	2	0	182654	0	0	0	0
72	0	1	0	0	114	84	26	3	1	119178	0	0	0	0
73	0	2	0	0	86	56	29	1	0	77396	0	0	0	0
74	1	2	0	0	101	70	27	4	0	177419	0	0	0	0
75	0	2	0	0	88	63	23	2	0	84434	0	0	0	0
76	0	3	0	0	78	55	23	0	0	21407	0	0	0	0
77	0	2	0	0	93	65	27	1	0	62942	0	0	0	0
78	1	2	0	0	109	78	27	4	0	72083	0	0	0	0
79	2	2	1	0	91	80	10	1	0	11642	0	0	0	0
80	0	2	0	0	102	69	29	4	0	6103	0	0	0	0
81	0	2	1	0	112	80	28	4	0	2845	0	0	0	0
82	1	2	1	0	112	80	28	4	0	13002	0	0	0	0

Sheet 12

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
83	0	2	0	0	100	67	29	4	0	2511	0	0	0	0
84	0	2	0	0	105	72	29	4	0	3069	0	0	0	0
85	1	2	0	0	109	76	29	4	0	5004	0	0	0	0
86	1	2	1	0	112	79	29	4	0	45389	0	0	0	0
87	1	1	1	0	187	148	34	4	1	68180	0	0	0	0
88	2	1	0	0	193	153	35	4	1	177992	3	0	0	0
89	2	2	0	0	168	135	30	3	0	131077	7	0.01	0	0
90	2	1	0	0	214	169	33	8	4	140840	0	0	31	0.02
91	3	1	0	0	262	184	55	14	9	42855	7	0.02	995	2.32
92	5	2	1	0	236	169	46	13	8	3120	2	0.06	0	0
93	1	1	1	0	231	167	45	13	6	24539	102	0.42	0	0
94	1	1	0	0	226	165	43	13	5	76083	0	0	0	0
95	1	2	1	0	172	131	33	7	1	107030	0	0	0	0
96	1	1	0	0	239	173	52	11	3	176196	57	0.03	752	0.43
97	3	1	0	0	252	171	50	17	14	83501	117	0.14	1330	1.59
98	5	1	1	1	259	176	49	16	18	69305	207	0.3	665	0.96
99	2	1	1	0	252	170	48	17	17	168436	89	0.05	2814	1.67
100	0	1	1	0	182	135	37	8	2	89564	3	0	0	0
101	2	1	1	0	194	143	37	11	3	203891	89	0.04	1517	0.74
102	2	0	1	0	129	109	18	2	0	7639	0	0	0	0
103	1	2	1	0	155	116	32	6	1	95088	0	0	0	0
104	1	2	1	0	112	80	28	4	0	18572	0	0	0	0
105	1	2	1	0	115	82	29	4	0	17583	23	0.13	0	0
106	1	1	0	0	111	95	16	0	0	2337	0	0	0	0
107	1	1	0	0	125	107	16	2	0	7903	0	0	0	0
108	1	1	0	0	126	106	19	1	0	6264	0	0	0	0
109	1	1	0	0	142	119	19	4	0	10193	30	0.29	0	0

Sheet 13

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
110	1	1	0	0	137	119	18	0	0	6344	0	0	0	0
111	1	1	0	0	131	112	18	1	0	3109	0	0	0	0
112	2	1	0	0	136	115	20	1	0	29435	15	0.05	0	0
113	1	1	0	0	116	102	14	0	0	5426	0	0	0	0
114	1	1	0	0	139	119	18	2	0	34146	62	0.18	0	0
115	1	1	0	0	120	105	13	2	0	509	0	0	0	0
116	2	1	0	0	119	105	13	1	0	1824	0	0	0	0
117	2	1	2	0	209	154	39	12	4	66205	48	0.07	9284	14.02
118	2	0	1	0	206	146	39	13	8	23748	8	0.03	318	1.34
119	2	0	1	0	195	135	39	13	8	5107	0	0	14	0.27
120	2	0	2	0	208	148	39	13	8	3116	6	0.19	394	12.64
121	3	0	2	0	223	163	39	13	8	12402	52	0.42	290	2.34
122	2	0	1	0	231	171	39	13	8	30016	164	0.55	1129	3.76
123	3	0	1	0	64	43	10	7	4	4165	36	0.86	478	11.48
124	2	0	1	0	201	139	40	13	9	16221	11	0.07	28	0.17
125	1	0	1	0	194	138	35	13	8	5830	31	0.53	0	0
126	3	0	1	0	193	136	36	13	8	4572	3	0.07	1297	28.37
127	2	0	1	0	192	135	36	13	8	6414	103	1.61	100	1.56
128	3	0	1	0	199	142	36	13	8	15326	127	0.83	438	2.86
129	2	0	1	0	178	125	32	13	8	2368	0	0	0	0
130	3	0	1	0	179	141	26	9	3	5422	16	0.3	2870	52.93
131	1	0	1	0	.	110	.	.	.	248	0	0	0	0
132	5	1	2	0	253	172	49	19	13	41400	1069	2.58	27984	67.59
133	6	2	1	1	248	166	48	17	17	840	0	0	484	57.62
134	1	1	1	0	270	172	51	21	26	47076	613	1.3	27865	59.19
135	0	0	2	0	280	166	52	30	32	25093	1824	7.27	20729	82.61
136	2	1	1	0	192	151	36	4	1	46930	0	0	0	0

Sheet 14

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
137	1	1	0	0	204	153	45	5	1	43150	0	0	1095	2.54
138	1	1	0	0	205	163	36	5	1	66881	13	0.02	22256	33.28
139	1	1	0	0	194	152	36	5	1	7923	0	0	2	0.03
140	1	1	0	0	196	155	36	4	1	3156	0	0	0	0
141	1	1	1	0	191	150	36	4	1	11636	0	0	0	0
142	1	1	0	0	206	164	36	5	1	49317	7	0.01	84	0.17
143	1	1	0	0	199	157	36	5	1	11169	0	0	464	4.15
144	3	0	0	0	207	166	36	4	1	24672	0	0	746	3.02
145	3	0	0	0	224	166	48	8	2	71737	7	0.01	266	0.37
146	5	1	0	0	226	150	58	10	8	1612	0	0	0	0
147	2	1	0	0	213	173	35	4	1	116892	0	0	360	0.31
148	2	0	0	0	225	175	41	7	2	63321	3	0	775	1.22
149	1	0	0	0	227	175	43	6	3	97839	60	0.06	46084	47.1
150	1	1	1	0	210	161	41	5	3	6594	0	0	668	10.13
151	2	1	1	0	219	173	41	4	1	3221	0	0	0	0
152	1	1	1	0	215	169	41	4	1	8536	0	0	841	9.85
153	3	1	1	0	219	161	46	6	6	5252	0	0	801	15.25
154	2	0	1	0	214	156	46	6	6	4609	0	0	624	13.54
155	3	0	1	0	247	185	46	9	7	33688	28	0.08	7774	23.08
156	1	0	0	0	225	167	46	6	6	169380	613	0.36	132370	78.15
157	2	0	1	0	203	148	41	7	7	97526	249	0.26	76071	78
158	4	0	1	0	224	148	58	10	8	14666	261	1.78	11863	80.89
159	3	0	1	1	226	145	58	10	13	130840	84	0.06	67395	51.51
160	7	0	1	1	210	146	46	6	12	8268	0	0	1851	22.39
161	3	1	1	0	219	161	46	6	6	2170	0	0	1762	81.2
162	3	0	1	0	247	185	46	9	7	29264	352	1.2	18515	63.27
163	5	0	1	0	218	156	46	9	7	1505	0	0	1143	75.95

Sheet 15

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
164	6	0	1	0	222	148	54	9	11	556	0	0	93	16.73
165	1	3	0	0	118	93	25	0	0	24827	0	0	0	0
166	2	3	0	0	112	89	23	0	0	13149	0	0	0	0
167	2	3	0	0	101	76	25	0	0	5521	0	0	0	0
168	2	3	0	0	134	103	30	1	0	35708	0	0	0	0
169	2	3	0	0	127	96	30	1	0	19329	0	0	0	0
170	2	3	0	0	141	105	35	1	0	81893	0	0	0	0
171	2	4	0	0	158	122	35	1	0	68081	0	0	0	0
172	2	4	0	0	155	120	34	1	0	35106	0	0	0	0
173	2	3	0	0	167	119	46	2	0	22314	0	0	0	0
174	2	3	0	0	176	128	46	2	0	21469	0	0	0	0
175	2	4	0	0	163	128	34	1	0	25344	0	0	0	0
176	2	3	0	0	155	119	35	1	0	53936	0	0	0	0
177	1	3	0	0	180	132	46	2	0	33546	8	0.02	0	0
178	1	4	0	0	166	128	37	1	0	33536	0	0	0	0
179	1	3	0	0	179	130	46	3	0	23373	0	0	0	0
180	1	4	0	0	182	134	43	4	1	99897	0	0	0	0
181	1	4	0	0	169	127	40	2	0	32433	0	0	0	0
182	1	4	0	0	169	128	40	1	0	24559	0	0	0	0
183	1	4	0	0	174	131	39	3	1	35911	0	0	0	0
184	2	3	0	0	152	119	30	3	0	3709	0	0	0	0
185	2	2	0	0	155	120	32	3	0	2533	0	0	0	0
186	1	3	0	0	172	125	40	5	2	23002	0	0	0	0
187	1	3	0	0	175	127	43	4	1	5374	0	0	0	0
188	2	1	0	0	85	67	17	1	0	6084	0	0	0	0
189	2	1	0	0	85	67	17	1	0	2609	0	0	0	0
190	1	2	0	0	183	128	47	6	2	12305	3	0.02	0	0

Sheet 16

ER	SNLb	SNLm	SNLa	SNLr	SRt	SRb	SRm	SRa	SRr	Area	ABuiltup	% ABuiltup	ACropland	% ACropland
191	1	2	0	0	187	132	47	6	2	46601	0	0	0	0
192	1	0	0	0	218	165	43	7	3	58304	4	0.01	2	0
193	1	1	0	0	180	139	29	8	4	18065	0	0	0	0
194	1	1	0	0	189	139	32	12	6	13251	235	1.77	0	0
195	2	0	0	0	180	148	18	8	6	1120	0	0	0	0
196	1	0	1	0	241	163	53	17	8	4448	766	17.22	960	21.58
197	1	0	1	0	242	164	53	17	8	270	0	0	0	0
198	1	3	0	0	178	130	43	4	1	21958	0	0	0	0
199	1	3	0	0	192	144	43	4	1	33470	1	0	0	0
200	1	4	0	0	205	155	45	4	1	35404	0	0	0	0
201	1	3	0	0	185	130	47	6	2	2754	0	0	0	0
202	3	1	0	0	240	170	54	8	8	88423	0	0	0	0
203	1	2	0	0	226	167	52	5	2	44356	14	0.03	0	0
204	1	3	0	0	217	164	43	7	3	11511	0	0	0	0
205	4	1	1	1	256	177	60	10	9	86590	5	0.01	0	0
206	2	3	0	0	240	161	60	10	9	23276	0	0	0	0
207	2	3	0	0	239	160	60	10	9	38896	0	0	0	0
208	2	0	0	0	238	168	54	8	8	15020	0	0	0	0
209	5	1	0	1	246	176	54	8	8	37456	69	0.18	491	1.31
210	4	1	0	1	276	173	70	17	16	4349	0	0	49	1.13
211	5	2	0	1	262	172	68	8	14	1011	0	0	45	4.45
212	3	2	0	1	274	184	68	8	14	7794	12	0.15	0	0
213	2	3	0	0	243	164	60	10	9	7551	7	0.09	0	0
214	4	2	0	0	240	158	59	12	11	15273	0	0	145	0.95
215	1	2	1	0	141	109	30	2	0	58528	0	0	0	0
216	1	4	1	0	142	109	29	4	0	129208	0	0	0	0
217	1	1	1	0	170	130	33	6	1	170843	0	0	0	0

Sheet 17

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
1	0	0	0	0	35	0	0	0	33588	0
2	0	0	0	0	0	0	0	0	24746	0
3	0	0	0	0	0	0	0	0	12934	0
4	0	0	0	0	19	0	0	0	45960	0
5	0	0	0	0	104	0	0	0	80734	0
6	0	0	0	0	56	0	0	0	8325	0
7	0	0	0	0	181	0	0	0	29418	0
8	0	0	0	0	153	0	0	0	40078	0
9	0	0	0	0	615	0	0	0	78073	0
10	0	0	0	0	0	0	0	0	11768	0
11	0	0	0	0	0	0	0	0	62606	0
12	0	0	0	0	0	0	0	0	56321	0
13	0	0	0	0	15	0	0	0	98598	0
14	0	0	0	0	0	0	0	0	9903	0
15	0	0	0	0	0	0	0	0	47402	0
16	0	0	0	0	2569	0	0	0	82333	0
17	0	0	0	0	0	0	0	0	21551	0
18	0	0	0	0	3761	0	0	0	172849	0
19	0	0	0	0	178	0	0	0	15893	0
20	0	0	0	0	932	0	0	0	32457	0
21	0	0	0	0	757	0	0	0	23146	0
22	0	0	0	0	170	0	0	0	29366	0
23	0	0	0	0	2345	0	0	0	104543	0
24	0	0	0	0	1092	0	0	0	75178	0
25	0	0	0	0	952	0	0	0	48679	0
26	0	0	0	0	217	0	0	0	29275	0
27	0	0	0	0	296	0	0	0	33040	0
28	0	0	0	0	4099	0	0	0	68485	0

Sheet 18

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
29	0	0	0	0	79	0	0	0	15037	0
30	0	0	0	0	5041	0	0	0	235494	0
31	0	0	0	0	81	0	0	0	33722	0
32	0	0	0	0	0	0	0	0	5421	0
33	0	0	258	1.4	702	0	0	0	18379	0
34	0	0	994	6.69	36	0	0	0	14851	0
35	0	0	29876	55.58	897	0	0	0	53754	0
36	0	0	137	0.26	1038	0	0	0	53478	0
37	0	0	501	2.3	61	0	0	0	21736	0
38	0	0	0	0	0	0	0	0	8245	0
39	0	0	0	0	817	0	0	0	61010	0
40	0	0	0	0	413	0	0	0	18849	0
41	0	0	5749	5.23	7884	0	0	0	109996	0
42	0	0	7	0.01	3288	0	0	0	79528	0
43	0	0	0	0	2448	0	0	0	35967	0
44	0	0	176	0.37	4230	0	0	0	47156	0
45	0	0	0	0	4303	0	0	0	72844	0
46	0	0	0	0	296	0	0	0	35218	0
47	0	0	145	0.1	7463	0	0	0	143499	0
48	0	0	0	0	39	0	0	0	183	0
49	0	0	0	0	344	0	0	0	2509	0
50	0	0	6657	79.56	867	0	0	0	8367	0
51	0	0	43070	75.41	151	0	0	0	57115	0
52	0	0	69725	93.68	1744	0	0	0	74428	0
53	0	0	27645	97.27	771	0	0	0	28421	0
54	0	0	16082	85.74	2626	0	0	0	18756	0
55	0	0	37117	94.16	2031	0	0	0	39418	0

Sheet 19

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
56	0	0	14023	91.93	1231	0	0	0	15254	0
57	0	0	1832	26.39	42	0	0	0	6943	0
58	0	0	5781	95.52	271	0	0	0	6052	0
59	0	0	23948	94.98	1265	0	0	0	25213	0
60	0	0	32716	92.25	2747	0	0	0	35463	0
61	0	0	7759	67.25	0	0	0	0	11538	0
62	0	0	12402	96.78	108	0	0	0	12815	0
63	0	0	22794	98.05	453	0	0	0	23247	0
64	0	0	112692	97.42	2981	0	0	0	115673	0
65	0	0	56681	97.31	1569	0	0	0	58250	0
66	0	0	22793	99.74	51	0	0	0	22853	0
67	0	0	12180	98.81	147	0	0	0	12327	0
68	0	0	91950	73.08	10333	0	0	0	125817	0
69	0	0	91057	95.26	4413	4	0	0	95587	0
70	0	0	39245	23.39	13763	0	0	0	167771	0
71	0	0	154707	84.7	14207	0	0	0	182654	0
72	0	0	116262	97.55	2916	0	0	0	119178	0
73	0	0	20138	26.02	6239	0	0	0	77396	0
74	0	0	147891	83.36	11550	0	0	0	177419	0
75	0	0	51576	61.08	4825	0	0	0	84434	0
76	0	0	161	0.75	766	0	0	0	21407	0
77	0	0	6444	10.24	3244	0	0	0	62942	0
78	0	0	56453	78.32	5701	0	0	0	72083	0
79	0	0	4024	34.56	171	0	0	0	11642	0
80	0	0	5725	93.81	223	0	0	0	6103	0
81	0	0	2016	70.86	17	0	0	0	2845	0
82	0	0	12518	96.28	462	0	0	0	13002	0

Sheet 20

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
83	0	0	1644	65.47	107	0	0	0	2511	0
84	0	0	2295	74.78	54	0	0	0	3069	0
85	0	0	4911	98.14	93	0	0	0	5004	0
86	0	0	44585	98.23	804	0	0	0	45389	0
87	0	0	64952	95.27	3228	0	0	0	68180	0
88	0	0	159171	89.43	18815	3	0	0	177989	0
89	0	0	120309	91.78	10761	7	0.01	0	131070	0
90	0	0	132829	94.31	7980	31	0.02	0	140809	0
91	0	0	35610	83.09	6243	1002	2.34	0	41853	0
92	0	0	2622	84.04	496	2	0.06	0	3118	0
93	0	0	22734	92.64	1703	102	0.42	0	24437	600
94	0	0	72440	95.21	3643	0	0	0	76083	600
95	0	0	101498	94.83	5532	0	0	0	107030	0
96	0	0	169399	96.14	5918	809	0.46	0	175387	300
97	0	0	79046	94.66	3008	1447	1.73	0	82054	300
98	0	0	65820	94.97	2613	872	1.26	4.75028	68433	79500
99	0	0	159303	94.58	6228	2903	1.72	4.86754	165533	172000
100	0	0	82860	92.51	6614	3	0	0	89561	0
101	0	0	191646	93.99	9400	1606	0.79	4.62354	202285	3000
102	0	0	7586	99.31	0	0	0	0	7639	0
103	0	0	91090	95.8	2748	0	0	0	95088	2100
104	0	0	18271	98.38	244	0	0	0	18572	0
105	0	0	16856	95.87	188	23	0.13	0	17560	0
106	0	0	2183	93.41	17	0	0	0	2337	0
107	0	0	7527	95.24	190	0	0	0	7903	0
108	0	0	4354	69.51	35	0	0	0	6264	0
109	0	0	9218	90.43	456	30	0.29	0	10163	0

Sheet 21

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
110	0	0	5592	88.15	65	0	0	0	6344	0
111	0	0	1802	57.96	35	0	0	0	3109	0
112	0	0	26645	90.52	999	15	0.05	0	29420	0
113	0	0	5404	99.59	21	0	0	0	5426	13100
114	0	0	29827	87.35	632	62	0.18	0	34084	131000
115	0	0	509	100	0	0	0	0	509	0
116	0	0	1608	88.16	0	0	0	0	1824	0
117	0	0	56627	85.53	199	9332	14.1	5.39235	56873	212000
118	0	0	23360	98.37	62	326	1.37	4.10209	23422	27300
119	0	0	5093	99.73	0	14	0.27	0	5093	0
120	0	0	2716	87.16	0	400	12.84	4.59804	2716	27000
121	0	0	11517	92.86	185	342	2.76	4.94585	12060	63600
122	0	0	27906	92.97	201	1293	4.31	5.35597	28723	107000
123	0	0	3585	86.07	0	514	12.34	4.49941	3651	76300
124	0	0	15753	97.11	376	39	0.24	4.59944	16182	25200
125	0	0	5573	95.59	26	31	0.53	4.50068	5799	90300
126	0	0	3167	69.27	12	1300	28.43	5.01757	3272	34500
127	0	0	6015	93.78	10	203	3.16	4.28117	6211	9600
128	0	0	13957	91.07	99	565	3.69	5.19945	14761	76500
129	0	0	2320	97.97	0	0	0	0	2368	0
130	0	0	2470	45.56	23	2886	53.23	5.25592	2536	94000
131	0	0	18	7.26	1	0	0	0	248	3300
132	0	0	11864	28.66	483	29053	70.18	6.25136	12347	921000
133	0	0	322	38.33	34	484	57.62	0	356	17800
134	0	0	16699	35.47	1899	28478	60.49	5.83516	18598	647000
135	0	0	2325	9.27	185	22553	89.88	5.74791	2540	616000
136	0	0	44387	94.58	2540	0	0	0	46930	0

Sheet 22

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
137	0	0	42055	97.46	0	1095	2.54	0	42055	0
138	0	0	43242	64.66	1370	22269	33.3	0	44612	0
139	0	0	7921	99.97	0	2	0.03	0	7921	0
140	0	0	2982	94.49	174	0	0	0	3156	0
141	0	0	11591	99.61	45	0	0	0	11636	0
142	0	0	48890	99.13	336	91	0.18	0	49226	0
143	0	0	10634	95.21	71	464	4.15	0	10705	0
144	173	0.7	23194	94.01	559	919	3.72	0	23753	0
145	2500	3.48	68854	95.98	1	2773	3.87	0	68964	0
146	806	50	806	50	0	806	50	0	806	0
147	0	0	109108	93.34	7424	360	0.31	0	116532	0
148	0	0	54587	86.21	7956	778	1.23	0	62543	0
149	16647	17.01	33686	34.43	1362	62791	64.18	0	35048	0
150	9	0.14	5750	87.2	167	677	10.27	0	5917	0
151	0	0	3221	100	0	0	0	0	3221	0
152	0	0	7668	89.83	27	841	9.85	0	7695	0
153	0	0	4451	84.75	0	801	15.25	0	4451	0
154	437	9.48	3533	76.65	15	1061	23.02	0	3548	0
155	0	0	24179	71.77	1618	7802	23.16	0	25886	1800
156	26612	15.71	7799	4.6	1985	159595	94.22	0	9785	300
157	20229	20.74	83	0.09	894	96549	99	0	977	0
158	2180	14.86	362	2.47	0	14304	97.53	0	362	0
159	61878	47.29	0	0	1483	129357	98.87	0	1483	0
160	5898	71.34	519	6.28	0	7749	93.72	0	519	0
161	0	0	408	18.8	0	1762	81.2	0	408	0
162	3082	10.53	6533	22.32	735	21949	75	0	7315	13500
163	355	23.59	7	0.47	0	1498	99.53	0	7	0

Sheet 23

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
164	45	8.09	418	75.18	0	138	24.82	0	418	0
165	0	0	3641	14.67	0	0	0	0	24827	0
166	0	0	7698	58.54	0	0	0	0	13149	0
167	0	0	4783	86.63	0	0	0	0	5521	0
168	0	0	20670	57.89	0	0	0	0	35708	0
169	0	0	18313	94.74	0	0	0	0	19329	0
170	0	0	27031	33.01	0	0	0	0	81893	0
171	0	0	29914	43.94	21	0	0	0	68081	0
172	0	0	16473	46.92	138	0	0	0	35106	0
173	0	0	3017	13.52	44	0	0	0	22314	0
174	0	0	7745	36.08	625	0	0	0	21469	0
175	0	0	16975	66.98	56	0	0	0	25344	0
176	0	0	41554	77.04	322	0	0	0	53936	0
177	0	0	22926	68.34	1018	8	0.02	0	33538	0
178	0	0	17400	51.88	142	0	0	0	33536	0
179	0	0	11509	49.24	310	0	0	0	23373	0
180	0	0	51702	51.76	1336	0	0	0	99897	0
181	0	0	31195	96.18	242	0	0	0	32433	0
182	0	0	23322	94.96	0	0	0	0	24559	0
183	0	0	22234	61.91	1	0	0	0	35911	0
184	0	0	0	0	36	0	0	0	3709	0
185	0	0	204	8.05	0	0	0	0	2533	0
186	0	0	9847	42.81	0	0	0	0	23002	0
187	0	0	4793	89.19	0	0	0	0	5374	0
188	0	0	6084	100	0	0	0	0	6084	0
189	0	0	2609	100	0	0	0	0	2609	0
190	0	0	10497	85.31	0	3	0.02	0	12302	0

Sheet 24

ER	ARange	% ARange	AForest	% AForest	AWater	AHD1	% AHD1	AC1861	ANatural	Pop1871
191	0	0	38530	82.68	668	0	0	0	46601	0
192	0	0	41799	71.69	721	6	0.01	0	58298	600
193	0	0	17830	98.7	100	0	0	0	18065	0
194	0	0	12677	95.67	120	235	1.77	0	13016	5500
195	0	0	1120	100	0	0	0	0	1120	0
196	0	0	2694	60.57	28	1726	38.8	0	2722	1500
197	0	0	270	100	0	0	0	0	270	0
198	0	0	13553	61.72	0	0	0	0	21958	0
199	3	0	24168	72.21	1276	4	0.01	0	33466	0
200	0	0	31875	90.03	400	0	0	0	35404	0
201	0	0	2434	88.38	0	0	0	0	2754	0
202	1039	1.18	84543	95.61	2094	1039	1.18	0	87384	0
203	0	0	42670	96.2	1591	14	0.03	0	44342	1200
204	0	0	7963	69.18	242	0	0	0	11511	0
205	32	0.04	74169	85.66	2131	37	0.04	0	86553	600
206	0	0	17243	74.08	7	0	0	0	23276	0
207	0	0	25750	66.2	0	0	0	0	38896	0
208	425	2.83	12858	85.61	0	425	2.83	0	14595	600
209	4458	11.9	31973	85.36	465	5018	13.4	0	32438	0
210	294	6.76	4006	92.11	0	343	7.89	0	4006	0
211	396	39.17	570	56.38	0	441	43.62	0	570	0
212	0	0	7768	99.67	0	12	0.15	0	7782	0
213	0	0	7327	97.03	77	7	0.09	0	7544	0
214	856	5.6	12348	80.85	0	1001	6.55	0	14272	0
215	0	0	39943	68.25	37	0	0	0	58528	0
216	0	0	127740	98.86	293	0	0	0	129208	0
217	0	0	169993	99.5	850	0	0	0	170843	0

Sheet 25

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0
5	482	0	0.00597	482	0	0	0	0	0	0
6	565	0	0.06787	565	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0
12	171	0	0.00304	171	0	0	0	0	0	0
13	232	0	0.00235	232	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0
15	125	0	0.00264	125	0	0	0	0	0	0
16	1484	0	0.01802	1484	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0
18	1363	0	0.00789	1363	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0
21	409	0	0.01767	409	0	0	0	0	0	0
22	1811	0	0.06167	1811	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0
24	47	0	0.00063	47	0	0	0	0	0	0
25	1462	0	0.03003	1462	0	0	0	0	0	0
26	1135	0	0.03877	1135	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0
28	4954	0	0.07234	4954	0	0	0	0	0	0

Sheet 26

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
29	0	0	0	0	0	0	0	0	0	0
30	1674	0	0.00711	1674	0	0	0	0	0	0
31	1461	0	0.04332	1461	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0
33	988	0	0.05376	988	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0
35	255	0	0.00474	255	0	0	0	0	0	0
36	1059	0	0.01980	1059	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0
38	18	0	0.00218	18	0	0	0	0	0	0
39	53	0	0.00087	53	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0
45	3580	0	0.04915	3580	0	0	0	0	0	0
46	578	0	0.01641	578	0	0	0	0	0	0
47	3257	0	0.02270	3257	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0
49	526	0	0.20965	526	0	0	0	0	0	0
50	3979	0	0.47556	3979	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0
53	920	0	0.03237	920	0	0	0	0	0	0
54	69	0	0.00368	69	0	0	0	0	0	0
55	1153	0	0.02925	1153	0	0	0	0	0	0

Sheet 27

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
56	1176	0	0.07709	1176	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0
60	392	0	0.01105	392	0	0	0	0	0	0
61	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0
64	13155	0	0.11373	13155	65985	149663	215648	36.78	9.42	52.52
65	574	0	0.00985	574	0	0	0	0	0	0
66	10	0	0.00044	10	0	0	0	0	0	0
67	1	0	0.00008	1	0	0	0	0	0	0
68	530	0	0.00421	530	0	0	0	0	0	0
69	18078	0	0.18912	18078	0	0	0	0	0	0
70	2	0	0.00001	2	0	0	0	0	0	0
71	1562	0	0.00855	1562	0	0	0	0	0	0
72	5326	0	0.04469	5326	0	0	0	0	0	0
73	284	0	0.00367	284	0	0	0	0	0	0
74	47	0	0.00026	47	0	0	0	0	0	0
75	2654	0	0.03143	2654	0	0	0	0	0	0
76	529	0	0.02471	529	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0
78	234	0	0.00325	234	0	0	0	0	0	0
79	3536	0	0.30373	3536	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0

Sheet 28

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
83	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0
86	807	0	0.01778	807	0	0	0	0	0	0
87	1049	0	0.01539	1049	0	0	0	0	0	0
88	28027	0	0.15746	28027	2325	3355	5680	0	0	0.04
89	33751	0	0.25749	33751	0	0	0	.	.	.
90	18410	0	0.13072	18410	30041	84563	114604	8.45	2.12	14.47
91	52735	0	1.23054	52735	1894828	2917870	4812690	390.11	106.3	454.07
92	16780	0	5.37821	16780	217454	633188	850641	49.54	19.72	128.95
93	135793	0.02445	5.53376	135000	111313	692922	804235	17.39	3.55	77.74
94	22453	0.00789	0.29511	21853	2400	33468	35868	0.16	0	4.47
95	3325	0	0.03107	3325	0	0	0	0	0	0
96	247486	0.00170	1.40461	247000	174585	1398780	1573366	14.08	1.41	149.21
97	157170	0.00359	1.88225	157000	538728	1677230	2215959	142.9	9.05	241.42
98	473744	1.14710	6.83564	394000	737054	2710140	3447201	103.13	14.15	364.28
99	675567	1.02116	4.01082	504000	1519357	5575310	7094680	164.65	27.92	379.79
100	13622	0	0.15209	13622	0	0	0	.	.	.
101	386412	0.01471	1.89519	383000	1248446	4044440	5292900	151.26	23.94	344.14
102	264	0	0.03456	264	0	0	0	0	0	0
103	14908	0.02208	0.15678	12808	0	0	0	.	.	.
104	1845	0	0.09934	1845	0	0	0	0	0	0
105	10384	0	0.59057	10384	0	0	0	.	.	.
106	11885	0	5.08558	11885	0	0	0	.	.	.
107	12969	0	1.64102	12969	215	18406	18621	0.06	0	0.57
108	0	0	0	0	0	0	0	0	0	0
109	69399	0	6.80850	69399	53238	327587	380825	2.17	2.05	19.49

Sheet 29

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
110	603	0	0.09505	603	0	0	0	.	.	.
111	1164	0	0.37440	1164	0	0	0	0	0	0
112	75065	0	2.55020	75065	50341	282781	333122	1.5	1.06	10.6
113	46053	2.41430	8.48747	32953	18430	67653	86083	0.74	0.68	2.46
114	311536	3.83647	9.12365	181000	136759	488746	625505	1.21	1.69	19
115	209	0	0.41061	209	0	0	0	.	.	.
116	9216	0	5.05263	9216	0	29860	29860	0	0	1.61
117	707305	3.20218	10.68356	495000	3218102	21053200	24271270	415.36	66.59	1959.09
118	135404	1.14957	5.7017	108000	948898	2559730	3508620	104.08	34.94	190.63
119	0	0	0	0	0	0	0	0	0	0
120	47879	8.66496	15.36553	20879	5009795	8091960	13101710	255.7	181.15	332.88
121	150766	5.12821	12.15659	87166	429516	1831640	2261151	20.67	6.49	129.16
122	441805	3.56477	14.71898	335000	1096023	3615100	4711130	69.22	28.27	286.87
123	82496	18.31933	19.80696	6196	686735	1395540	2082268	32.75	22.84	99.35
124	87482	1.55354	5.39313	62282	151355	486877	638233	6.05	2.63	42.9
125	132437	15.48885	22.71647	42137	29754	173583	203337	0.75	0.77	14.19
126	108933	7.54593	23.82612	74433	2349199	4106130	6455310	96.67	67.91	315.15
127	271105	1.49673	42.26770	262000	110107	395794	505901	6.79	2.16	41.28
128	198674	4.99152	12.96320	122000	902276	2848390	3750676	52.71	31.37	209.75
129	2161	0	0.91258	2161	0	0	0	.	.	.
130	129765	17.33678	23.93305	35765	8962310	20016600	28978920	737.83	361.61	1021.16
131	13991	13.30645	56.41532	10691	983	14134	15117	0.06	0.01	0.3
132	5909970	22.24638	142.75292	4990000	44458007	146947000	191404900	6214.52	1040.44	9194.09
133	18467	21.19048	21.98452	667	246489	680600	927091	41.5	6.65	62.06
134	2149600	13.74373	45.66223	1500000	49787462	100641000	150428100	7329.63	1737.45	9893.4
135	5938070	24.54868	236.64241	5320000	88232787	142111000	230344400	8888.62	2570.52	9810.06
136	5559	0	0.11845	5559	0	0	0	.	.	.

Sheet 30

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
137	5055	0	0.11715	5055	637719	1913840	2551552	236.36	55.66	505.1
138	148040	0	2.21348	148000	24438243	46416800	70855300	7865.09	887.94	10176.5
139	298	0	0.03761	298	74501	240423	314925	26.87	4.75	48.4
140	586	0	0.18568	586	0	0	0	.	.	.
141	12	0	0.00103	12	0	0	0	0	0	0
142	38738	0	0.78549	38738	196720	298257	494977	74.48	1.11	83.78
143	4860	0	0.43513	4860	163733	555220	718955	58.31	2.82	124.67
144	16085	0	0.65195	16085	495050	1440180	1935234	188.68	5.08	295
145	55125	0	0.76843	55125	620525	2548760	3169285	169.24	8.94	677.28
146	3928	0	2.43672	3928	73004	374666	447670	22.15	5.58	60.69
147	20864	0	0.17849	20864	1225744	2515150	3740900	383.92	32.49	489.24
148	18240	0	0.28806	18240	836699	1169640	2006336	219.96	31.05	245.04
149	298064	0	3.04647	298000	63165508	118408000	181573100	20947.4	2191.12	26149.9
150	3167	0	0.48029	3167	1138911	2306050	3444960	438.77	50.19	588.68
151	25	0	0.00776	25	0	0	0	.	.	.
152	1330	0	0.15581	1330	736935	1428430	2165363	287.23	27.71	346.37
153	992	0	0.18888	992	579948	987518	1567463	197.55	18.43	207.73
154	2136	0	0.46344	2136	806918	1383080	2190002	250.92	20.63	268.19
155	84591	0.05343	2.51101	82791	10545082	19433900	29979000	2581.18	321.24	3551.56
156	1683880	0.00177	9.94142	1680000	184939636	286368000	471306000	66688.4	6655.37	70936.2
157	656011	0	6.72652	656000	74589895	77083900	151674100	36441.1	3949.65	26634.6
158	527962	0	35.99905	528000	13085489	28599800	41685400	5485.8	696.62	6427.7
159	187232	0	1.431	187000	57348227	45099900	102448600	33020.5	2644.21	13401.8
160	3898	0	0.47146	3898	1944866	1733070	3677930	985.18	125.16	609.63
161	5185	0	2.38940	5185	3680611	6451890	10132480	955.26	86.91	1105
162	782095	0.46132	26.72550	769000	48091685	77661100	125752300	11638.2	3189.85	13667.4
163	4829	0	3.20864	4829	3818650	5610840	9429470	958.52	98.07	1077.55

Sheet 31

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
164	0	0	0	0	0	0	0	0	0	0
165	0	0	0	0	0	0	0	0	0	0
166	0	0	0	0	0	0	0	0	0	0
167	256	0	0.04637	256	0	0	0	0	0	0
168	8	0	0.00022	8	0	0	0	0	0	0
169	0	0	0	0	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0
171	45	0	0.00066	45	0	0	0	0	0	0
172	1591	0	0.04532	1591	0	0	0	0	0	0
173	1	0	0.00004	1	0	0	0	0	0	0
174	666	0	0.03102	666	0	0	0	0	0	0
175	605	0	0.02387	605	0	0	0	0	0	0
176	2091	0	0.03877	2091	0	0	0	0	0	0
177	20880	0	0.62243	20880	0	0	0	0	0	0
178	33	0	0.00098	33	0	0	0	0	0	0
179	63	0	0.00270	63	0	0	0	0	0	0
180	3329	0	0.03332	3329	0	0	0	.	.	.
181	1413	0	0.04357	1413	0	0	0	0	0	0
182	137	0	0.00558	137	0	0	0	0	0	0
183	30	0	0.00084	30	0	0	0	0	0	0
184	0	0	0	0	0	0	0	0	0	0
185	0	0	0	0	0	0	0	0	0	0
186	1409	0	0.06126	1409	0	0	0	0	0	0
187	1666	0	0.31001	1666	99	6823	6922	0.39	0.33	4.92
188	2312	0	0.38001	2312	0	0	0	0	0	0
189	3004	0	1.15140	3004	0	0	0	.	.	.
190	24332	0	1.97741	24332	35977	77298	113275	1.49	0.09	9.95

Sheet 32

ER	Pop1991	PopD1871	PopD1991	PopGr	$ Pesticide	$ Fertilizer	$ P + F	AHerb	AIns	AFert
191	35540	0	0.76264	35540	0	0	0	.	.	.
192	36511	0.01029	0.62622	35911	184841	532224	717066	5.44	2.99	21.27
193	20485	0	1.13396	20485	0	0	0	.	.	.
194	547592	0.41506	41.32458	542000	514102	2711930	3226036	18.28	8.15	125.08
195	20847	0	18.61339	20847	21953	144116	166069	0.3	0.27	7.63
196	1810020	0.33723	406.92963	1810000	7109842	18942100	26052000	173.26	113.21	401.8
197	672	0	2.48889	672	3160	32456	35616	0.37	0.05	1.14
198	0	0	0	0	0	0	0	0	0	0
199	6070	0	0.18136	6070	0	0	0	0	0	0
200	3778	0	0.10671	3778	27253	67283	94536	6.77	0	14.35
201	931	0	0.33805	931	175	23026	23201	0	0.04	6.27
202	69396	0	0.78482	69396	205882	2030790	2236670	15.72	1.2	427.95
203	110605	0.02705	2.49357	109000	103382	1200860	1304242	6.34	0.27	286.27
204	337	0	0.02928	337	0	22960	22960	0	0	2.85
205	57037	0.00693	0.65870	56437	528189	1044610	1572800	46	9.54	109.79
206	1235	0	0.05306	1235	7291	49801	57092	3.44	0	10.36
207	10100	0	0.25967	10100	0	0	0	.	.	.
208	6897	0.03995	0.45919	6297	21312	93906	115218	1.25	3.63	11.01
209	344502	0	9.19751	345000	3824810	4287520	8112340	123.57	74.96	352.5
210	3937	0	0.90527	3937	332950	393608	726558	6.23	7.14	20.15
211	22979	0	22.72898	22979	1110094	1101860	2211950	21.84	24.46	51.6
212	33716	0	4.32589	33716	11033	71967	83000	0.59	0	9.46
213	44995	0	5.95881	44995	53910	558613	612523	12.01	2.42	94
214	35246	0	2.30773	35246	112428	436951	549379	54.81	2.5	99.37
215	1628	0	0.02782	1628	0	0	0	.	.	.
216	1218	0	0.00943	1218	0	0	0	.	.	.
217	7092	0	0.04151	7092	0	0	0	0	0	0

Sheet 33

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
1	0	0	5	0.00015	99	0	-19
2	0	0	1	0.00004	100	0	-19
3	0	0	1	0.00008	100	0	-19
4	0	0	8	0.00017	49	0	-19
5	24.09	0.0003	56	0.00069	54	0	-12
6	0	0	14	0.00168	35	0	-12
7	0	0	15	0.00051	99	0	-6
8	0	0	30	0.00075	37	0	-16
9	0	0	36	0.00046	33	0	-17
10	0	0	15	0.00127	66	0	-16
11	0	0	38	0.00061	25	0	-18
12	8.62	0.00015	48	0.00085	49	0	-18
13	0	0	42	0.00043	37	0	-13
14	0	0	3	0.00030	100	0	-14
15	0	0	3	0.00006	100	0	-16
16	24.49	0.0003	39	0.00047	85	0	-14
17	0	0	5	0.00023	100	0	-16
18	14.83	0.00009	32	0.00019	51	0	-14
19	0	0	10	0.00063	56	0	-16
20	0	0	10	0.00031	77	0	-13
21	11.85	0.00051	17	0.00073	39	0	-15
22	41.04	0.0014	17	0.00058	75	0	-13
23	22.14	0.00021	23	0.00022	81	0	-13
24	83.79	0.00111	9	0.00012	98	0	-12
25	24.29	0.0005	37	0.00076	44	0	-11
26	0	0	47	0.00161	20	0	-10
27	0	0	2	0.00006	100	0	-12
28	0	0	57	0.00083	57	0	-12

Sheet 34

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
29	0	0	1	0.00007	100	0	-12
30	11.48	0.00005	34	0.00014	93	0	-11
31	63.56	0.00188	9	0.00027	99	1	-9
32	0	0	9	0.00166	97	0	-11
33	150.28	0.00818	36	0.00196	39	3	-12
34	0	0	8495	0.57202	39	0	-12
35	0	0	3	0.00006	100	0	-11
36	0	0	9	0.00017	100	0	-11
37	0	0	1	0.00005	100	0	-11
38	0	0	35	0.00424	40	0	-13
39	0	0	13	0.00021	99	0	-11
40	0	0	13	0.00069	73	0	-12
41	0	0	8	0.00007	100	0	-11
42	0	0	6	0.00008	100	0	-11
43	0	0	3	0.00008	100	0	-11
44	0	0	2	0.00004	100	0	-11
45	0	0	20	0.00027	99	0	-10
46	18.73	0.00053	8	0.00023	69	0	-11
47	0	0	21	0.00015	100	0	-7
48	0	0	5	0.02732	44	0	-9
49	0	0	15	0.00598	48	0	-6
50	0	0	7	0.00084	99	0	-10
51	174.34	0.00305	11	0.00019	51	0	-6
52	334.81	0.0045	55	0.00074	74	1	-8
53	59.22	0.00208	16	0.00056	99	1	-8
54	0	0	1	0.00005	100	0	-10
55	553.17	0.01403	21	0.00053	51	1	-7

Sheet 35

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
56	138.7	0.00909	34	0.00223	94	1	-7
57	0	0	2	0.00029	100	0	-8
58	322.84	0.05334	15	0.00248	75	16	-6
59	29.64	0.00118	4	0.00016	99	0	-7
60	458.14	0.01292	25	0.0007	70	3	-6
61	0	0	3	0.00026	100	0	-5
62	0	0	4	0.00031	100	0	-5
63	364.44	0.01568	13	0.00056	62	3	-6
64	2595.46	0.02244	136	0.00118	46	5	-3
65	349.84	0.00601	20	0.00034	88	1	-2
66	267.49	0.0117	17	0.00074	38	2	-1
67	0	0	6	0.00049	100	0	-2
68	145.09	0.00115	25	0.0002	99	0	-8
69	296.72	0.0031	71	0.00074	97	1	-5
70	0	0	7	0.00004	100	0	-8
71	0	0	17	0.00009	100	0	-5
72	332.48	0.00279	28	0.00023	91	1	-4
73	0	0	10	0.00013	100	0	-6
74	0	0	21	0.00012	100	0	-5
75	35.16	0.00042	17	0.0002	98	0	-5
76	0	0	5	0.00023	100	0	-5
77	0	0	13	0.00021	99	0	-4
78	395.19	0.00548	123	0.00171	52	0	-4
79	0	0	141	0.01211	17	0	-4
80	0	0	2	0.00033	100	0	-1
81	0	0	1	0.00035	100	0	-4
82	0	0	1	0.00008	100	0	1

Sheet 36

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
83	0	0	1	0.0004	100	0	-1
84	29.77	0.0097	5	0.00163	93	4	-3
85	58.14	0.01162	3	0.0006	92	4	-4
86	179.53	0.00396	16	0.00035	94	1	-1
87	155.97	0.00229	63	0.00092	98	1	-4
88	1623.59	0.00912	121	0.00068	37	1	-3
89	519.59	0.00396	52	0.0004	93	1	-4
90	1303.84	0.00926	66	0.00047	89	2	1
91	2398.76	0.05597	99	0.00231	19	21	2
92	487.06	0.15611	26	0.00833	20	47	2
93	1300.4	0.05299	57	0.00232	39	10	1
94	3026.99	0.03979	108	0.00142	51	13	2
95	204.84	0.00191	25	0.00023	99	0	-2
96	6201.35	0.0352	178	0.00101	26	12	1
97	3560.29	0.04264	123	0.00147	14	15	3
98	3504.89	0.05057	232	0.00335	17	19	4
99	8304.4	0.0493	313	0.00186	34	15	2
100	431.04	0.00481	52	0.00058	75	1	0
101	4562.49	0.02238	197	0.00097	89	7	0
102	332.22	0.04349	284	0.03718	71	0	2
103	238.63	0.00251	123	0.00129	2	0	1
104	35.47	0.00191	8	0.00043	99	1	0
105	252.66	0.01437	18	0.00102	59	6	-2
106	236.74	0.1013	27	0.01155	39	18	3
107	418.95	0.05301	60	0.00759	33	7	3
108	4	0.00064	9	0.00144	99	0	4
109	784.73	0.07699	59	0.00579	22	26	4

Sheet 37

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
110	51.16	0.00806	16	0.00252	96	3	4
111	5.01	0.00161	6	0.00193	97	1	4
112	2114.61	0.07184	115	0.00391	12	23	5
113	597.52	0.11012	134	0.0247	13	9	4
114	1929.06	0.05649	175	0.00513	31	9	6
115	45.19	0.08878	5	0.00982	54	33	6
116	177.03	0.09706	19	0.01042	21	17	6
117	6663.39	0.10065	370	0.00559	8	25	4
118	2095.64	0.08824	146	0.00615	20	22	4
119	199.77	0.03912	18	0.00352	75	8	3
120	585.59	0.18793	54	0.01733	8	57	5
121	1283.17	0.10346	82	0.00661	17	19	5
122	3660.84	0.12196	197	0.00656	7	43	5
123	749.96	0.18006	123	0.02953	4	13	6
124	1416.65	0.08733	68	0.00419	33	27	7
125	857.74	0.14713	166	0.02847	6	7	7
126	696.96	0.15244	78	0.01706	10	55	7
127	565.65	0.08819	70	0.01091	17	15	7
128	2000.8	0.13055	163	0.01064	3	34	6
129	33.37	0.01409	19	0.00802	80	2	5
130	843.49	0.15557	59	0.01088	3	75	6
131	67.63	0.2727	13	0.05242	8	48	5
132	5146.82	0.12432	482	0.01164	1	82	5
133	92.03	0.10956	16	0.01905	17	71	5
134	4244.64	0.09017	491	0.01043	2	70	6
135	3283.72	0.13086	196	0.00781	0	95	8
136	740.23	0.01577	42	0.00089	57	4	-2

Sheet 38

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
137	986.71	0.02287	65	0.00151	73	8	-1
138	5920.68	0.08853	241	0.0036	13	41	1
139	29.12	0.00368	10	0.00126	98	1	0
140	66.93	0.02121	4	0.00127	82	9	0
141	0	0	10	0.00086	99	0	0
142	552.65	0.01121	38	0.00077	91	1	1
143	772.03	0.06912	58	0.00519	10	16	1
144	928.47	0.03763	66	0.00268	27	5	0
145	4359.44	0.06077	212	0.00296	11	20	2
146	93.56	0.05804	13	0.00806	15	58	2
147	3633.37	0.03108	135	0.00115	51	9	0
148	1780.01	0.02811	186	0.00294	30	5	-1
149	12841.46	0.13125	436	0.00446	2	75	1
150	480.61	0.07289	34	0.00516	21	22	0
151	83.43	0.0259	15	0.00466	86	11	0
152	623.03	0.07299	24	0.00281	19	19	0
153	444.13	0.08456	18	0.00343	14	39	0
154	353.82	0.07677	23	0.00499	17	42	0
155	3410.04	0.10122	167	0.00496	12	33	1
156	22680.79	0.1339	178	0.00105	0	96	2
157	13228.43	0.13564	24	0.00025	0	99	3
158	1742.8	0.11883	12	0.00082	0	99	4
159	17181.96	0.13132	31	0.00024	0	99	4
160	934.62	0.11304	13	0.00157	1	97	3
161	317.93	0.14651	9	0.00415	8	87	2
162	4326.47	0.14784	104	0.00355	2	85	3
163	200.6	0.13329	3	0.00199	0	100	1

Sheet 39

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
164	34.59	0.06221	9	0.01619	22	39	1
165	75.98	0.00306	6	0.00024	83	1	-10
166	0	0	2	0.00015	100	0	-10
167	0	0	2	0.00036	100	0	-10
168	113.2	0.00317	5	0.00014	69	1	-6
169	180.35	0.00933	5	0.00026	76	4	-7
170	287.12	0.00351	13	0.00016	74	1	-5
171	337.41	0.00496	15	0.00022	69	1	-5
172	1513.24	0.0431	56	0.0016	40	12	-6
173	12.47	0.00056	15	0.00067	99	0	-2
174	638.63	0.02975	25	0.00116	56	6	-3
175	652.44	0.02574	28	0.0011	23	9	-4
176	1139.12	0.02112	34	0.00063	60	5	-4
177	1024.94	0.03055	39	0.00116	22	9	-3
178	226.89	0.00677	24	0.00072	57	1	-3
179	252.63	0.01081	25	0.00107	50	3	-1
180	1536.3	0.01538	50	0.0005	59	5	-2
181	796.26	0.02455	15	0.00046	30	9	-3
182	98.81	0.00402	8	0.00033	98	1	-2
183	212.84	0.00593	7	0.00019	88	2	-1
184	0	0	2	0.00054	100	0	0
185	14.48	0.00572	3	0.00118	63	3	-1
186	107.57	0.00468	26	0.00113	75	1	-1
187	507.05	0.09435	23	0.00428	38	22	2
188	127.18	0.0209	39	0.00641	52	6	8
189	72.63	0.02784	23	0.00882	44	9	8
190	533	0.04332	28	0.00228	33	15	5

Sheet 40

ER	RR	RRD	# P	PDens	LPI_nat	LPI_hum	MAT
191	257.45	0.00552	148	0.00318	57	1	7
192	616.01	0.01057	123	0.00211	73	2	8
193	1162.16	0.06433	89	0.00493	18	15	9
194	1985.71	0.14985	110	0.0083	15	51	9
195	211.98	0.18927	71	0.06339	10	19	9
196	616.08	0.13851	56	0.01259	10	59	9
197	25.78	0.09548	6	0.02222	31	34	9
198	156.96	0.00715	31	0.00141	79	2	1
199	681.84	0.02037	21	0.00063	89	4	2
200	323.76	0.00914	40	0.00113	50	1	2
201	30.97	0.01125	6	0.00218	93	2	3
202	4102.83	0.0464	149	0.00169	49	10	3
203	2182.02	0.04919	92	0.00207	34	15	3
204	49.08	0.00426	14	0.00122	98	1	4
205	2962.65	0.03421	179	0.00207	29	9	5
206	717.06	0.03081	52	0.00223	37	9	4
207	996.15	0.02561	77	0.00198	37	6	3
208	792.88	0.05279	35	0.00233	29	18	6
209	3245.59	0.08665	157	0.00419	10	36	6
210	202.43	0.04655	20	0.0046	42	12	7
211	185.53	0.18351	21	0.02077	12	45	8
212	487.76	0.06258	29	0.00372	52	15	6
213	1090.78	0.14446	74	0.0098	17	37	5
214	1329.98	0.08708	86	0.00563	14	32	4
215	0	0	22	0.00038	53	0	-4
216	0	0	14	0.00011	98	0	-4
217	266.81	0.00156	35	0.0002	94	0	-2

Appendix 9: Correlation matrices for variables examined in Chapter 3

For explanations of abbreviations used in the following tables, see Appendix 10.

A) Spearman rank correlation matrix for variables examined in regression analyses of all 217 Canadian terrestrial ecoregions.

B) Spearman rank correlation matrix for variables examined in regression analyses of the 80 Canadian terrestrial ecoregions with detected human landcover.

A (217 ecoregions) Sheet 1

	SRt	SRb	SRm	SRa	SRr	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr
SRt	1	0.985	0.927	0.877	0.868	0.750	0.759	-0.032	0.607	0.375	0.821	0.741	0.780	0.382	0.268
SRb	0.985	1	0.880	0.836	0.828	0.736	0.741	-0.020	0.595	0.333	0.813	0.731	0.777	0.413	0.226
SRm	0.927	0.880	1	0.801	0.779	0.746	0.666	0.120	0.467	0.361	0.703	0.635	0.681	0.281	0.248
SRa	0.877	0.836	0.801	1	0.900	0.570	0.691	-0.270	0.717	0.329	0.813	0.725	0.738	0.340	0.253
SRr	0.868	0.828	0.779	0.900	1	0.594	0.697	-0.244	0.663	0.423	0.782	0.716	0.728	0.332	0.306
ISRt	0.750	0.736	0.746	0.570	0.594	1	0.809	0.323	0.472	0.361	0.594	0.552	0.541	0.367	0.273
ISRb	0.759	0.741	0.666	0.691	0.697	0.809	1	-0.190	0.594	0.362	0.724	0.684	0.657	0.290	0.277
ISRm	-0.032	-0.020	0.120	-0.270	-0.244	0.323	-0.190	1	-0.399	-0.091	-0.303	-0.282	-0.250	0.055	-0.138
ISRa	0.607	0.595	0.467	0.717	0.663	0.472	0.594	-0.399	1	0.160	0.729	0.628	0.603	0.455	0.178
ISRr	0.375	0.333	0.361	0.329	0.423	0.361	0.362	-0.091	0.160	1	0.297	0.304	0.252	0.047	0.711
SLt	0.821	0.813	0.703	0.813	0.782	0.594	0.724	-0.303	0.729	0.297	1	0.930	0.935	0.392	0.253
SLb	0.741	0.731	0.635	0.725	0.716	0.552	0.684	-0.282	0.628	0.304	0.930	1	0.776	0.337	0.263
SLm	0.780	0.777	0.681	0.738	0.728	0.541	0.657	-0.250	0.603	0.252	0.935	0.776	1	0.365	0.184
SLa	0.382	0.413	0.281	0.340	0.332	0.367	0.290	0.055	0.455	0.047	0.392	0.337	0.365	1	0.124
SLr	0.268	0.226	0.248	0.253	0.306	0.273	0.277	-0.138	0.178	0.711	0.253	0.263	0.184	0.124	1
Area	-0.058	-0.036	-0.025	-0.104	-0.081	0.179	-0.056	0.340	0.017	0.011	-0.046	-0.005	-0.074	0.215	0.103
Pop1871	0.426	0.402	0.297	0.537	0.520	0.298	0.435	-0.308	0.524	0.231	0.460	0.466	0.341	0.135	0.249
PopD1871	0.423	0.398	0.294	0.536	0.521	0.294	0.434	-0.313	0.522	0.232	0.458	0.462	0.340	0.137	0.241
Pop1991	0.663	0.659	0.516	0.687	0.684	0.509	0.617	-0.216	0.578	0.285	0.688	0.672	0.594	0.377	0.247
PopD1991	0.666	0.655	0.504	0.695	0.699	0.445	0.639	-0.336	0.553	0.295	0.686	0.666	0.599	0.294	0.232
PopGr	0.663	0.660	0.520	0.677	0.672	0.507	0.607	-0.196	0.566	0.267	0.685	0.668	0.595	0.388	0.248
$Pest	0.739	0.727	0.604	0.732	0.779	0.547	0.691	-0.281	0.594	0.365	0.758	0.734	0.707	0.360	0.286
$Fert	0.743	0.733	0.602	0.738	0.779	0.531	0.682	-0.288	0.586	0.344	0.750	0.721	0.703	0.359	0.278
$P+F	0.744	0.734	0.603	0.738	0.780	0.533	0.684	-0.288	0.585	0.353	0.751	0.722	0.705	0.356	0.281

Sheet 2

	SRt	SRb	SRm	SRa	SRr	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr
AC	0.749	0.742	0.614	0.730	0.777	0.547	0.683	-0.267	0.579	0.349	0.751	0.718	0.712	0.371	0.279
%AC	0.742	0.728	0.611	0.734	0.785	0.523	0.683	-0.303	0.567	0.347	0.742	0.712	0.701	0.328	0.267
AC1861	0.283	0.248	0.174	0.441	0.428	0.193	0.355	-0.346	0.451	0.164	0.344	0.358	0.226	-0.048	0.271
AI	0.701	0.688	0.575	0.704	0.750	0.515	0.689	-0.318	0.578	0.342	0.741	0.720	0.692	0.305	0.285
AH	0.733	0.724	0.600	0.716	0.765	0.550	0.693	-0.282	0.590	0.350	0.759	0.736	0.711	0.358	0.277
Afert	0.746	0.739	0.612	0.730	0.775	0.541	0.682	-0.272	0.579	0.339	0.753	0.722	0.712	0.365	0.271
AR	0.412	0.385	0.432	0.321	0.428	0.396	0.449	-0.096	0.208	0.317	0.415	0.386	0.451	0.121	0.132
AB	0.534	0.520	0.424	0.595	0.563	0.432	0.504	-0.199	0.567	0.270	0.572	0.561	0.482	0.324	0.282
%AB	0.527	0.510	0.415	0.599	0.567	0.417	0.498	-0.212	0.568	0.258	0.566	0.554	0.475	0.305	0.262
AHD1	0.725	0.710	0.612	0.722	0.756	0.571	0.713	-0.303	0.633	0.367	0.763	0.723	0.712	0.348	0.288
AHD2	0.690	0.679	0.565	0.699	0.721	0.542	0.680	-0.314	0.669	0.361	0.750	0.724	0.680	0.359	0.291
%AHD1	0.721	0.699	0.612	0.724	0.764	0.561	0.715	-0.331	0.627	0.374	0.761	0.720	0.713	0.313	0.279
%AHD2	0.687	0.671	0.567	0.702	0.729	0.533	0.683	-0.335	0.664	0.365	0.749	0.722	0.680	0.329	0.283
RR	0.765	0.768	0.655	0.701	0.683	0.643	0.665	-0.036	0.522	0.241	0.697	0.652	0.649	0.403	0.216
RRD	0.761	0.743	0.631	0.740	0.734	0.526	0.705	-0.275	0.523	0.270	0.721	0.686	0.665	0.261	0.205
AF	0.519	0.549	0.501	0.443	0.286	0.511	0.365	0.283	0.299	0.015	0.447	0.410	0.379	0.309	0.012
AW	0.008	0.044	-0.014	-0.028	-0.067	0.124	-0.025	0.190	0.080	-0.001	0.090	0.137	0.028	0.198	0.084
AN	-0.152	-0.120	-0.116	-0.191	-0.189	0.057	-0.185	0.382	-0.087	-0.077	-0.173	-0.133	-0.199	0.169	-0.000
LPI_nat	-0.555	-0.536	-0.428	-0.562	-0.619	-0.454	-0.611	0.277	-0.467	-0.283	-0.566	-0.546	-0.516	-0.231	-0.242
LPI_hum	0.785	0.761	0.683	0.741	0.749	0.564	0.719	-0.256	0.517	0.309	0.737	0.695	0.699	0.265	0.236
# P	0.491	0.510	0.345	0.502	0.512	0.432	0.489	-0.059	0.447	0.164	0.511	0.508	0.425	0.372	0.175
PDens	0.551	0.546	0.388	0.579	0.578	0.274	0.533	-0.378	0.415	0.194	0.559	0.520	0.511	0.162	0.124
MAT	0.763	0.739	0.646	0.822	0.733	0.436	0.646	-0.328	0.524	0.308	0.737	0.670	0.678	0.258	0.214

Sheet 3

	Area	Pop1871	PopD1871	Pop1991	PopD1991	PopGr	$Pest	$Fert	$P+F	AC	%AC	AC1861	AI	AH
SRt	-0.058	0.426	0.423	0.663	0.666	0.663	0.739	0.743	0.744	0.749	0.742	0.283	0.701	0.733
SRb	-0.036	0.402	0.398	0.659	0.655	0.660	0.727	0.733	0.734	0.742	0.728	0.248	0.688	0.724
SRm	-0.025	0.297	0.294	0.516	0.504	0.520	0.604	0.602	0.603	0.614	0.611	0.174	0.575	0.600
SRa	-0.104	0.537	0.536	0.687	0.695	0.677	0.732	0.738	0.738	0.730	0.734	0.441	0.704	0.716
SRr	-0.081	0.520	0.521	0.684	0.699	0.672	0.779	0.779	0.780	0.777	0.785	0.428	0.750	0.765
ISRt	0.179	0.298	0.294	0.509	0.445	0.507	0.547	0.531	0.533	0.547	0.523	0.193	0.515	0.550
ISRb	-0.056	0.435	0.434	0.617	0.639	0.607	0.691	0.682	0.684	0.683	0.683	0.355	0.689	0.693
ISRm	0.340	-0.308	-0.313	-0.216	-0.336	-0.196	-0.281	-0.288	-0.288	-0.267	-0.303	-0.346	-0.318	-0.282
ISRa	0.017	0.524	0.522	0.578	0.553	0.566	0.594	0.586	0.585	0.579	0.567	0.451	0.578	0.590
ISRr	0.011	0.231	0.232	0.285	0.295	0.267	0.365	0.344	0.353	0.349	0.347	0.164	0.342	0.350
SLt	-0.046	0.460	0.458	0.688	0.686	0.685	0.758	0.750	0.751	0.751	0.742	0.344	0.741	0.759
SLb	-0.005	0.466	0.462	0.672	0.666	0.668	0.734	0.721	0.722	0.718	0.712	0.358	0.720	0.736
SLm	-0.074	0.341	0.340	0.594	0.599	0.595	0.707	0.703	0.705	0.712	0.701	0.226	0.692	0.711
SLa	0.215	0.135	0.137	0.377	0.294	0.388	0.360	0.359	0.356	0.371	0.328	-0.048	0.305	0.358
SLr	0.103	0.249	0.241	0.247	0.232	0.248	0.286	0.278	0.281	0.279	0.267	0.271	0.285	0.277
Area	1	0.037	0.020	0.153	-0.114	0.171	-0.042	-0.049	-0.052	-0.031	-0.122	-0.017	-0.059	-0.039
Pop1871	0.037	1	0.998	0.596	0.576	0.565	0.592	0.607	0.602	0.566	0.548	0.739	0.585	0.560
PopD1871	0.020	0.998	1	0.593	0.577	0.560	0.591	0.605	0.601	0.563	0.550	0.730	0.585	0.559
Pop1991	0.153	0.596	0.593	1	0.947	0.996	0.764	0.773	0.771	0.760	0.740	0.439	0.731	0.743
PopD1991	-0.114	0.576	0.577	0.947	1	0.937	0.777	0.788	0.787	0.770	0.782	0.443	0.751	0.755
PopGr	0.171	0.565	0.560	0.996	0.937	1	0.753	0.763	0.761	0.752	0.727	0.415	0.719	0.734
$Pest	-0.042	0.592	0.591	0.764	0.777	0.753	1	0.989	0.990	0.986	0.980	0.462	0.971	0.987
$Fert	-0.049	0.607	0.605	0.773	0.788	0.763	0.989	1	1.000	0.995	0.988	0.471	0.960	0.977
$P+F	-0.052	0.602	0.601	0.771	0.787	0.761	0.990	1.000	1	0.995	0.989	0.468	0.962	0.978

Sheet 4

	Area	Pop1871	PopD1871	Pop1991	PopD1991	PopGr	$Pest	$Fert	$P+F	AC	%AC	AC1861	AI	AH
AC	-0.031	0.566	0.563	0.760	0.770	0.752	0.986	0.995	0.995	1	0.988	0.435	0.953	0.978
%AC	-0.122	0.548	0.550	0.740	0.782	0.727	0.980	0.988	0.989	0.988	1	0.425	0.953	0.971
AC1861	-0.017	0.739	0.730	0.439	0.443	0.415	0.462	0.471	0.468	0.435	0.425	1	0.466	0.433
AI	-0.059	0.585	0.585	0.731	0.751	0.719	0.971	0.960	0.962	0.953	0.953	0.466	1	0.966
AH	-0.039	0.560	0.559	0.743	0.755	0.734	0.987	0.977	0.978	0.978	0.971	0.433	0.966	1
Afert	-0.042	0.568	0.566	0.760	0.773	0.752	0.987	0.997	0.997	0.999	0.989	0.436	0.958	0.980
AR	-0.034	0.003	0.003	0.299	0.306	0.308	0.451	0.435	0.440	0.454	0.462	-0.102	0.466	0.461
AB	0.152	0.675	0.668	0.743	0.677	0.739	0.700	0.708	0.702	0.681	0.647	0.561	0.682	0.666
%AB	0.109	0.681	0.677	0.738	0.685	0.733	0.698	0.705	0.700	0.675	0.650	0.581	0.681	0.663
AHD1	0.007	0.552	0.550	0.742	0.723	0.733	0.901	0.894	0.894	0.894	0.879	0.451	0.903	0.896
AHD2	0.013	0.560	0.557	0.729	0.707	0.718	0.881	0.870	0.870	0.867	0.852	0.476	0.879	0.874
%AHD1	-0.061	0.537	0.538	0.720	0.722	0.707	0.893	0.883	0.884	0.880	0.882	0.438	0.897	0.888
%AHD2	-0.045	0.551	0.551	0.712	0.707	0.697	0.874	0.862	0.863	0.856	0.855	0.468	0.874	0.867
RR	0.180	0.512	0.505	0.795	0.728	0.797	0.736	0.741	0.739	0.742	0.701	0.375	0.700	0.728
RRD	-0.244	0.494	0.499	0.734	0.809	0.722	0.773	0.782	0.782	0.768	0.791	0.388	0.754	0.762
AF	0.438	0.209	0.196	0.402	0.257	0.414	0.215	0.220	0.217	0.231	0.165	0.108	0.177	0.210
AW	0.724	0.088	0.075	0.225	0.022	0.237	-0.007	-0.007	-0.010	0.002	-0.071	-0.002	-0.024	-0.010
AN	0.935	-0.013	-0.029	0.034	-0.218	0.050	-0.192	-0.196	-0.200	-0.181	-0.269	-0.043	-0.214	-0.191
LPI_nat	0.115	-0.484	-0.486	-0.684	-0.733	-0.672	-0.719	-0.721	-0.721	-0.711	-0.728	-0.365	-0.704	-0.713
LPI_hum	-0.256	0.462	0.464	0.704	0.780	0.694	0.787	0.794	0.795	0.785	0.803	0.361	0.774	0.782
# P	0.343	0.530	0.523	0.759	0.654	0.760	0.568	0.575	0.571	0.566	0.519	0.400	0.530	0.556
PDens	-0.504	0.446	0.451	0.570	0.716	0.555	0.580	0.593	0.592	0.573	0.606	0.367	0.563	0.566
MAT	-0.322	0.500	0.503	0.689	0.772	0.679	0.661	0.679	0.679	0.659	0.677	0.374	0.628	0.637

Sheet 5

	Afert	AR	AB	%AB	AHD1	AHD2	%AHD1	%AHD2	RR	RRD	AF	AW	AN	LPI_nat
SRt	0.746	0.412	0.534	0.527	0.725	0.690	0.721	0.687	0.765	0.761	0.519	0.008	-0.152	-0.555
SRb	0.739	0.385	0.520	0.510	0.710	0.679	0.699	0.671	0.768	0.743	0.549	0.044	-0.120	-0.536
SRm	0.612	0.432	0.424	0.415	0.612	0.565	0.612	0.567	0.655	0.631	0.501	-0.014	-0.116	-0.428
SRa	0.730	0.321	0.595	0.599	0.722	0.699	0.724	0.702	0.701	0.740	0.443	-0.028	-0.191	-0.562
SRr	0.775	0.428	0.563	0.567	0.756	0.721	0.764	0.729	0.683	0.734	0.286	-0.067	-0.189	-0.619
ISRt	0.541	0.396	0.432	0.417	0.571	0.542	0.561	0.533	0.643	0.526	0.511	0.124	0.057	-0.454
ISRb	0.682	0.449	0.504	0.498	0.713	0.680	0.715	0.683	0.665	0.705	0.365	-0.025	-0.185	-0.611
ISRm	-0.272	-0.096	-0.199	-0.212	-0.303	-0.314	-0.331	-0.335	-0.036	-0.275	0.283	0.190	0.382	0.277
ISRa	0.579	0.208	0.567	0.568	0.633	0.669	0.627	0.664	0.522	0.523	0.299	0.080	-0.087	-0.467
ISRr	0.339	0.317	0.270	0.258	0.367	0.361	0.374	0.365	0.241	0.270	0.015	-0.001	-0.077	-0.283
SLt	0.753	0.415	0.572	0.566	0.763	0.750	0.761	0.749	0.697	0.721	0.447	0.090	-0.173	-0.566
SLb	0.722	0.386	0.561	0.554	0.723	0.724	0.720	0.722	0.652	0.686	0.410	0.137	-0.133	-0.546
SLm	0.712	0.451	0.482	0.475	0.712	0.680	0.713	0.680	0.649	0.665	0.379	0.028	-0.199	-0.516
SLa	0.365	0.121	0.324	0.305	0.348	0.359	0.313	0.329	0.403	0.261	0.309	0.198	0.169	-0.231
SLr	0.271	0.132	0.282	0.262	0.288	0.291	0.279	0.283	0.216	0.205	0.012	0.084	-0.000	-0.242
Area	-0.042	-0.034	0.152	0.109	0.007	0.013	-0.061	-0.045	0.180	-0.244	0.438	0.724	0.935	0.115
Pop1871	0.568	0.003	0.675	0.681	0.552	0.560	0.537	0.551	0.512	0.494	0.209	0.088	-0.013	-0.484
PopD1871	0.566	0.003	0.668	0.677	0.550	0.557	0.538	0.551	0.505	0.499	0.196	0.075	-0.029	-0.486
Pop1991	0.760	0.299	0.743	0.738	0.742	0.729	0.720	0.712	0.795	0.734	0.402	0.225	0.034	-0.684
PopD1991	0.773	0.306	0.677	0.685	0.723	0.707	0.722	0.707	0.728	0.809	0.257	0.022	-0.218	-0.733
PopGr	0.752	0.308	0.739	0.733	0.733	0.718	0.707	0.697	0.797	0.722	0.414	0.237	0.050	-0.672
$Pest	0.987	0.451	0.700	0.698	0.901	0.881	0.893	0.874	0.736	0.773	0.215	-0.007	-0.192	-0.719
$Fert	0.997	0.435	0.708	0.705	0.894	0.870	0.883	0.862	0.741	0.782	0.220	-0.007	-0.196	-0.721
$P+F	0.997	0.440	0.702	0.700	0.894	0.870	0.884	0.863	0.739	0.782	0.217	-0.010	-0.200	-0.721

Sheet 6

	Afert	AR	AB	%AB	AHD1	AHD2	%AHD1	%AHD2	RR	RRD	AF	AW	AN	LPI_nat
AC	0.999	0.454	0.681	0.675	0.894	0.867	0.880	0.856	0.742	0.768	0.231	0.002	-0.181	-0.711
%AC	0.989	0.462	0.647	0.650	0.879	0.852	0.882	0.855	0.701	0.791	0.165	-0.071	-0.269	-0.728
AC1861	0.436	-0.102	0.561	0.581	0.451	0.476	0.438	0.468	0.375	0.388	0.108	-0.002	-0.043	-0.365
AI	0.958	0.466	0.682	0.681	0.903	0.879	0.897	0.874	0.700	0.754	0.177	-0.024	-0.214	-0.704
AH	0.980	0.461	0.666	0.663	0.896	0.874	0.888	0.867	0.728	0.762	0.210	-0.010	-0.191	-0.713
Afert	1	0.454	0.682	0.678	0.893	0.866	0.881	0.857	0.740	0.773	0.224	-0.006	-0.191	-0.713
AR	0.454	1	0.191	0.172	0.526	0.412	0.544	0.427	0.325	0.376	-0.008	-0.086	-0.219	-0.389
AB	0.682	0.191	1	0.995	0.771	0.802	0.739	0.775	0.672	0.582	0.286	0.203	0.009	-0.547
%AB	0.678	0.172	0.995	1	0.763	0.794	0.738	0.775	0.660	0.593	0.264	0.171	-0.023	-0.553
AHD1	0.893	0.526	0.771	0.763	1	0.967	0.992	0.961	0.725	0.726	0.244	0.037	-0.146	-0.678
AHD2	0.866	0.412	0.802	0.794	0.967	1	0.960	0.994	0.711	0.710	0.237	0.058	-0.141	-0.660
%AHD1	0.881	0.544	0.739	0.738	0.992	0.960	1	0.967	0.693	0.741	0.192	-0.018	-0.213	-0.690
%AHD2	0.857	0.427	0.775	0.775	0.961	0.994	0.967	1	0.685	0.724	0.195	0.010	-0.196	-0.671
RR	0.740	0.325	0.672	0.660	0.725	0.711	0.693	0.685	1	0.854	0.568	0.164	0.060	-0.702
RRD	0.773	0.376	0.582	0.593	0.726	0.710	0.741	0.724	0.854	1	0.267	-0.156	-0.358	-0.796
AF	0.224	-0.008	0.286	0.264	0.244	0.237	0.192	0.195	0.568	0.267	1	0.423	0.467	-0.079
AW	-0.006	-0.086	0.203	0.171	0.037	0.058	-0.018	0.010	0.164	-0.156	0.423	1	0.687	0.139
AN	-0.191	-0.219	0.009	-0.023	-0.146	-0.141	-0.213	-0.196	0.060	-0.358	0.467	0.687	1	0.241
LPI_nat	-0.713	-0.389	-0.547	-0.553	-0.678	-0.660	-0.690	-0.671	-0.702	-0.796	-0.079	0.139	0.241	1
LPI_hum	0.789	0.432	0.585	0.590	0.763	0.738	0.776	0.749	0.815	0.957	0.240	-0.173	-0.385	-0.771
# P	0.564	0.127	0.587	0.579	0.543	0.538	0.502	0.507	0.740	0.567	0.448	0.291	0.288	-0.679
PDens	0.579	0.189	0.400	0.422	0.519	0.503	0.541	0.525	0.529	0.753	0.046	-0.318	-0.510	-0.742
MAT	0.664	0.285	0.527	0.539	0.601	0.579	0.611	0.589	0.666	0.808	0.342	-0.180	-0.395	-0.575

Sheet 7

	LPI_hum	# P	PDens	MAT
SRt	0.785	0.491	0.551	0.763
SRb	0.761	0.510	0.546	0.739
SRm	0.683	0.345	0.388	0.646
SRa	0.741	0.502	0.579	0.822
SRr	0.749	0.512	0.578	0.733
ISRt	0.564	0.432	0.274	0.436
ISRb	0.719	0.489	0.533	0.646
ISRm	-0.256	-0.059	-0.378	-0.328
ISRa	0.517	0.447	0.415	0.524
ISRr	0.309	0.164	0.194	0.308
SLt	0.737	0.511	0.559	0.737
SLb	0.695	0.508	0.520	0.670
SLm	0.699	0.425	0.511	0.678
SLa	0.265	0.372	0.162	0.258
SLr	0.236	0.175	0.124	0.214
Area	-0.256	0.343	-0.504	-0.322
Pop1871	0.462	0.530	0.446	0.500
PopD1871	0.464	0.523	0.451	0.503
Pop1991	0.704	0.759	0.570	0.689
PopD1991	0.780	0.654	0.716	0.772
PopGr	0.694	0.760	0.555	0.679
$Pest	0.787	0.568	0.580	0.661
$Fert	0.794	0.575	0.593	0.679
$P+F	0.795	0.571	0.592	0.679

Sheet 8

	LPI_hum	# P	PDens	MAT
AC	0.785	0.566	0.573	0.659
%AC	0.803	0.519	0.606	0.677
AC1861	0.361	0.400	0.367	0.374
AI	0.774	0.530	0.563	0.628
AH	0.782	0.556	0.566	0.637
Afert	0.789	0.564	0.579	0.664
AR	0.432	0.127	0.189	0.285
AB	0.585	0.587	0.400	0.527
%AB	0.590	0.579	0.422	0.539
AHD1	0.763	0.543	0.519	0.601
AHD2	0.738	0.538	0.503	0.579
%AHD1	0.776	0.502	0.541	0.611
%AHD2	0.749	0.507	0.525	0.589
RR	0.815	0.740	0.529	0.666
RRD	0.957	0.567	0.753	0.808
AF	0.240	0.448	0.046	0.342
AW	-0.173	0.291	-0.318	-0.180
AN	-0.385	0.288	-0.510	-0.395
LPI_nat	-0.771	-0.679	-0.742	-0.575
LPI_hum	1	0.487	0.712	0.782
# P	0.487	1	0.600	0.472
PDens	0.712	0.600	1	0.726
MAT	0.782	0.472	0.726	1

B (80 ecoregions) Sheet 1

	SRt	SRb	SRm	SRa	SRr	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr
SRt	1	0.859	0.833	0.602	0.730	0.630	0.523	0.141	0.330	0.521	0.448	0.428	0.332	0.206	0.385
SRb	0.859	1	0.568	0.330	0.405	0.557	0.423	0.233	0.238	0.347	0.433	0.426	0.346	0.300	0.213
SRm	0.833	0.568	1	0.440	0.661	0.527	0.377	0.276	0.082	0.472	0.231	0.188	0.270	0.064	0.306
SRa	0.602	0.330	0.440	1	0.833	0.314	0.401	-0.258	0.578	0.325	0.318	0.345	0.004	0.041	0.314
SRr	0.730	0.405	0.661	0.833	1	0.491	0.557	-0.178	0.425	0.587	0.341	0.342	0.120	-0.051	0.439
ISRt	0.630	0.557	0.527	0.314	0.491	1	0.819	0.304	0.429	0.472	0.656	0.563	0.601	0.357	0.391
ISRb	0.523	0.423	0.377	0.401	0.557	0.819	1	-0.229	0.507	0.435	0.776	0.699	0.661	0.136	0.389
ISRm	0.141	0.233	0.276	-0.258	-0.178	0.304	-0.229	1	-0.294	-0.005	-0.218	-0.235	-0.016	0.311	-0.112
ISRa	0.330	0.238	0.082	0.578	0.425	0.429	0.507	-0.294	1	0.003	0.613	0.534	0.323	0.343	0.118
ISRr	0.521	0.347	0.472	0.325	0.587	0.472	0.435	-0.005	0.003	1	0.221	0.233	0.095	-0.067	0.717
SLt	0.448	0.433	0.231	0.318	0.341	0.656	0.776	-0.218	0.613	0.221	1	0.936	0.818	0.241	0.320
SLb	0.428	0.426	0.188	0.345	0.342	0.563	0.699	-0.235	0.534	0.233	0.936	1	0.632	0.139	0.337
SLm	0.332	0.346	0.270	0.004	0.120	0.601	0.661	-0.016	0.323	0.095	0.818	0.632	1	0.227	0.090
SLa	0.206	0.300	0.064	0.041	-0.051	0.357	0.136	0.311	0.343	-0.067	0.241	0.139	0.227	1	0.071
SLr	0.385	0.213	0.306	0.314	0.439	0.391	0.389	-0.112	0.118	0.717	0.320	0.337	0.090	0.071	1
Area	0.186	0.362	0.029	-0.005	-0.071	0.444	0.174	0.400	0.215	0.051	0.286	0.264	0.257	0.429	0.170
Pop1871	0.093	-0.001	-0.145	0.549	0.335	0.082	0.200	-0.332	0.490	0.096	0.150	0.222	-0.172	-0.128	0.193
PopD1871	0.065	-0.039	-0.162	0.542	0.332	0.055	0.191	-0.362	0.478	0.097	0.125	0.192	-0.184	-0.123	0.167
Pop1991	0.199	0.140	-0.000	0.449	0.310	0.375	0.395	-0.078	0.437	0.157	0.375	0.422	0.131	0.132	0.283
PopD1991	0.098	-0.087	-0.042	0.500	0.415	0.107	0.337	-0.413	0.318	0.168	0.198	0.268	-0.058	-0.174	0.217
PopGr	0.236	0.192	0.057	0.401	0.281	0.397	0.371	0.016	0.391	0.140	0.389	0.426	0.183	0.186	0.289
$Pest	0.335	0.314	0.171	0.311	0.346	0.564	0.712	-0.226	0.527	0.233	0.757	0.691	0.618	0.061	0.278
$Fert	0.338	0.314	0.164	0.361	0.340	0.522	0.664	-0.232	0.539	0.161	0.705	0.651	0.557	0.073	0.255
$P+F	0.345	0.317	0.172	0.355	0.356	0.537	0.682	-0.229	0.532	0.193	0.721	0.667	0.574	0.058	0.266
AC	0.367	0.390	0.229	0.226	0.270	0.620	0.689	-0.103	0.473	0.179	0.732	0.638	0.665	0.122	0.260

Sheet 2

	SRt	SRb	SRm	SRa	SRr	ISRt	ISRb	ISRm	ISRa	ISRr	SLt	SLb	SLm	SLa	SLr
%AC	0.307	0.210	0.248	0.270	0.367	0.448	0.672	-0.349	0.393	0.167	0.649	0.560	0.581	-0.076	0.208
AC1861	-0.004	-0.110	-0.186	0.543	0.368	0.034	0.199	-0.406	0.488	0.080	0.175	0.231	-0.157	-0.225	0.234
AI	0.296	0.267	0.154	0.290	0.334	0.527	0.691	-0.241	0.478	0.205	0.746	0.680	0.637	0.009	0.247
AH	0.315	0.325	0.177	0.185	0.246	0.595	0.704	-0.175	0.498	0.161	0.789	0.683	0.720	0.111	0.234
%ACI	0.049	-0.040	0.000	0.183	0.221	0.116	0.336	-0.308	0.145	0.158	0.337	0.352	0.276	-0.168	0.136
%ACH	0.187	0.151	0.119	0.041	0.166	0.419	0.562	-0.242	0.367	0.140	0.666	0.555	0.666	0.076	0.163
Afert	0.347	0.359	0.217	0.226	0.263	0.583	0.676	-0.133	0.474	0.141	0.747	0.667	0.668	0.096	0.225
AR	0.272	0.199	0.410	-0.064	0.226	0.434	0.512	0.053	-0.047	0.223	0.377	0.301	0.549	-0.013	0.057
AB	0.207	0.136	0.038	0.453	0.308	0.347	0.381	-0.124	0.455	0.163	0.394	0.436	0.142	0.104	0.289
%AB	0.135	0.043	-0.028	0.480	0.330	0.242	0.309	-0.202	0.459	0.115	0.326	0.376	0.057	0.031	0.220
AHD1	0.380	0.331	0.261	0.301	0.357	0.610	0.748	-0.172	0.442	0.234	0.712	0.628	0.638	0.085	0.276
AHD2	0.278	0.267	0.095	0.295	0.286	0.532	0.664	-0.244	0.554	0.203	0.716	0.651	0.554	0.106	0.277
%AHD1	0.327	0.201	0.254	0.297	0.416	0.529	0.744	-0.322	0.400	0.264	0.679	0.591	0.618	-0.051	0.243
%AHD2	0.241	0.169	0.091	0.301	0.338	0.458	0.655	-0.362	0.528	0.217	0.675	0.614	0.519	-0.004	0.248
RR	0.249	0.325	0.067	0.209	0.142	0.506	0.377	0.197	0.344	0.091	0.442	0.448	0.323	0.297	0.208
AF	0.088	0.353	-0.092	-0.066	-0.222	0.113	-0.169	0.440	0.032	-0.120	-0.042	-0.038	-0.046	0.383	-0.066
RRD	0.010	-0.163	-0.049	0.294	0.342	0.074	0.359	-0.447	0.283	0.057	0.258	0.295	0.079	-0.207	0.109
AW	0.200	0.410	-0.085	0.059	-0.070	0.315	0.085	0.302	0.227	0.036	0.242	0.274	0.105	0.356	0.154
AN	0.137	0.373	-0.066	-0.014	-0.171	0.194	-0.098	0.421	0.099	-0.035	0.036	0.044	-0.012	0.430	0.062
LPI_nat	-0.112	0.040	-0.044	-0.265	-0.342	-0.365	-0.619	0.391	-0.353	-0.186	-0.509	-0.478	-0.380	0.084	-0.266
LPI_hum	0.278	0.047	0.278	0.349	0.462	0.342	0.558	-0.343	0.322	0.210	0.473	0.443	0.373	-0.127	0.216
# P	0.133	0.271	-0.144	0.206	0.045	0.292	0.200	0.142	0.291	0.035	0.251	0.305	0.061	0.314	0.157
PDens	-0.065	-0.213	-0.167	0.290	0.213	-0.231	0.035	-0.420	0.074	0.020	-0.068	0.001	-0.240	-0.248	0.028
MAT	0.079	-0.173	0.098	0.444	0.456	-0.047	0.101	-0.232	0.060	0.305	-0.186	-0.122	-0.340	-0.156	0.205

Sheet 3

	Area	Pop1871	PopD1871	Pop1991	PopD1991	PopGr	$Pest	$Fert	$P+F	AC	%AC	AC1861	AI	AH
SRt	0.186	0.093	0.065	0.199	0.098	0.236	0.335	0.338	0.345	0.367	0.307	-0.004	0.296	0.315
SRb	0.362	-0.001	-0.039	0.140	-0.087	0.192	0.314	0.314	0.317	0.390	0.210	-0.110	0.267	0.325
SRm	0.029	-0.145	-0.162	-0.000	-0.042	0.057	0.171	0.164	0.172	0.229	0.248	-0.186	0.154	0.177
SRa	-0.005	0.549	0.542	0.449	0.500	0.401	0.311	0.361	0.355	0.226	0.270	0.543	0.290	0.185
SRr	-0.071	0.335	0.332	0.310	0.415	0.281	0.346	0.340	0.356	0.270	0.367	0.368	0.334	0.246
ISRt	0.444	0.082	0.055	0.375	0.107	0.397	0.564	0.522	0.537	0.620	0.448	0.034	0.527	0.595
ISRb	0.174	0.200	0.191	0.395	0.337	0.371	0.712	0.664	0.682	0.689	0.672	0.199	0.691	0.704
ISRm	0.400	-0.332	-0.362	-0.078	-0.413	0.016	-0.226	-0.232	-0.229	-0.103	-0.349	-0.406	-0.241	-0.175
ISRa	0.215	0.490	0.478	0.437	0.318	0.391	0.527	0.539	0.532	0.473	0.393	0.488	0.478	0.498
ISRr	0.051	0.096	0.097	0.157	0.168	0.140	0.233	0.161	0.193	0.179	0.167	0.080	0.205	0.161
SLt	0.286	0.150	0.125	0.375	0.198	0.389	0.757	0.705	0.721	0.732	0.649	0.175	0.746	0.789
SLb	0.264	0.222	0.192	0.422	0.268	0.426	0.691	0.651	0.667	0.638	0.560	0.231	0.680	0.683
SLm	0.257	-0.172	-0.184	0.131	-0.058	0.183	0.618	0.557	0.574	0.665	0.581	-0.157	0.637	0.720
SLa	0.429	-0.128	-0.123	0.132	-0.174	0.186	0.061	0.073	0.058	0.122	-0.076	-0.225	0.009	0.111
SLr	0.170	0.193	0.167	0.283	0.217	0.289	0.278	0.255	0.266	0.260	0.208	0.234	0.247	0.234
Area	1	0.129	0.051	0.470	-0.231	0.533	0.249	0.296	0.279	0.406	-0.137	0.069	0.184	0.278
Pop1871	0.129	1	0.985	0.665	0.632	0.555	0.296	0.382	0.360	0.184	0.113	0.783	0.256	0.121
PopD1871	0.051	0.985	1	0.622	0.649	0.494	0.274	0.352	0.332	0.146	0.130	0.752	0.243	0.100
Pop1991	0.470	0.665	0.622	1	0.724	0.975	0.563	0.662	0.634	0.504	0.288	0.526	0.473	0.387
PopD1991	-0.231	0.632	0.649	0.724	1	0.641	0.416	0.482	0.466	0.232	0.419	0.543	0.372	0.208
PopGr	0.533	0.555	0.494	0.975	0.641	1	0.538	0.640	0.612	0.503	0.246	0.430	0.445	0.379
$Pest	0.249	0.296	0.274	0.563	0.416	0.538	1	0.966	0.982	0.915	0.839	0.341	0.964	0.937
$Fert	0.296	0.382	0.352	0.662	0.482	0.640	0.966	1	0.995	0.930	0.819	0.396	0.918	0.896
$P+F	0.279	0.360	0.332	0.634	0.466	0.612	0.982	0.995	1	0.929	0.828	0.384	0.939	0.910
AC	0.406	0.184	0.146	0.504	0.232	0.503	0.915	0.930	0.929	1	0.816	0.245	0.874	0.944

Sheet 4

	Area	Pop1871	PopD1871	Pop1991	PopD1991	PopGr	$Pest	$Fert	$P+F	AC	%AC	AC1861	AI	AH
%AC	-0.137	0.113	0.130	0.288	0.419	0.246	0.839	0.819	0.828	0.816	1	0.196	0.841	0.849
AC1861	0.069	0.783	0.752	0.526	0.543	0.430	0.341	0.396	0.384	0.245	0.196	1	0.307	0.206
AI	0.184	0.256	0.243	0.473	0.372	0.445	0.964	0.918	0.939	0.874	0.841	0.307	1	0.931
AH	0.278	0.121	0.100	0.387	0.208	0.379	0.937	0.896	0.910	0.944	0.849	0.206	0.931	1
%ACI	-0.180	0.271	0.307	0.262	0.432	0.215	0.534	0.446	0.480	0.271	0.429	0.218	0.644	0.414
%ACH	0.022	-0.070	-0.049	0.085	0.095	0.077	0.730	0.603	0.639	0.623	0.690	-0.012	0.774	0.819
Afert	0.342	0.197	0.164	0.507	0.278	0.507	0.937	0.954	0.954	0.982	0.837	0.251	0.903	0.953
AR	0.081	-0.310	-0.310	0.043	-0.012	0.086	0.362	0.309	0.331	0.396	0.422	-0.308	0.366	0.386
AB	0.408	0.607	0.565	0.929	0.670	0.908	0.534	0.619	0.593	0.473	0.299	0.498	0.463	0.383
%AB	0.213	0.639	0.625	0.866	0.758	0.820	0.470	0.552	0.525	0.364	0.301	0.563	0.420	0.305
AHD1	0.312	0.242	0.212	0.557	0.346	0.541	0.903	0.904	0.908	0.926	0.802	0.287	0.862	0.884
AHD2	0.308	0.325	0.293	0.589	0.384	0.559	0.913	0.902	0.907	0.897	0.777	0.361	0.869	0.891
%AHD1	-0.033	0.198	0.215	0.392	0.443	0.344	0.854	0.814	0.831	0.795	0.906	0.242	0.847	0.828
%AHD2	0.016	0.304	0.315	0.476	0.495	0.415	0.884	0.850	0.862	0.803	0.879	0.341	0.854	0.848
RR	0.843	0.359	0.287	0.748	0.177	0.775	0.524	0.613	0.589	0.625	0.190	0.281	0.467	0.486
AF	0.787	0.121	0.045	0.228	-0.358	0.283	-0.088	-0.017	-0.044	0.062	-0.447	0.047	-0.159	-0.068
RRD	-0.443	0.304	0.347	0.366	0.764	0.289	0.466	0.479	0.481	0.296	0.634	0.307	0.489	0.347
AW	0.823	0.182	0.122	0.439	-0.115	0.484	0.187	0.232	0.217	0.287	-0.162	0.046	0.122	0.176
AN	0.850	0.176	0.100	0.295	-0.316	0.348	-0.028	0.038	0.012	0.116	-0.411	0.107	-0.101	-0.011
LPI_nat	0.127	-0.293	-0.312	-0.488	-0.650	-0.430	-0.664	-0.667	-0.670	-0.577	-0.743	-0.319	-0.668	-0.605
LPI_hum	-0.238	0.155	0.172	0.357	0.584	0.335	0.655	0.654	0.663	0.560	0.802	0.189	0.679	0.603
# P	0.681	0.544	0.480	0.686	0.258	0.678	0.312	0.403	0.373	0.341	-0.046	0.453	0.240	0.218
PDens	-0.646	0.384	0.435	0.111	0.645	0.015	0.007	0.027	0.022	-0.191	0.184	0.390	0.033	-0.120
MAT	-0.373	0.439	0.470	0.330	0.658	0.271	-0.049	-0.016	-0.016	-0.276	-0.044	0.360	-0.079	-0.292

Sheet 5

	%ACI	%ACH	Afert	AR	AB	%AB	AHD1	AHD2	%AHD1	%AHD2	RR	AF	RRD	AW	AN
SRt	0.049	0.187	0.347	0.272	0.207	0.135	0.380	0.278	0.327	0.241	0.249	0.088	0.010	0.200	0.137
SRb	-0.040	0.151	0.359	0.199	0.136	0.043	0.331	0.267	0.201	0.169	0.325	0.353	-0.163	0.410	0.373
SRm	0.000	0.119	0.217	0.410	0.038	-0.028	0.261	0.095	0.254	0.091	0.067	-0.092	-0.049	-0.085	-0.066
SRa	0.183	0.041	0.226	-0.064	0.453	0.480	0.301	0.295	0.297	0.301	0.209	-0.066	0.294	0.059	-0.014
SRr	0.221	0.166	0.263	0.226	0.308	0.330	0.357	0.286	0.416	0.338	0.142	-0.222	0.342	-0.070	-0.171
ISRt	0.116	0.419	0.583	0.434	0.347	0.242	0.610	0.532	0.529	0.458	0.506	0.113	0.074	0.315	0.194
ISRb	0.336	0.562	0.676	0.512	0.381	0.309	0.748	0.664	0.744	0.655	0.377	-0.169	0.359	0.085	-0.098
ISRm	-0.308	-0.242	-0.133	0.053	-0.124	-0.202	-0.172	-0.244	-0.322	-0.362	0.197	0.440	-0.447	0.302	0.421
ISRa	0.145	0.367	0.474	-0.047	0.455	0.459	0.442	0.554	0.400	0.528	0.344	0.032	0.283	0.227	0.099
ISRr	0.158	0.140	0.141	0.223	0.163	0.115	0.234	0.203	0.264	0.217	0.091	-0.120	0.057	0.036	-0.035
SLt	0.337	0.666	0.747	0.377	0.394	0.326	0.712	0.716	0.679	0.675	0.442	-0.042	0.258	0.242	0.036
SLb	0.352	0.555	0.667	0.301	0.436	0.376	0.628	0.651	0.591	0.614	0.448	-0.038	0.295	0.274	0.044
SLm	0.276	0.666	0.668	0.549	0.142	0.057	0.638	0.554	0.618	0.519	0.323	-0.046	0.079	0.105	-0.012
SLa	-0.168	0.076	0.096	-0.013	0.104	0.031	0.085	0.106	-0.051	-0.004	0.297	0.383	-0.207	0.356	0.430
SLr	0.136	0.163	0.225	0.057	0.289	0.220	0.276	0.277	0.243	0.248	0.208	-0.066	0.109	0.154	0.062
Area	-0.180	0.022	0.342	0.081	0.408	0.213	0.312	0.308	-0.033	0.016	0.843	0.787	-0.443	0.823	0.850
Pop1871	0.271	-0.070	0.197	-0.310	0.607	0.639	0.242	0.325	0.198	0.304	0.359	0.121	0.304	0.182	0.176
PopD1871	0.307	-0.049	0.164	-0.310	0.565	0.625	0.212	0.293	0.215	0.315	0.287	0.045	0.347	0.122	0.100
Pop1991	0.262	0.085	0.507	0.043	0.929	0.866	0.557	0.589	0.392	0.476	0.748	0.228	0.366	0.439	0.295
PopD1991	0.432	0.095	0.278	-0.012	0.670	0.758	0.346	0.384	0.443	0.495	0.177	-0.358	0.764	-0.115	-0.316
PopGr	0.215	0.077	0.507	0.086	0.908	0.820	0.541	0.559	0.344	0.415	0.775	0.283	0.289	0.484	0.348
$Pest	0.534	0.730	0.937	0.362	0.534	0.470	0.903	0.913	0.854	0.884	0.524	-0.088	0.466	0.187	-0.028
$Fert	0.446	0.603	0.954	0.309	0.619	0.552	0.904	0.902	0.814	0.850	0.613	-0.017	0.479	0.232	0.038
$P+F	0.480	0.639	0.954	0.331	0.593	0.525	0.908	0.907	0.831	0.862	0.589	-0.044	0.481	0.217	0.012
AC	0.271	0.623	0.982	0.396	0.473	0.364	0.926	0.897	0.795	0.803	0.625	0.062	0.296	0.287	0.116

Sheet 6

	%ACI	%ACH	Afert	AR	AB	%AB	AHD1	AHD2	%AHD1	%AHD2	RR	AF	RRD	AW	AN
%AC	0.429	0.690	0.837	0.422	0.299	0.301	0.802	0.777	0.906	0.879	0.190	-0.447	0.634	-0.162	-0.411
AC1861	0.218	-0.012	0.251	-0.308	0.498	0.563	0.287	0.361	0.242	0.341	0.281	0.047	0.307	0.046	0.107
AI	0.644	0.774	0.903	0.366	0.463	0.420	0.862	0.869	0.847	0.854	0.467	-0.159	0.489	0.122	-0.101
AH	0.414	0.819	0.953	0.386	0.383	0.305	0.884	0.891	0.828	0.848	0.486	-0.068	0.347	0.176	-0.011
%ACI	1	0.573	0.347	0.200	0.258	0.329	0.354	0.351	0.499	0.457	0.057	-0.339	0.491	-0.141	-0.298
%ACH	0.573	1	0.661	0.364	0.115	0.081	0.586	0.627	0.670	0.682	0.129	-0.309	0.320	-0.030	-0.255
Afert	0.347	0.661	1	0.396	0.476	0.391	0.915	0.886	0.807	0.815	0.596	0.008	0.358	0.237	0.060
AR	0.200	0.364	0.396	1	-0.013	-0.096	0.477	0.236	0.520	0.263	0.188	-0.223	0.169	-0.097	-0.221
AB	0.258	0.115	0.476	-0.013	1	0.950	0.515	0.599	0.376	0.491	0.653	0.148	0.330	0.382	0.219
%AB	0.329	0.081	0.391	-0.096	0.950	1	0.410	0.507	0.355	0.479	0.499	0.019	0.450	0.231	0.081
AHD1	0.354	0.586	0.915	0.477	0.515	0.410	1	0.919	0.896	0.842	0.583	-0.033	0.368	0.165	0.019
AHD2	0.351	0.627	0.886	0.236	0.599	0.507	0.919	1	0.828	0.923	0.561	-0.041	0.395	0.222	0.017
%AHD1	0.499	0.670	0.807	0.520	0.376	0.355	0.896	0.828	1	0.913	0.283	-0.367	0.562	-0.120	-0.322
%AHD2	0.457	0.682	0.815	0.263	0.491	0.479	0.842	0.923	0.913	1	0.320	-0.305	0.577	-0.019	-0.252
RR	0.057	0.129	0.596	0.188	0.653	0.499	0.583	0.561	0.283	0.320	1	0.568	0.025	0.692	0.630
AF	-0.339	-0.309	0.008	-0.223	0.148	0.019	-0.033	-0.041	-0.367	-0.305	0.568	1	-0.643	0.702	0.976
RRD	0.491	0.320	0.358	0.169	0.330	0.450	0.368	0.395	0.562	0.577	0.025	-0.643	1	-0.350	-0.622
AW	-0.141	-0.030	0.237	-0.097	0.382	0.231	0.165	0.222	-0.120	-0.019	0.692	0.702	-0.350	1	0.757
AN	-0.298	-0.255	0.060	-0.221	0.219	0.081	0.019	0.017	-0.322	-0.252	0.630	0.976	-0.622	0.757	1
LPI_nat	-0.491	-0.485	-0.597	-0.363	-0.466	-0.488	-0.663	-0.648	-0.768	-0.744	-0.297	0.457	-0.814	0.164	0.404
LPI_hum	0.475	0.516	0.601	0.394	0.355	0.377	0.631	0.591	0.777	0.712	0.177	-0.562	0.795	-0.227	-0.522
# P	0.040	-0.098	0.321	-0.129	0.562	0.470	0.318	0.322	0.030	0.112	0.790	0.681	-0.023	0.630	0.732
PDens	0.317	-0.077	-0.129	-0.224	0.068	0.245	-0.067	-0.053	0.136	0.145	-0.311	-0.455	0.654	-0.440	-0.460
MAT	0.278	-0.258	-0.220	-0.078	0.302	0.420	-0.106	-0.120	0.023	0.007	-0.142	-0.369	0.470	-0.342	-0.341

Sheet 7

	LPI_nat	LPI_hum	# P	PDens	MAT
SRt	-0.112	0.278	0.133	-0.065	0.079
SRb	0.040	0.047	0.271	-0.213	-0.173
SRm	-0.044	0.278	-0.144	-0.167	0.098
SRa	-0.265	0.349	0.206	0.290	0.444
SRr	-0.342	0.462	0.045	0.213	0.456
ISRt	-0.365	0.342	0.292	-0.231	-0.047
ISRb	-0.619	0.558	0.200	0.035	0.101
ISRm	0.391	-0.343	0.142	-0.420	-0.232
ISRa	-0.353	0.322	0.291	0.074	0.060
ISRr	-0.186	0.210	0.035	0.020	0.305
SLt	-0.509	0.473	0.251	-0.068	-0.186
SLb	-0.478	0.443	0.305	0.001	-0.122
SLm	-0.380	0.373	0.061	-0.240	-0.340
SLa	0.084	-0.127	0.314	-0.248	-0.156
SLr	-0.266	0.216	0.157	0.028	0.205
Area	0.127	-0.238	0.681	-0.646	-0.373
Pop1871	-0.293	0.155	0.544	0.384	0.439
PopD1871	-0.312	0.172	0.480	0.435	0.470
Pop1991	-0.488	0.357	0.686	0.111	0.330
PopD1991	-0.650	0.584	0.258	0.645	0.658
PopGr	-0.430	0.335	0.678	0.015	0.271
$Pest	-0.664	0.655	0.312	0.007	-0.049
$Fert	-0.667	0.654	0.403	0.027	-0.016
$P+F	-0.670	0.663	0.373	0.022	-0.016
AC	-0.577	0.560	0.341	-0.191	-0.276

Sheet 8

	LPI_nat	LPI_hum	# P	PDens	MAT
%AC	-0.743	0.802	-0.046	0.184	-0.044
AC1861	-0.319	0.189	0.453	0.390	0.360
AI	-0.668	0.679	0.240	0.033	-0.079
AH	-0.605	0.603	0.218	-0.120	-0.292
%ACI	-0.491	0.475	0.040	0.317	0.278
%ACH	-0.485	0.516	-0.098	-0.077	-0.258
Afert	-0.597	0.601	0.321	-0.129	-0.220
AR	-0.363	0.394	-0.129	-0.224	-0.078
AB	-0.466	0.355	0.562	0.068	0.302
%AB	-0.488	0.377	0.470	0.245	0.420
AHD1	-0.663	0.631	0.318	-0.067	-0.106
AHD2	-0.648	0.591	0.322	-0.053	-0.120
%AHD1	-0.768	0.777	0.030	0.136	0.023
%AHD2	-0.744	0.712	0.112	0.145	0.007
RR	-0.297	0.177	0.790	-0.311	-0.142
AF	0.457	-0.562	0.681	-0.455	-0.369
RRD	-0.814	0.795	-0.023	0.654	0.470
AW	0.164	-0.227	0.630	-0.440	-0.342
AN	0.404	-0.522	0.732	-0.460	-0.341
LPI_nat	1	-0.813	-0.167	-0.400	-0.283
LPI_hum	-0.813	1	-0.092	0.338	0.260
# P	-0.167	-0.092	1	0.048	0.023
PDens	-0.400	0.338	0.048	1	0.599
MAT	-0.283	0.260	0.023	0.599	1

Appendix 10: Descriptions of abbreviations from Tables 10 and 11 and Appendices 8 and 9

Unless otherwise stated, human landuse data are from the 1991 census (Statistics Canada 1999).

AB(uiltup)	Builtup area (km2; from AVHRR data); e.g. residential development
% AB	% of ER dominated by builtup landcover (from AVHRR data)
AC(ropland)	Cropland area (km2; from AVHRR data)
% AC	% of ER dominated by cropland (from AVHRR data)
%ACH	% of cropland treated with herbicides
%ACI	% of cropland treated with insecticides
AC1861	Cropland area in 1861 (km2)
AF(orest)	Forest landcover area (km2; from AVHRR data)
AFert	Area treated with agricultural fertilizers (km2)
AH(erb)	Area treated with agricultural herbicides (km2)
AHD1	Human-dominated landcover (km2; from AVHRR data); builtup + cropland + rangeland
% AHD1	% of ER dominated by total human landcover (from AVHRR data)
AHD2	Builtup + Cropland (km2; from AVHRR data)
% AHD2	% of ER dominated by Builtup + Cropland (from AVHRR data)
AI(ns)	Area treated with agricultural insecticides (km2)
AN(atural)	Area dominated by natural landcover (km2; from AVHRR data)
AR(ange)	Rangeland area (km2; from AVHRR data)
% ARange	% of ER dominated by rangeland (from AVHRR data)
Area	Ecoregion area (km2; from AVHRR data)
AW(ater)	Freshwater area (km2; from AVHRR data)
Ecoregion	Ecoregion Name

Ecozone	Ecozone Name
ER	Ecoregion number
$ Fert(ilizer)	Agricultural fertilizers ($ purchased)
ISRa	# COSEWIC-listed Amphibian species remaining in ER (out of 6 in study)
ISRb	# COSEWIC-listed Bird species remaining in ER (out of 37 in study)
ISRm	# COSEWIC-listed Mammal species remaining in ER (out of 12 in study)
ISRr	# COSEWIC-listed Reptile species remaining in ER (out of 7 in study)
ISRt	Total # COSEWIC-listed (imperiled) species remaining in ER (out of 62 in study)
LPI_hum	Largest Patch Index for human-dominated landcover (% of total ER area covered by the largest patch of human-dominated landcover)
LPI_nat	Largest Patch Index for natural-dominated landcover (% of total ER area covered by the largest patch of natural landcover)
MAT	Mean annual temperature (C)
# P	Total number of patches, or polygons, of human + natural-dominated landcover (from AVHRR data)
PDens	Patch, or polygon, density (# patches/km2)
$ Pest(icide)	Agricultural pesticides ($ purchased)
$ P + F	Agricultural pesticides + fertilizers ($ purchased)
Pop1871	Human population in 1871
Pop1991	Human population in 1991
PopD1871	Human population density in 1871
PopD1991	Human population density in 1991
PopGr	Human population growth between 1871 and 1991
RR	Length of roads and railways (km)
RRD	Road and railway density (km/km2)
SLa	# COSEWIC-listed amphibian species lost from part of or entire ER (out of 6 in study)
SLb	# COSEWIC-listed bird species lost from part of or entire ER (out of 37 in study)

SLm	# COSEWIC-listed mammal species lost from part of or entire ER (out of 12 in study)
SLr	# COSEWIC-listed reptile species lost from part of or entire ER (out of 7 in study)
SLt	Total # COSEWIC-listed species lost from part of or entire ER (out of 62 in study)
SNLa	# of COSEWIC-listed amphibian species remaining without any loss in ER (out of 6 in study)
SNLb	# of COSEWIC-listed bird species remaining without any loss in ER (out of 37 in study)
SNLm	# of COSEWIC-listed mammal species remaining without any loss in ER (out of 12 in study)
SNLr	# of COSEWIC-listed reptile species remaining without any loss in ER (out of 7 in study)
SNLt	Total # of COSEWIC-listed species remaining without any loss in ER (out of 63 in study)
SRa	Amphibian species richness (from feral distribution maps)
SRb	Bird species richness (from feral distribution maps)
SRm	Mammal species richness (from feral distribution maps)
SRr	Reptile species richness (from feral distribution maps)
SRt	Total species richness (from feral distribution maps; birds + mammals + amphibians + reptiles)