Complexity versus certainty in understanding species' declines

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ABSTRACT

Aim Our understanding of and ability to predict species declines is limited, despite decades of study. We sought to expand our understanding of species declines within a regional landscape by testing models using both traditional hypotheses and those derived from a complex adaptive systems approach.

Location Our study area was the dry mixed grassland of south-eastern Alberta, Canada, one of the largest remnants of native grassland in North America, and the adjacent grassland in Saskatchewan.

Methods We used the breeding birds of the grassland to test the relationship between species declines and a suite of traits associated with decline (such as size, specialization and rarity, as well as distance to edge of a discontinuity, and edge of geographic range) in a stepwise regression with AICc values and bootstrapping via model averaging, followed by a refit procedure to obtain model-averaged parameter estimates. We used both provincial government and Breeding Bird Survey (BBS) classifications of decline. We also modelled degree of decline in the Alberta and Saskatchewan grasslands, which differ in amount of habitat remaining, to test whether severity of decline was explained by the same traits as species decline/not- decline.

Results We found that the model for government-defined decline fulfilled government expectations that species' extinction risk is a function of being large, specialized, rare and carnivorous, whereas the model for BBS-defined decline suggested that the biological reality of decline is more complex, requiring the need to explicitly model scale-specific patterns. Furthermore, species decline/not- decline was explained by different traits than those that fit degree of decline, though complex systems- derived traits featured in both sets of models.

Main conclusions Traditional approaches to predict species declines (e.g. government processes or IUCN Red Lists), may be too simplistic and may therefore misguide management and conservation. Using complex systems approaches that account for scale-specific patterns and processes have the potential to overcome these limitations.

Keywords
Body mass distributions, complex adaptive systems, cross-scale, discontinuity hypothesis, extinction risk, North American Breeding Bird Survey.

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INTRODUCTION

The changing focus of conservation efforts from single species to communities of species and regional landscapes has propelled a need to understand the dynamics of species decline at these higher levels of ecological organization and over longer time scales. Simply put, the knowledge gained from an exquisite understanding of the life cycles or interspecific interactions of individual species often does not scale up to explain the long-term dynamics or declines of species at the ecosystem, regional landscape or biome scale (Colles *et al.*, 2009). The textural discontinuity hypothesis (hereafter called the discontinuity hypothesis), offers insight into community assembly and disassembly processes at spatial and temporal meso-scales that lie between the local and immediate role of vegetative processes, competition and

stochastic disturbances, and the long sweep of evolution and phylogeny (Holling, 1992; Bennett & Owens, 1997; Purvis *et al.*, 2000; Colles *et al.*, 2009). It expands our understanding of species declines at ecosystem, landscape and regional scales because the processes that shape the assembly of communities are pertinent to understanding their collapse. We explain the theoretical foundations for the discontinuity hypothesis and its relationship to species declines and extinction risk and then test this relationship in a grassland system in Alberta, Canada.

The discontinuity hypothesis, rising out of complex adaptive systems (CAS) theory, proposes that resource structure is shaped by relatively few processes that occur at discrete spatial and temporal scales. These structuring processes create discontinuous ecological structure because they differ sufficiently in characteristic extent and rate. For example, the spatial and temporal dimensions of the needles on a pine tree differ markedly from the spatial extent and temporal frequency associated with individual trees, stands of trees or the location of boreal forests on a continent, because the key processes structuring pine needles are different than those that determine the location of boreal forests (Holling, 1992).

Wiens (1989) described this discontinuous structure as 'domains of scale'. At the spatial and temporal extent of one scale domain, patterns either change monotonically or do not change at all. Scale domains are separated by scale breaks, which are a relatively abrupt nonlinear transition from one set of scaling processes to another. Because species interact with ecological structure at a scale relative to their body mass (Peters, 1983; Fisher *et al.*, 2011), species pools are predicted to be sorted, or morphologies to evolve, such that species with body sizes suited to the scale domains of ecological structure are more likely to persist, creating a discontinuous body mass distribution with aggregations of similarly sized species separated by gaps that correspond to scale breaks (Holling, 1992).

Discontinuities in body mass distributions have been demonstrated in hundreds of ecosystems, from terrestrial (Holling, 1992; Sendzimir *et al.*, 2002; Allen, 2006a; Allen *et al.*, 2006; Skillen & Maurer, 2008), to aquatic (Havlicek & Carpenter, 2001; Angeler *et al.*, 2011; Nash *et al.*, 2013), and paleo-ecological (Lambert, 2006), using a variety of methods (Allen, 2006a; Fisher *et al.*, 2011; Nash *et al.*, 2013). Empirical evidence demonstrating that species exploit resources at a scale domain relative to their body mass is accumulating (Haskell *et al.*, 2002; De La Montaña *et al.*, 2006; Szabó & Meszéna, 2006; Fischer *et al.*, 2008; Fisher *et al.*, 2011; Borthagaray *et al.*, 2012). The discontinuity hypothesis is a theory of community assembly at meso-scales and fits into a hierarchy of theories explaining the distribution pattern of species in time and space (for example, Hutchinson, 1959; Allen *et al.*, 2006; Vergnon *et al.*, 2012).

The search for patterns in species extinction risk has been a topic of interest since at least the time of Darwin (McKinney, 1997), but efforts have accelerated due to the current high rate of global extinctions and the increasing number of species classified as 'at risk'. There is an extensive literature on species extinction and decline that assesses macro-evolutionary variables such as the role of phylogeny (Purvis *et al.*, 2000), evolutionarily conserved traits such as body size and trophic level (Gaston & Blackburn, 1995) and intrinsic properties such as fecundity (Bennett & Owens, 1997), specialization (Colles *et al.*, 2009), rarity (Gaston & Fuller, 2007), dispersal ability, and abundance, among others (Purvis *et al.*, 2000).

General patterns have emerged, although the interactions among many of these traits are not understood. Extinction risk at global scales appears to be associated with a larger body size (Gaston & Blackburn, 1995; Bennett & Owens, 1997), but other studies differing in spatial scale or taxonomic focus found a negative, or no correlation, between body size and extinction risk (Forys & Allen, 1999). Studies on specialization show similarly conflicting results, as studies focused at the species level and at spatial scales of a region or smaller show that habitat specialization is strongly correlated with an increased extinction risk, while phylogenetic and paleo-ecological studies show either a small or no increased risk for specialization (Colles *et al.*, 2009). Despite apparent contradictions, studies on body mass, specialization and other such traits provide insight into factors affecting risk across species and species groups.

Species-specific studies, on the other hand, have limited generality. Habitat loss and/or habitat fragmentation are widely believed to be the primary causes of species declines, but it is likely that extinction risk is caused by multiple factors interacting in complex ways. Authors have commented on the importance of explicitly assessing multiple scales in studies of species decline or extinction (Koper & Schmiegelow, 2006). For example, area sensitivity and habitat use of grassland birds not only varies among species, but often varies within species depending on the study site (Johnson and Igl 2001). Idiosyncratic responses such as this reduce the utility of these studies for management applications, and for understanding general patterns of extinction risk within and across ecosystems and regional landscapes.

Despite contradictory evidence regarding risk, government listing programmes must nonetheless classify species by their extinction risk, and the IUCN Red List Categories and Criteria is perhaps the most commonly used vehicle for doing so (IUCN 2012). Their listing criteria are focused on changes in population size, extent and area of occupancy, rarity and threats to the population and habitat. These basic population demographics commonly underpin governmental listing programmes but may neglect risk factors arising from complex systems theory.

The discontinuity hypothesis adds a novel dimension to the ongoing struggle to understand extinction risk. As ecological structure occurs as a series of hierarchically nested scale domains of structure separated by scale breaks (Wiens, 1989; Holling, 1992), the implication for species persistence is that not all locations within that discontinuous distribution of resources are equivalent. Species with a mass that

places them close to a scale break likely interact differently with biotic and abiotic patterns and processes than species centrally located in their body mass aggregation. For example, scale breaks are associated with high spatio-temporal variability such as at the edges of geographic ranges (Araújo *et al.*, 2002). Species with traits like migration and nomadism that exploit highly variable resources tend to have body masses that place them near the edges of their aggregations (Allen & Saunders, 2002, 2006; Allen, 2006a; Alai, 2010). Higher spatial and temporal variability in population abundance (Wardwell & Allen, 2009) and the probability of successful invasion have been associated with proximity to scale breaks (Allen *et al.*, 1999; Allen, 2006b). More specifically, Allen *et al.* (1999) have shown that the risk of extinction is also higher when species' masses place them proximate to scale breaks, highlighting the usefulness of a CAS approach for analysing how scale-specific processes moderate extinction risk.

The purpose of our analyses is to consider variables associated with decline that reflect processes and patterns typically not considered in extinction risk studies. If species decline is multicausal and driven by processes occurring at multiple spatial and temporal scales, then both discontinuity variables and traditional variables will be supported. We test this by modelling decline based on two classifications of decline–provincial government versus Breeding Bird Survey. We use the breeding birds from a grassland system in Alberta, Canada, and a small suite of traditional and discontinuity variables associated with avian species decline and extinction risk (body size, trophic status, abundance, rarity, dietary and habitat specialization, endemism, distance to edge of a scale break, migratory status and edge of geographic range).

We also ask whether, given severity of decline as the response variable, the same variables are identified. We compared the Alberta grassland with the adjacent grassland in Saskatchewan, which has experienced greater levels of habitat loss and fragmentation (Hammermeister *et al.*, 2001).

METHODS

Data sets and defining decline: analysing extinction risk

We used the breeding birds of the dry mixed grassland of south-eastern Alberta, including both grassland obligates and species that also breed in other ecosystems (Table S1 in Supporting Information). We compiled a species list from Alberta government data (Banasch & Samuel, 1998; Dale *et al.*, 1999; Gutsell *et al.*, 2005a,b), the North American Breeding Bird Survey (BBS) (Sauer *et al.*, 2011), the Royal Alberta Museum, and the Federation of Alberta Naturalists (P. Penner, pers. comm.). Two data sets using the same suite of species were created. In the first, species were classified as declining if they were listed in the top three Alberta government risk categories (At Risk, May Be At Risk, and

Sensitive). In the second data set, species were classified as declining if BBS trend data (1966–2010) for Alberta was significantly declining. Government listings are concerned with endangerment, which is more than just decline trends, but can also be controversial and affected by political agendas, so we created the second data set based solely on BBS trend data. The Alberta process is similar to the IUCN Red List criteria in their focus on basic population demographics (Fish and Wildlife Division, 2005), but places greater emphasis on perceived threats to the population and their habitat and less on the raw amount of decline, increasing the subjectivity of their process. The BBS data also have biases, because it is a roadside survey and likely underestimates wary and wetland birds and birds with small populations or those that use habitat that falls primarily outside the survey area (Sauer *et al.*, 2011). It is assumed that significant decline trends indicate an increased risk of extinction as compared to species whose populations have remained stable. We chose to analyse government-defined decline and BBS-defined decline separately, to avoid having the limitations of either assessment confound the results.

There are 101 non-aquatic breeding bird species in our study area. Aquatic species were not included because different mechanisms structure aquatic body mass distributions (Holling, 1992). The government-defined data set had 34 species classified as declining, and the BBS data set had 28 species classed as declining. Fifteen of the BBS-defined declining species were unique to that data set.

To test the degree of decline, we used BBS trend data for Alberta and Saskatchewan (1966–2010), which provides a percent change in abundance over time for each species (Sauer *et al.*, 2011) (Table S2 in supporting Information). The Albertan dry mixed grassland system extends east into south-western Saskatchewan. Alberta has a more information-rich species tracking system and thus had data for the first research question, while Saskatchewan did not. However, BBS data allows for a comparative analysis of long-term abundance trend estimates for the two portions of the grassland ecosystem. The dry mixed grassland in Alberta has more than 50% remaining in native vegetation cover (Prairie Consesrvation Forum, 2008), and the Saskatchewan portion has about 20% remaining (Hammermeister *et al.*, 2001). Our data sets included only those species defined as declining by the BBS, a calculation they make using a hierarchical model analysis. If the confidence interval does not include zero, then it is considered a statistically significant decline. In rare instances, the sample size is too small and a species will not be flagged as declining by the BBS despite the significant confidence interval. Species known to be highly endangered such as the burrowing owl (*Athene cunicularia*) are not listed as declining by the BBS because of their rarity ($n = 12$ for Alberta and $n = 12$ for Saskatchewan, where $n =$ the number of survey routes on which the species was encountered). As a result, a few species recognized by the provinces but not by BBS data to be endangered are not included in these data sets.

Predictor variables for both analyses

We selected variables that were the best studied and most widely accepted determinants of extinction risk and then added a small suite of discontinuity variables that we predicted could also contribute to extinction risk. The traditional variables were body mass, habitat and dietary specialization, grassland specialization, carnivory, abundance and rarity.

Larger body size has been presumed to increase extinction risk because larger species have lower fecundity, larger home ranges and tend to be more rare, thus are more vulnerable to habitat loss and fragmentation (Arita et al., 1990; Gaston & Blackburn, 1995; Bennett & Owens, 1997; Haskell et al., 2002), but the evidence for this is equivocal (Lawton et al., 1994). Trophic status has also been well studied as a predictor of extinction risk, but like body size, results have conflicted, and it is clear that both body size and trophic status interact in complex and poorly understood ways, as neither consistently explain much variance in extinction risk (Laurance, 1991; Davies et al., 2000; Cardillo et al., 2004). Carnivory has been associated with an increased extinction risk because of the larger home range requirements and increased vulnerability to human-caused mortality, including exposure to pesticides, which is a particular risk to avian species (Haskell et al., 2002; Henny et al., 2008; Walker et al., 2008; Imre & Derboowka, 2011). Specialization is thought to confer increased risk because of a reduced ability to cope with habitat transformation or fragmentation (Faaborg, 1979; Krüger & Radford, 2008). Grassland specialization is a form of habitat specialization in that specialists are restricted to the ecosystem type in which they evolved (Knopf, 1996), but they may use multiple types of habitat within the grassland. Abundance and rarity are often discussed as degrees of the same phenomenon (Vazquez & Gaston, 2004), but Alberta considers abundance to be a function of the overall size of the breeding population within Alberta, and rarity to be a measure of the number of different sites where the species occur. Both having low abundances and rarity in occurrence and/or restricted ranges are correlated to extinction risk (Davies et al., 2000; Gaston & Fuller, 2007).

Our discontinuity variables were 'distance to the edge of a discontinuity', 'migratory status' and 'edge of geographic range'. Studies have shown that declining species are more likely to be associated with the edges of body mass aggregations (thus near discontinuities) than are stable species (Allen et al., 1999; Skillen & Maurer, 2008). The strategy of migration, which takes advantage of both spatial and temporal variation in resources, has been associated with discontinuity edges (Allen, 1997; Alai, 2010). Though migration has been discounted as increasing extinction risk in grassland birds by some (McCracken, 2005), it also been shown to increase extinction risk when compared to non-migrants (Pimm et al., 1988). Species whose populations are at the edge of their range may be at greater decline risk and may have body masses that place them close to a discontinuity (Brown,

1984; Skillen & Maurer, 2008). Populations at the edge of their geographic range are believed to have lower and more variable abundances and densities and to be at increased extinction risk because of the decreased habitat suitability compared to the centre of their range, but there is increasingly equivocal evidence for these assertions (Brown, 1984; Sagarin & Gaines, 2002; Skillen & Maurer, 2008; Feldhamer et al., 2012; Lloyd et al., 2012).

Data sources for predictor variables

Average body size was determined from local data sources (Royal Alberta Museum specimen database), and when n was <30, average body size was determined from a literature review of studies conducted in geographically proximate ecosystems. Adult male and female body masses were averaged and log10 transformed. Habitat and dietary specialization were determined by counting the number of different habitats and food items used by a species in the breeding season using studies specific to the northern North American grassland region (Fisher et al., 1998; Poole, 2010). Because of uneven representation within bins, habitat specialization was compressed from 10 to 3 bins (classified as using 1 habitat, 2 habitats, or 3 or more habitats), and dietary specialization was compressed from 8 to 3 bins (classified as using 1 food type, 2 food types, or 3 or more food types). Grassland specialization came from Knopf (1996).

Abundance and rarity classifications came from government reports (Gutsell et al., 2005a,b) that classify species into one of four population abundance and rarity categories based on total number of mature individuals capable of breeding and the number of estimated sites within the province where the species currently persists. Saskatchewan uses one number to encompass both abundance and rarity based on a 1–5 ranking (Saskatchewan Conservation Data Centre, 2012). We averaged abundance and rarity in the Alberta data set to enable a direct comparison between the two data sets.

Distance to edge was determined by first identifying the discontinuities in the body mass distribution using BCART (Bayesian classification and regression tree; see Allen & Holling, 2002) and then calculating the distance in terms of log10 body mass units of each species from the nearest species that defined the edges of the aggregation. Migratory status and geographic range were based on migration range maps, range maps and detailed species accounts (Poole, 2010).

Modelling species declines

We used a stepwise regression in a general linear model (Proc GLMSELECT; SAS Institute, 2011), using AICc values to compare a forward addition and backward elimination at each step. For the first analysis, we used a binomial classification of decline for all 101 species. For the second analysis, we used the percent change in abundance over time as the response variable, including only those species considered

declining. Bootstrapping via model averaging was performed by running 10,000 iterations (resampling with replacement) and averaging the parameter estimates for each variable across all iterations. To make this averaged model more parsimonious and improve the predictive performance while avoiding Type II error, we refit the averaged model by including only those variables that were selected in at least 40% of the samples in the initial round of model averaging (SAS Institute, 2011). This method stringently shrinks the parameter estimates. We resampled this reduced model 10,000 times to attain model-averaged parameter estimates for the refit model. Refitting allows us to draw inference from a subset of models selected by the regression, akin to information/theoretic approaches (Burnham & Anderson, 2002), rather than estimating parameter estimates based on a single 'best' model. We used this methodology for both of our analyses.

All variables were tested for correlations using Pearson correlation. Abundance and rarity were highly correlated ($r = 0.846$, $P < 0.0001$), as expected. Both variables were still included in the analysis because of the different values for abundance and rarity exhibited by birds of prey, in particular.

RESULTS

The Alberta government-defined decline data set had 34 declining species. The initial stepwise regression included four variables with a minimum variable selection percentage of ≥40%; body mass, grassland specialization, carnivory and abundance (see Table S3 in Supporting Information). The model-averaged parameter estimates from the refit procedure indicate that being larger, a grassland specialist, a carnivore and less abundant best-fit government-defined decline (decline = 0.38 + 0.08 body mass + 0.33 grassland specialist + 0.17 carnivore − 0.09 abundance) (Fig. 1).

The BBS-defined decline data set had 28 declining species, based on 50-year trend data (1960–2010). The regression had four variables with a minimum variable selection percentage of ≥40%; edge of geographic range, migration, abundance and distance to edge (see Table S4 in Supporting Information). The model-averaged parameter estimates from the refit procedure indicate that *not* being at the edge of their geographic range, being migratory, having *greater* abundance and *not* being at the edge of a discontinuity best fit the BBS-defined decline (decline = −0.25 + 0.01 distance to edge − 0.23 edge of geographic range + 0.26 migratory + 0.10 abundance) (Fig. 2).

In the final analysis, we assessed the relationship between the independent variables of extinction risk and the severity of decline as per BBS trend data. There were 28 species in the Alberta portion of the grassland with statistically significant decline (Sauer *et al.*, 2011). The degree of decline in the 28 species ranged from 0.7% for the savanna sparrow (*Passerculus sandwichensis*) to 8.9% for the McCown's longspur (*Calcarius mccownii*). The regression had six variables with a

minimum variable selection percentage of ≥40%; food and habitat specialization, abundance/rarity, distance to edge of a discontinuity, grassland specialization and edge of geographic range (see Table S5 in Supporting Information). The model-averaged parameter estimates from the refit procedure indicate that being a habitat and dietary specialist, less abundant, at the edge of a discontinuity and *not* at the edge of their geographic range best explained severity of decline in the Alberta grassland (severity of decline = 22.39 − 0.76 grassland specialization − 1.09 dietary specialization − 2.97 abrarity − 1.74 habitat specialization − 0.13 distance to edge + 1.56 edge of geographic range) (Fig. 3).

There were 28 species with significant decline in the Saskatchewan portion of the dry mixed grassland (Sauer *et al.*, 2011) (Fig. 4). Nine of those species differed from the Alberta data set, and 19 were in common. The degree of decline ranged from 1.0% for the eastern kingbird (*Tyrannus tyrannus*) to 10.9% for the McCown's longspur (*Calcarius mccownii*). The regression had three variables with a minimum variable selection percentage of ≥40%; food and habitat specialization and rarity (see Table S6 in Supporting Information). The model-averaged parameter estimates from the refit procedure indicate that being a dietary and habitat specialist and less abundant best explained severity of decline in the Saskatchewan grassland (severity of decline = 12.41 − 0.80 dietary specialization − 1.14 abrarity − 0.88 habitat specialization) (Fig. 4).

DISCUSSION

Analyses of extinction risk often focus on intrinsic traits, while we propose that the interaction of species with habitat and resource structure also plays a role in decline and risk (Allen, 2006b). Although the relationship between distance to edge and decline was not consistent, our results support that discontinuity variables play a role in explaining decline. Discontinuity variables like distance to edge of a body mass aggregation directly reflect the scales at which species interact with their landscapes, and this provides a richer understanding of risk, just as previous work on success rate of introduced species demonstrated that successful invasion was best explained by species' distance to a discontinuity rather than intrinsic traits such as a high r or a small body mass (Allen, 2006b).

Government-defined decline versus BBS-defined decline in Alberta, Canada

Our analysis compared two data sets of decline, one defined by the provincial government of Alberta, and the other by BBS data. The regression assessed variables that have historically been linked to extinction risk as well as more novel variables related to the discontinuity hypothesis (Allen *et al.*, 1999). The government-defined declining species met the conventional expectations of extinction risk and none of the expectations of the discontinuity hypothesis; that is,
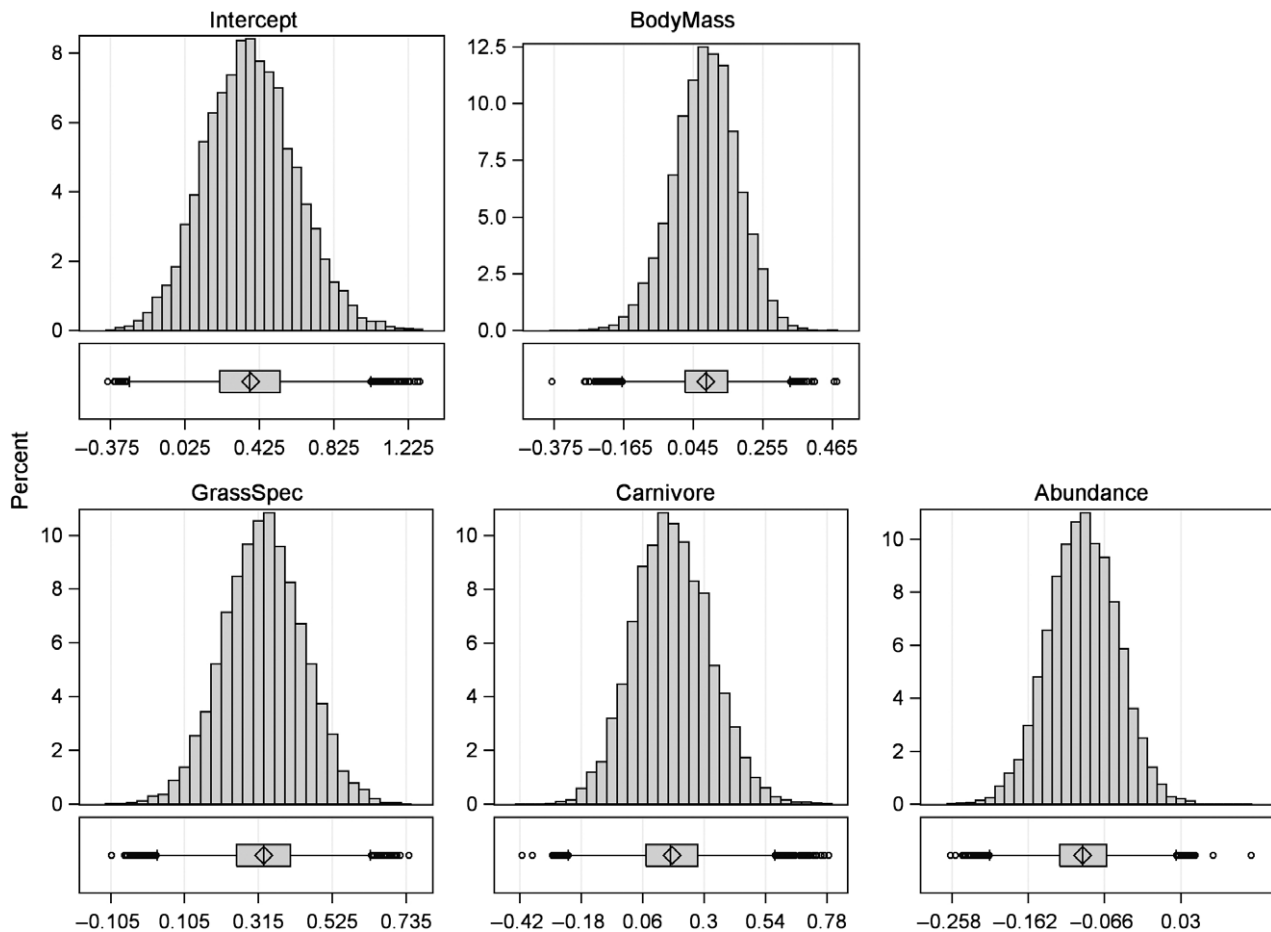
Figure 1 Parameter estimate distributions after refit procedure (10,000 iterations) for variables in best-fit model for Alberta government-defined declining breeding birds in the dry mixed grassland, Alberta, Canada.

declining species are larger-bodied, carnivorous, grassland specialists and rare. However, Alberta does not consider large declines in common and widespread species as sufficient to list a species, particularly when the cause is unknown (Fish and Wildlife Division 2005), whereas the IUCN criteria weight declines with unknown causes higher than declines with known and reversible causes and considers substantial decline trends as sufficient for listing (IUCN 2012).

The best-fit model for the BBS data suggests that the factors involved in decline are multifaceted, as the variables in the model are migratory, *not* at edge of their geographic range, *greater* abundance, and *not* at the edge of a discontinuity. In short, the model includes the discontinuity variable distance to edge and related variables of migration and edge of geographic range and has an opposite trend for the one variable in common with the government model (abundance). BBS data are objective where government listing processes may be affected by expectations of the traits driving extinction risk, but it has known limitations with regards to wary or extremely rare species, which may account for 'more abundant' in the best-fit model. Weaknesses in BBS collection methods do not account for the presence of all three non-traditional variables in the final

model nor do they explain the absence of many of the traditional extinction risk variables such as specialization, body mass, or trophic status.

About one-third of the species in the data sets were at the edge of their geographic range (32 of 101 species). Only 2 of the 28 BBS-defined declining species were at the edge of their range (*c.* 4%), while of the 73 stable species, 30 were at the edge of their range (*c.* 41%). BBS-defined declining species were strongly *not* at the edge of their geographic range. Although previous analyses have suggested that populations far from the centre of their geographic range can have high variability in abundances and densities because of decreasing environmental suitability, thus increasing their likelihood for extinction (part of the Abundant Centre Hypothesis) (Brown, 1984; Skillen & Maurer, 2008), other studies have suggested that general rules of thumb regarding abundance, variability in population size, extinction risk and their relationship to edge of geographic range cannot be supported (Sagarin & Gaines, 2002; Feldhamer *et al.*, 2012; Lloyd *et al.*, 2012). Our results confirm that while decline is associated with the location of a species within its geographic range, that relationship is mediated by unknown factors that define the nature of that association.
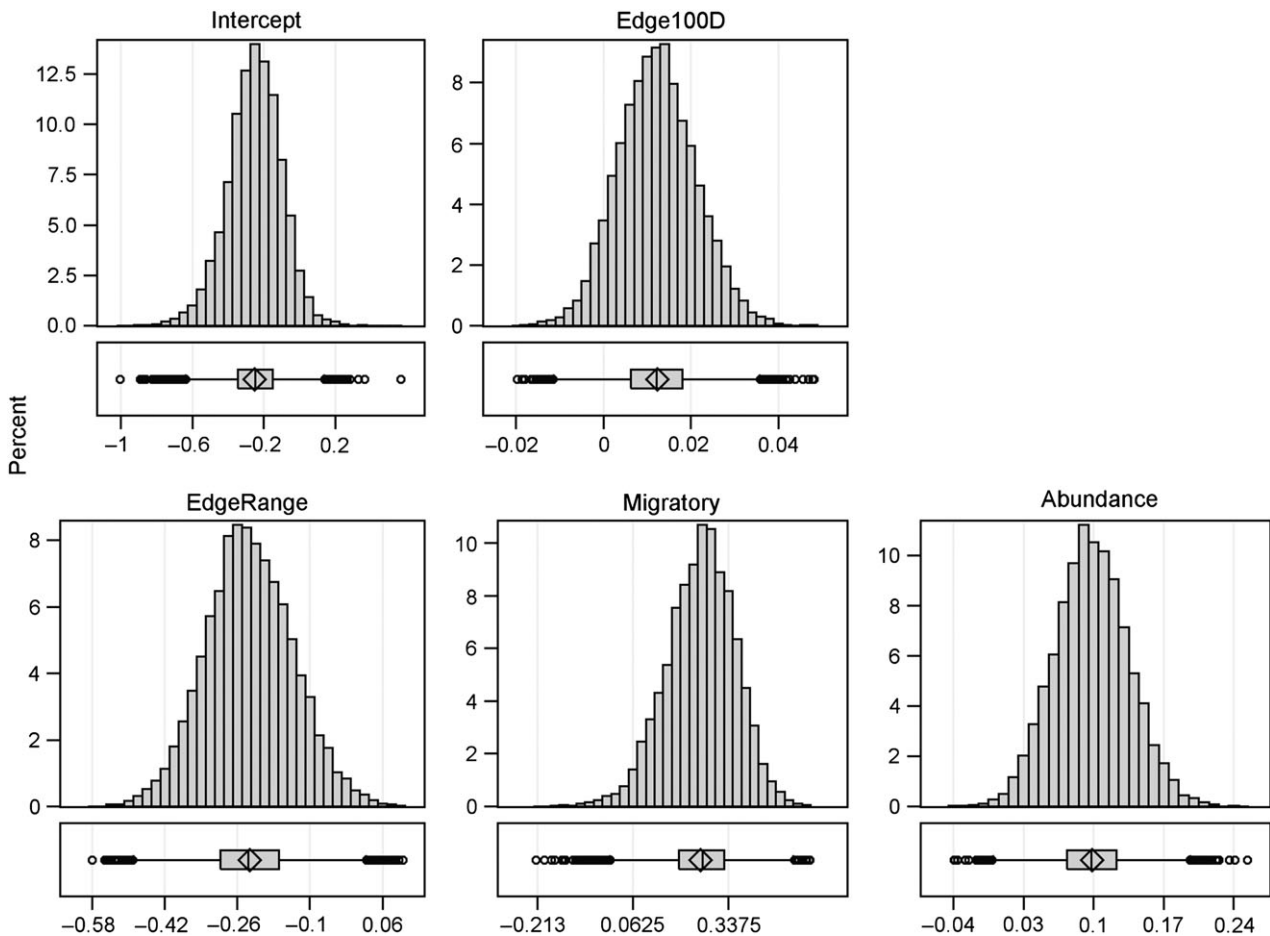
Figure 2 Parameter estimate distributions after refit procedure (10,000 iterations) for variables in best-fit model for Breeding Bird Survey-defined declining breeding birds in the dry mixed grassland, Alberta, Canada.

Similarly, *not* being close to a discontinuity best-fit BBS-defined declining species. Discontinuities reflect abrupt changes in scaling processes (Wiens, 1989; Gunderson, 2010), and resources at the edges of a scale domain are hypothesized to be more variable in space and time, as in at the edges of geographic ranges, or in ecotones. Although previous research in the Everglades documented a significant association between endangerment and proximity to discontinuities (Allen *et al.*, 1999), the BBS results for Alberta grassland birds indicate that species *not* close to the edge of a discontinuity are more likely to be declining, although it could also be a statistical artefact, as species near an edge are more variable in abundance (Wardwell & Allen, 2009), so may be less likely to meet the conditions of rigorous statistical methods determining decline. As with the geographic range result, other factors seem to be mediating the relationship between decline and distance to edge. The Everglades system and the dry mixed grassland have experienced different degrees of disturbance. Extinctions and invasions are one measure of human disturbance (King & Tschinkel, 2008), and the Everglades data set had 37 invasive avian species (c. 25% of the avifauna) and represented a highly

transformed ecosystem, while the Albertan dry mixed grassland had only five successful invasions and more than 54% of the grassland remained in native vegetation (Prairie Consesrvation Forum, 2008). If species whose body masses place them near discontinuities are using resources that are more variable in space and time, then it is a logical, though untested supposition that species whose body masses place them in the middle of a body mass aggregation are utilizing resources that are more consistent in space or time. If these species evolved around a certain spatio-temporal stability of resources, then their decline, as opposed to edge species, could reflect either a decline in resources, or another currently unmeasured form of environmental change. Unfortunately, a lack of long-term monitoring as well as a poor ability to measure resource structure that is stable and consistent versus that which is highly variable means we can only speculate.

Species that migrate take advantage of resources that vary in both time and space, and data has suggested that migratory species are more likely to have body masses that place them close to the edge of a scale break (Allen, 1997; Alai, 2010). Gaston & Fuller (2007) point out that many
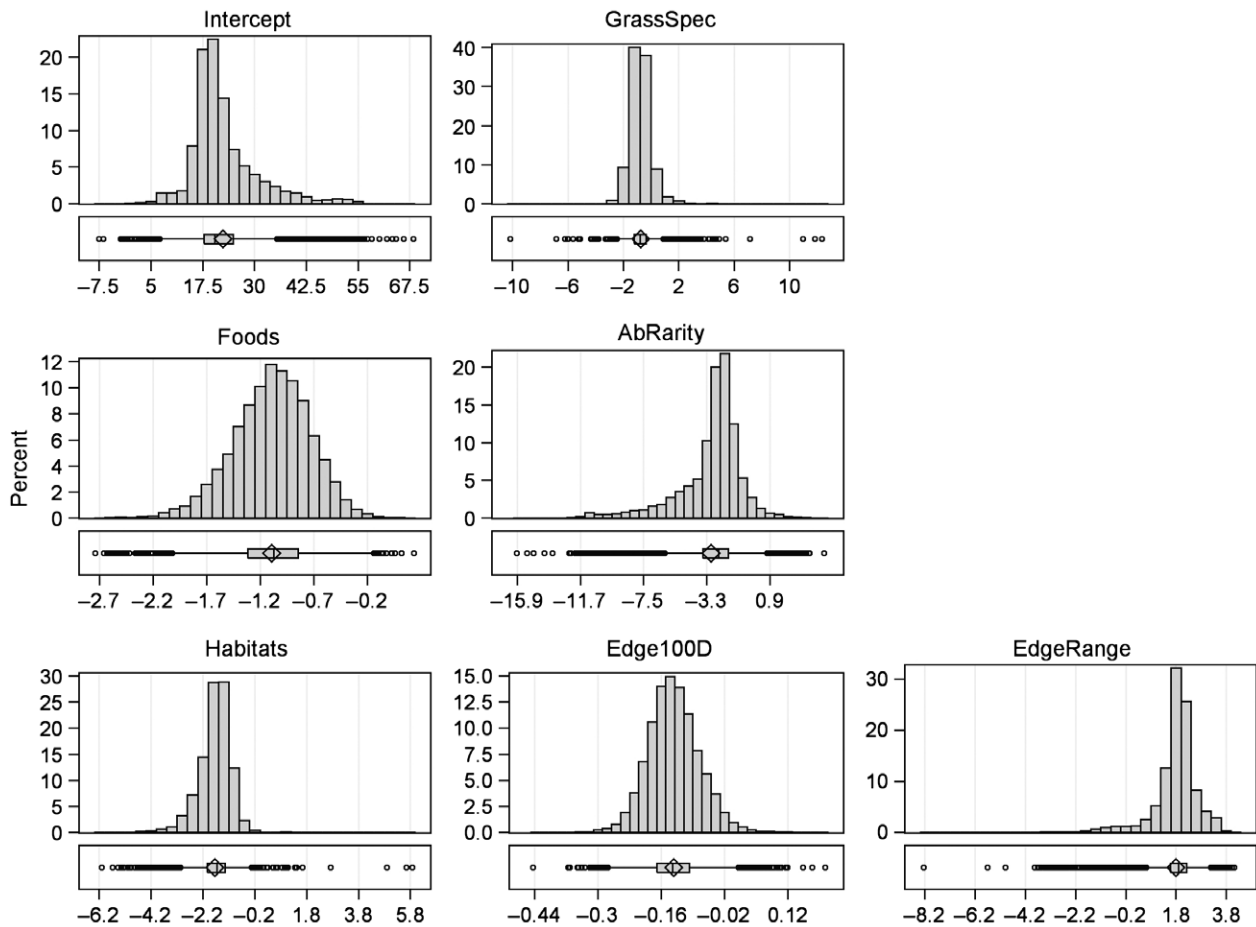
Figure 3 Parameter estimate distributions after refit procedure (10,000 iterations) for variables in the best-fit model for Breeding Bird Survey-defined declining breeding bird species in the dry mixed grassland of Alberta, Canada.

common species, particularly from temperate regions such as North America, either aggregate into relatively small areas at key points in their life cycle, such as when they migrate, or they breed in confined areas and that this is likely to be correlated to decline risk. It is not clear whether the strategy of migration itself, the indirect effects of migrating (Gaston & Fuller, 2007), or an artefact of the data set has included migration in the best-fit model. All but one of the BBS-declining species migrated, and all but four were in the highest abundance category (indicating commonness). Our results support the hypothesis that the strategy of migration is correlated with decline risk, though whether the decline is a result of habitat changes to their breeding grounds or to the habitat to which they migrate, or other factors entirely, is unknown.

What may be most notable is the almost complete non-overlap of variables between the two models, with the exception of abundance which appears in both but with an opposite trend. Clearly, the search for biologically sensible patterns of extinction risk, particularly when exploring new variables such as the discontinuity variables, requires that many more systems be evaluated.

Comparing degree of decline between Alberta and Saskatchewan

We also analysed the degree of decline using 50 years of BBS trend data. The Albertan dry mixed grassland extends into south-western Saskatchewan but has been substantially more transformed in Saskatchewan (roughly 20% remaining in native vegetation). The Alberta best-fit model had six variables that are a mix of traditional expectations and discontinuity variables, meeting the expectations of our working hypothesis. The model indicates that specialization in all forms (grassland specialization and habitat and dietary specialization), rarity, *proximity* to a discontinuity (distance to edge) and being at the edge of geographic range best explain degree of decline.

The Saskatchewan best-fit model included only dietary and habitat specialization and rarity. Proximity to a discontinuity figured in 35% of the Saskatchewan models during the Monte Carlo, so did not make the 40% cut-off to be included in the refit procedure. The presence of specialization and rarity confirms that fragmentation and habitat loss preferentially impact specialized and rare species (Davies
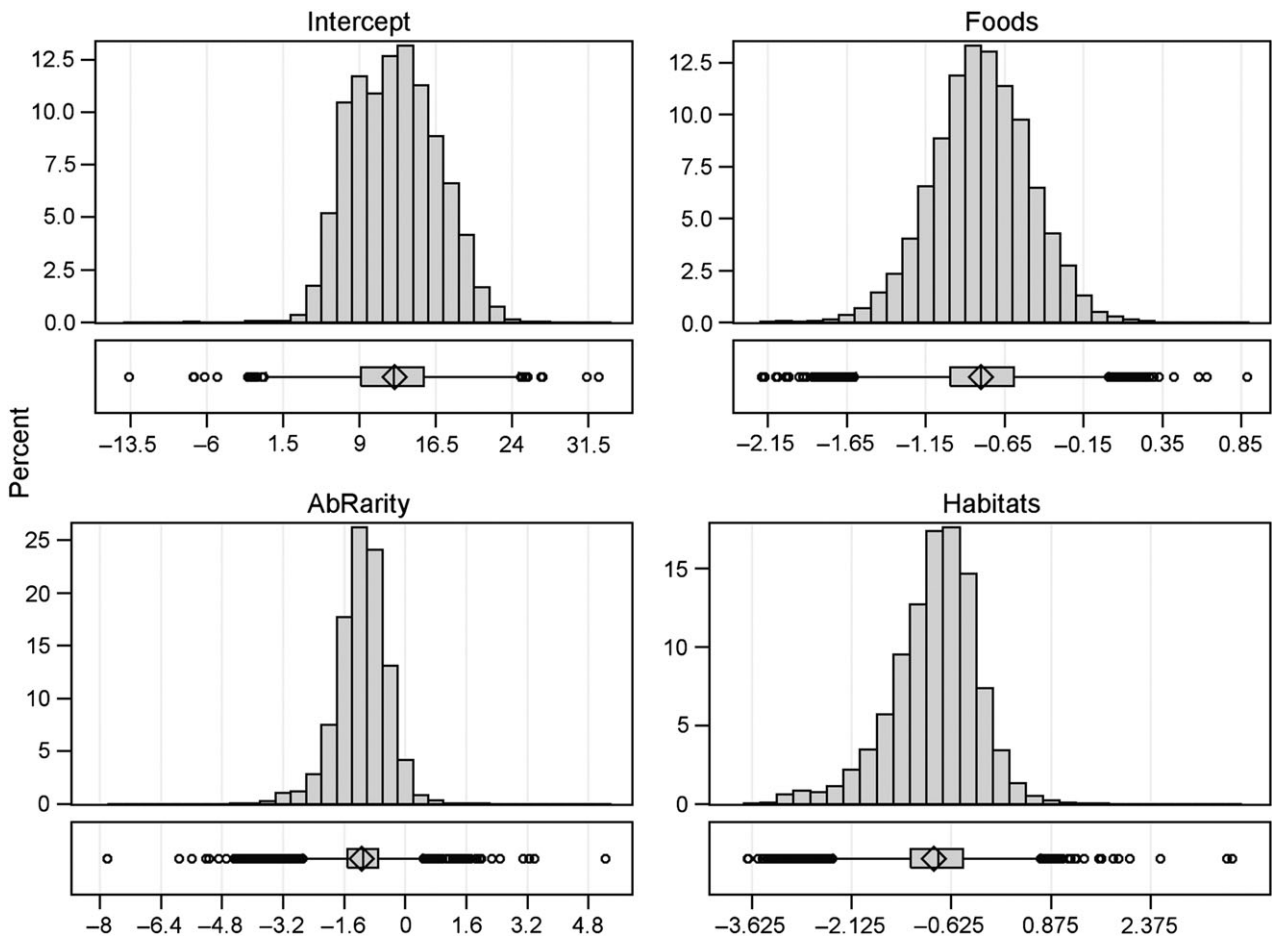
Figure 4 Parameter estimate distributions after refit procedure (10,000 iterations) for the best-fit model for the severity of decline in Breeding Bird Survey-defined declining breeding birds species in the dry mixed grassland of Saskatchewan, Canada.

et al., 2004; Pardini et al., 2010). The absence of distance to edge suggests that the relationship between distance to edge and extinction risk is complex.

CONCLUSION

Our results suggest that species decline and extinction risk are related to a broader set of traits than traditionally acknowledged by the scientific community. Discontinuity traits arise out of complex adaptive systems theory and reflect species-landscape interactions. Traditional approaches used by governments to predict species declines may be too simplistic and may therefore misguide management and conservation. Using CAS approaches that account for scale-specific patterns and processes have the potential to overcome these limitations and inform conservation biogeography.

Our analyses raised two issues that warrant further exploration. First, the suite of traits explaining decline/not-decline and those explaining severity of decline differed. This suggests that the processes or traits that push stable populations into declining populations may be different than those that push declining species towards extinction. Second is our

finding that species that are declining have body masses such that they are not at the edges of the aggregation, while severely declining species have body masses that place them near to the edge. These results raise questions about the relationship between type and scale of landscape transformation and the mechanisms responsible for decline and ultimately, extinction.

Finally, although decline and extinction risk are not precisely the same thing, both the Alberta listing process and the IUCN process from which it is derived omits any consideration of species' roles in contributing to ecological function. However, in contrast to the IUCN, species that are widespread and common but with significant decline trends are typically classified by Alberta as secure and are not given the same priority as rare species. The value placed on rare species by Alberta may be short-sighted, as commonness, which is itself a rarer condition than rarity, may be more critical for ecosystem functioning (Gaston & Fuller, 2007). Gaston and Fuller (2007, p. 14) argue that it is 'common species that shape the world around us' and disproportionately contribute to structure and ecosystem function. They urge conservation programmes to include common species

undergoing measurable population depletions. Food web network studies also demonstrate that species with many connections (common and widespread generalists) are more critical to the maintenance of the network than species with few connections (Dunne *et al.*, 2002). Our findings suggest that traditional perspectives of decline and extinction risk should be expanded to avoid having preconceived expectations of a declining species predict what we classify as a declining species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Data set for primary analysis on decline and extinction risk variables, using the breeding birds of the dry mixed grassland of Alberta, Canada.

Table S2 Data set for secondary analysis on degree of decline and extinction risk variables, using the breeding birds of the dry mixed grassland of Alberta and Saskatchewan.

Tables S3–S6 Tables of the variable selection percentages from the 4 regression analyses: Alberta government-defined decline, BBS-defined decline, Alberta decline trend and Saskatchewan decline trend.

BIOSKETCHES

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