Loss of community stability as a coherent ecological impact of a changing climate

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To my furry friends

Abstract

Climate models overwhelmingly show that 98% of the Earth experienced its highest level of warming during the twentieth century. During this period, a plethora of studies have demonstrated significant impacts on biota. The focus of my thesis is to study the stability of ecological communities to changes in climate, both observed and predicted. Climate change is often used synonymously with destabilization in the context of ecological systems. One of my objectives is to study whether specific types of ecological organization amplify or dampen potential destabilization due to specific types of climate change. I consider two types of highly non-equilibrium communities: a tropical planted forest and a seasonal Arctic tundra food web. Biodiversity may provide mechanisms through which to buffer community functioning to changing environmental conditions. In my first chapter, I use data from a ca. 15 year-old tropical planted forest experiment to study the stability of tree communities across a gradient of species richness to extreme climate events during this period. Using a bootstrapping procedure, I develop a statistical method for the detection of stress response in community growth and mortality as a measure of stability. In one-species communities, in contrast to higher richnesses, growth is strongly regulated by climate extremes and mortality is higher during a long period of drought. Using indicators of loss of resilience or critical slowing down, I show that for the drought extremes experienced at the experiment there may be an effect of diversity on loss of resilience, with one-species communities being more prone to massive die-off. In my second and third chapters, I consider a simplified Arctic tundra food web in a strongly seasonal community on Bylot Island (lemming-fox-goose-owl) where biodiversity varies temporally due to migrating species. To ultimately study stability to changing climatic conditions in the Arctic, a model which captures the seasonality of the community is necessary. Without integrating seasonality in food web modelling, especially for communities at high altitudes or latitudes, predications about the impacts of climate change may be uncertain. I construct a multi-season model of predator-prey biomass dynamics based on a hybrid dynamical systems (HDS) framework which allows inclusion of both fast (i.e. migration) and slow (i.e. predator-prey) dynamics. Each season is associated with a different stable equilibrium to capture a food web whose topology changes with season. We estimate winter interaction coefficients for the HDS based on summer data from 1993 to 2018 to generate long-term time-series which match observed patterns in species biomass fluctuations. I show that multi-season models, compared to models which do not incorporate seasonality, can expose indirect interactions between migrants and residents. Furthermore, I find that seasonality prevents specialist migratory predators from overexploiting available prey potentially suggesting that temporally changing food web topology may stabilize community dynamics. In my third chapter, I develop theoretical tools based on the HDS stability theory in order to study stability using the model I develop in my second chapter for a seasonal community with migrations. These tools accomplish two goals: 1) to separate the contribution of biomass coming from migrants and from residents and 2) define a measure of resilience which applies to systems with more than one equilibrium depending on the length of time spent in that season. I then use historical and projection data from Representative Concentration Pathway (RCP) climate scenarios to estimate summer season length for low, moderate, and high emissions scenarios. Two mechanisms contribute to the stability in seasonal systems. The first is the length of time spent in summer. I find that the longer migrants spend coupled to resident communities in summer, the longer the amount of time is needed for residents to recover within a certain threshold of their equilibrium. Second, the larger the distance between winter and summer equilibria, the less resilient the community is; migrants can drive larger distances depending on their dynamics in both seasons. I find that certain types of migrations (i.e. by migrant prey) may serve to amplify destabilizing effects of longer summers. Collectively, the three chapters of my thesis provide insight into the relationship between biodiversity and stability for certain types of complex systems and provide new methodologies to model communities in temporally-forced environments. They suggest that loss of stability may be a coherent impact of climate change on communities likely due to the exposure of communities to more extreme conditions or patterns over longer periods of time. Importantly, tension may be provided by the interaction of these patterns with the underlying species interactions in ways that are difficult to anticipate due to the complex nature of ecological communities.

Résumé

Les modèles climatiques montrent à une écrasante majorité que 98 % de la terre a connu son plus haut niveau de réchauffement au cours du XXe siècle. Au cours de cette période, une pléthore d'études ont démontré des impacts importants sur le biote. L'objectif de ma thèse est d'étudier la stabilité des communautés écologiques aux changements climatiques observés et prédits. Le changement climatique est souvent utilisé comme synonyme de déstabilisation dans le contexte des systèmes écologiques. L'un de mes objectifs est d'étudier si des types spécifiques d'organisation écologique amplifient ou atténuent la déstabilisation potentielle due à des types spécifiques de changement climatique. Je considère deux types de communautés très déséquilibrées : une forêt tropicale plantée et un réseau trophique saisonnier de la toundra arctique. La biodiversité peut fournir des mécanismes permettant d'amortir le fonctionnement de la communauté aux conditions environnementales changeantes. Dans mon premier chapitre, j'utilise des données d'une forêt plantée tropicale, âgée de c. 15 ans, pour étudier la stabilité des communautés d'arbres à travers un gradient de richesse en espèces aux événements climatiques extrêmes au cours de cette période. En utilisant une procédure d'amorçage, je développe une méthode statistique pour la détection de la réponse au stress dans la croissance et la mortalité de la communauté comme mesure de stabilité. Dans les communautés monospécifiques, contrairement aux richesses plus élevées, la croissance est fortement régulée par les extrêmes climatiques et la mortalité est plus élevée pendant une longue période de sécheresse. En utilisant des indicateurs de perte de résilience ou de ralentissement critique, je montre que pour les extrêmes de sécheresse rencontrés lors de l'expérience, il peut y avoir un effet de la diversité sur la perte de résilience, les communautés d'une seule espèce étant plus sujettes à la mort massive. Dans mon deuxième et mon troisième chapitres, je considère un réseau alimentaire simplifié de la toundra arctique dans une communauté fortement saisonnière sur l'île Bylot (lemming-renard-oie-hibou) où la biodiversité varie dans le temps en raison des espèces migratrices. Pour finalement étudier la stabilité aux conditions climatiques changeantes de l'Arctique, un modèle qui saisit la saisonnalité de la communauté est nécessaire. Sans intégrer la saisonnalité dans la modélisation du réseau trophique, en particulier pour les communautés à haute altitude ou latitude, les prévisions concernant les impacts du changement climatique peuvent être incertaines. Je construis un modèle multi-saison de la dynamique de la biomasse prédateur-proie basé sur un cadre de systèmes dynamiques hybrides (HDS) qui permet d'inclure à la fois la dynamique rapide (c.-à-d. la migration) et lente (c.-à-d. le prédateur-proie). Chaque saison est associée à un équilibre stable différent pour capturer un réseau trophique dont la topologie change avec la saison. Nous estimons les coefficients d'interaction hivernale pour l'HDS sur la base des données estivales de 1993 à 2018 afin de générer des séries chronologiques à long terme qui correspondent aux tendances observées dans les fluctuations de la biomasse des espèces. Je montre que les modèles multi-saisons, par rapport aux modèles qui n'intègrent pas la saisonnalité, peuvent révéler des interactions indirectes entre migrants et résidents. De plus, je détermine que la saisonnalité empêche les prédateurs migrateurs spécialisés de surexploiter les proies disponibles, ce qui suggère que la topologie du réseau trophique qui change dans le temps peut stabiliser la dynamique des communautés. Dans mon troisième chapitre, je développe des outils théoriques basés sur la théorie de la stabilité HDS afin d'étudier la stabilité en utilisant le modèle que je développe dans mon deuxième chapitre pour une communauté saisonnière avec des migrations. Ces outils atteignent deux objectifs : 1) séparer la contribution de la biomasse provenant des migrants et des résidents et 2) définir une mesure de résilience qui s'applique aux systèmes avec plus d'un équilibre en fonction de la durée de cette saison. J'utilise ensuite les données historiques et de projection des scénarios climatiques de la trajectoire de concentration représentative (RCP - "Representative Concentration Pathway") pour estimer la durée de la saison estivale pour les scénarios d'émissions faibles, modérées et élevées. Deux mécanismes contribuent à la stabilité des systèmes saisonniers. Le premier est la durée de l'été. Je observe que plus les migrants passent de temps à être couplés aux communautés résidentes en été, plus il faut de temps aux résidents pour récupérer dans un certain seuil de leur équilibre. Deuxièmement, plus la distance entre les équilibres d'hiver et d'été est grande, moins la communauté est résiliente ; les migrants peuvent parcourir de plus grandes distances en fonction de leur dynamique au cours des deux saisons. J'observe que certains types de migrations (c.-à-d. par des proies migrantes) peuvent servir à amplifier les effets déstabilisateurs des étés plus longs. Collectivement, les trois chapitres de ma thèse donnent un aperçu de la relation entre la biodiversité et la stabilité pour certains types de systèmes complexes et fournissent de nouvelles méthodologies pour modéliser les commu-

nautés dans des environnements temporellement forcés. Ils suggèrent que la perte de stabilité peut être un impact cohérent du changement climatique sur les communautés, probablement en raison de l'exposition des communautés à des conditions ou des modèles plus extrêmes sur des périodes plus longues. Il est important de noter que la tension peut être fournie par l'interaction de ces modèles avec les interactions des espèces sous-jacentes d'une manière qui est difficile à prévoir en raison de la nature complexe des communautés écologiques.

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Contents

Claims of Originality

(i) Long-term study (ca. 15 years) of the diversity-stability hypothesis based in Sardinilla, Panama, second oldest tree biodiversity-ecosystem functioning experiment in a global network of experiments known as TreeDivNet.

(ii) The development of a new methodological framework based on a nonparametric model to detect signals of stress response in communities where there can be large individual variability.

(iii) The application of indicators of loss of resilience to infer a possible diversity-slowing down relationship based on climate extremes observed at the study site in Sardinilla.

(iv) The development of a multi-season model for a tundra predator-prey community on Bylot Island, Canada. Explicit use of hybrid dynamical systems with multiple equilibria to model a seasonal food web taking into account migrations.

(v) The implementation of convergent cross mapping to study causal relationships (i.e. direct and indirect interactions) between resident and migrant species.

(vi) The application of Lyapunov stability theory from hybrid dynamical systems to a model with migration.

(vii) The derivation of an expression for the time derivative of a candidate Lyapunov function for a general class of predator-prey dynamics leading to a simple condition under which the function can be identified as being strictly Lyapunov.

(viii) The development of an algebra which allows the partitioning of the contributions of migrant and resident species to dynamic quantities related to stability.

(ix) The conceptualization and derivation of a measure of resilience for seasonal communities associated with multiple equilibria.

Contributions of Authors

Chapter 1 CH, DG, and CP conceived the project using the data from the study site where CP is principal investigator. CH developed the theory behind the manuscript and performed the data analyses. DG, FG, and CP had major input in technical discussions with CH. CH wrote the first draft of the manuscript, for which all authors contributed substantially to revisions.

Chapter 2 CH created the model and performed the modelling with significant input from FG and DG. GG, JB, DB and PL collected data. CH wrote the manuscript with input from all co-authors.

Chapter 3 CH developed the study with input from FG and DG. CH developed the novel theory and performed the analyses. CH wrote the manuscript with input from FG and DG.

List of Figures

Introduction

I.1 Changes in Earth's climate system and ecological responses

Reconstructions of warming events over the past two millennia find that anthropogenic warming exhibits spatiotemporal coherence as it is unmatched in terms of absolute temperature and spatial consistency [1, 2]: 98% of the Earth experienced the warmest period during the twentieth century. It is during this century that reviews comparing case-by-case studies provide strong evidence that biota have already been affected [3]. Furthermore, ecological responses seem to be coherent irrespective of taxonomic classification or geographic region: from polar to tropical and terrestrial to marine environments. According to Walther et al. [4], patterns of ecological responses to climate change fall into four categories: 1) phenology and physiology of organisms, 2) range and distribution of species, 3) composition and interactions within communities, and 4) the structure and dynamics of ecosystems. The timing of life history events is influenced by climatic conditions, such as advanced phytoplankton blooms due to earlier spring thermal stratification, but not all species (across trophic levels) respond in the same way [5]. They may not even respond to similar climatic factors [6, 7]. Surveys have documented northward range expansions for plants, insects, and mammals which are climatically limited; shifts in distribution and climate appear to be at the same spatiotemporal scales, occurring rapidly with warm periods and slowing down during cooling [8]. Changes in community composition (abundances) are another coherent pattern of change; for example, increases in woody shrub density and rare animals but extinction of other common ones have been found in a desert community [4, 9]. Lastly, large-scale climatic variability may alter the dynamical stability of communities. Changes in climate (i.e. direct changes to survival and indirect changes to prey vulnerability) are shown to alter the dynamics of a three level, straight chain community (balsam fir-moose-wolf) with the strongest effects at the top and bottom levels [10]. The ecological impacts of recent climate change are already visible and may become increasing evident as warming continues; therefore, assessing whether there are coherent patterns in the stability of ecological responses to climate is of paramount importance.

I.2 Thesis objectives

Impacts of climate change on ecological communities are often synonymous with destabilization, where stability is broadly defined as the ability of a community to defy change. Some types of ecological organization may amplify or dampen potential destabilization due to climate. A long standing problem in community ecology is whether biodiversity–a multifaceted type of organization such as those found in cells, organisms, and communities–begets stability. One issue is that there are many possible types of biodiversity and many indicators of stability; an ecological system may be stable with one set of definitions but unstable with respect to another. Generically, these measures of stability assume that an ecological system has a steady state (i.e. an equilibrium). To complicate the problem even further there are many ecological systems which are non-equilibrium in nature and require new definitions of stability. In this thesis, I consider two different communities which are highly non-equilibrium systems: a tropical planted forest and a seasonal Arctic tundra food web. My objective for the former community is to determine if biodiversity as measured by tree species richness can buffer growth and morality under extreme climate events, and whether species richness can help prevent loss of resilience, defined as massive tree die-off. The objective for the latter seasonal community is to determine whether food web diversity, which fluctuates over time due to migrating species, can increase resilience to increases in the summer season length. Collectively, I consider two measures of biodiversity: species richness and an overlooked dimension of biodiversity, seasonal changes in food web complexity due to migrations. Both are hypothesized to have similar mechanisms by which they infer stability through a level of asynchrony of species responses. The definitions of stability I develop in both cases apply to non-equilibrium systems. Taken together, I examine whether these studies, which employ an array of community types, may both exhibit a loss of stability to different patterns of climate change in the spirit of Walther et al.

I.3 Response of tropical forest communities to climate change: Known impacts and gaps in knowledge

I.3.1 Literature review on impacts

Forest ecosystems cover 30% of the land surface (including woodlands and savannas), support 80% of the world's terrestrial biodiversity, and perform essential ecosystem functions and services such as carbon sequestration [11, 12]. A changing climate system may impact forests in both positive and negative ways. Positive impacts include carbon accumulation from a greenhouse atmosphere (i.e. CO_2 fertilization) [13] but see [14]) and longer growing season (but see [15]). Reduced growth and increased mortality due to stress (i.e. changes in precipitation regimes) and due to the dynamics of forest insects and pathogens are possible negative consequences [16, 17]. Tropical forests may strongly counteract climate effects through high rates of carbon accumulation, but also through evaporative cooling compared to temperate and boreal forests [11]. However, as they loose their status as carbon sinks from increased deforestation and fires, their ability to regulate global climate is uncertain.

Intact, undisturbed tropical forests may be less vulnerable to a warmer, drier climate [18]. However, habitat loss and degradation driving biodiversity loss of tree species may increase the vulnerability of tropical forests to changing climatic conditions [19]. For example, deforestation and stress from changes in precipitation during the dry-season, may cause forest dieback and loss of resilience in the Amazonian forest biome [18]. Also, forest structure can be altered by logging and tree mortality resulting in the collapse of tree biomass. Using remote sensing techniques, Verbesselt et al. [20] use a vegetation index to study die-off (i.e. loss of resilience) in evergreen tropical forests in South America, Africa, and Southeast Asia. The authors find strong evidence of loss of resilience when mean annual precipitation fell below 1500 mm. Supplementing studies on the current state of tropical forests worldwide are controlled experimental forests which can be used to study how factors, such as biodiversity, may modify community response to changing climatic conditions. An important class of these experiments involve testing for biodiversity-ecosystem functioning relationships. Biodiversity-ecosystem functioning (BEF) is a broad research program which addresses the relationship between functioning (i.e. ecosystem processes which are affected by biota) and biodiversity (i.e. species richness) [21]. TreeDivNet is a global network of tree biodiversity experiments which aims at testing BEF in major forest types (http://www.treedivnet.ugent.be/). In the context of climate change impacts, the longest running experiments in this network can be used to study possible diversity-stability relationships with implications for mitigating impacts in natural tropical forests [22].

I.3.2 Diversity-stability relationships as BEF and insurance

Odum (1953), MacArthur (1955), Elton (1958), Hutchinson (1959), and Margalef (1969), argued that the larger the number of species, the more stable an ecological system is under fluctuations in the environment [23–27]; so called, diversity-stability relationships. This hypothesis was challenged along two fronts: McNaughton [28] demonstrated a lack of empirical support in a review of case studies while May [29] showed through mathematical models that stable equilibrium dynamics are not necessarily exhibited by more complex communities. Partially resolving these contradictory results, Pimm [30] argued that both the concepts of diversity and stability have many definitions; moreover, the choice of definition may change the nature of the relationship, a conclusion supported by Ives & Carpenter [31]. Tilman provided the first empirical evidence in the Cedar Creek experiment that species diversity can stabilize aggregate community variables while simultaneously decreasing population-level stability [32, 33].

Doak et al. [34] developed the statistical averaging mechanism for positive diversity-stability relationships assuming that the coefficient of variation is the same for all species and, moreover, that the variance is proportional to the square of the mean. Tilman [35] relaxed this assumption finding that interactions between species can change the exponent in the mean-variance relationship giving rise to a yielding effect. Yachi & Loreau [36] made these ideas more general by developing a statistical dynamical model. Their hypothesis, which they called the insurance hypothesis, posits that species richness can act as a buffer to fluctuations in the environment [28, 36–39]. Species asynchrony provides a mechanism for insurance where species may have different responses to similar environmental conditions; thus, some species may compensate by increasing their contribution to ecosystem processes while others decrease [40]. Two mechanisms for insurance are a complementarity effect (i.e. a reduction in temporal variance) and a selection effect (i.e. a performance-enhancing effect) [41].

I.3.3 Gap in our knowledge

Many studies which consider insurance effects under fluctuations do not consider perturbations of high frequencies or magnitude. Consequently, stress, such as that induced by extreme climate events in the form of drought and extreme heat, is largely ignored both empirically and theoretically in biodiversity-ecosystem functioning (BEF) research (with some exceptions see [41–46]). Multiple mechanisms may drive positive biodiversity-stability effects during stressful events. Niche complementary predicts that due to more efficient resource utilization by mixtures compared to monocultures mediates community-level response to stress intensive [47]. Complementarity may also allow the emergence of interspecific facilitative interactions among individuals in more diverse communities [48]. However, the ability of trees to recover may be dampened by periods of stress such as drought or extreme heat [49, 50]. When introducing the concept of stress, including extreme climate events and tree stress response, individual variation becomes important and a new detection problem emerges. Therefore, separating the background variation in functioning from the signal due to stress means developing an approach to measure stability accounting for this variation. Furthermore, a loss of resilience or critical slowing down can push forests to the boundary of massive die-off [20]; to the best of my knowledge, there has been no other study which has investigated the effect of diversity on loss of resilience; a relationship which may have important implications for natural tropical forests experiencing loss in tree species diversity.

I.3.4 General approach to address this gap

Holling [51] defines resilience as the capacity of an ecosystem to return of a *pre-condition* state following a perturbation. For a forest, multiple characteristics can be used to define its ecosystem state. It is common to define a forest state by the maintenance of taxonomic composition (i.e. a dominant collection of tree species at a certain spatial scale), of ecosystem functions or the specific functional roles that species have, of structures such as hight and stem density at maturity, and of process rates such as mortality [52].

At the landscape-level, there are two classical theories which attempt to describe forest dynamics: classical competition niche theory [24] and the neutral theory of biodiversity [53]. In competition niche theory, species coexistence is maintained through exclusive niches at equilibrium. Hubbell's neutral theory assumes that equilibrium is maintained through ecological drift of species with identical niches where species loss is balanced by dispersal and/or speciation. However, when applied to mega-diverse tropical forests, these theories fail to describe the non-equilibrium dynamics observed in large, permanent forest sites [54]. Non-stationary dynamics is evident within a timespan of 23 years, Barro Colorado Island in Panama has lost 37 species while Bukit Timah in Singapore looses species at an average rate of 8% between censuses [55].

On the other hand, in the case of a forest stand (defined as a uniform community of trees in age and spatial arrangement, for example), it may be possible to define a set of "normal behaviour" for the system: a pre-condition state. Tree-tree (neighbourhood) interactions can lead to the maintenance of ecosystem function such as community productivity and stability in mixed plots [22, 56, 57]. In this case, we define "normal behaviour" in a statistical sense assuming a null hypothesis of time-independent growth and mortality of individual trees. Using this null expectation, we may study the stand- or plot-level response to stress such as cased by extreme climate events.

I.4 Response of trophic interactions in Arctic communities to climate change: Known impacts and gaps in knowledge

I.4.1 Literature review on impacts

Earth's climate system is strongly regulated by the cryosphere. Some of its major functions include: a net cooling of the Earth's surface; driving air and ocean circulation globally; regulating availability of of freshwater at multiple time scales from seasonal to millennial; and helping to regulate methane and carbon storage [58]. The Arctic is experiencing larger rises in surface air temperature compared to the rest of the globe due to polar warming amplification [59]. Furthermore, there is a pronounced seasonality to polar warming amplification: winter warming is occurring four times faster than summer warming during to atmosphere processes such as dynamical feedbacks in energy transport (e.g. [60]). Arctic ecosystems are expected to be profoundly impacted by these aspects of climate change, as biological and chemical processes are structured by seasonal shifts in temperature, snow, ice cover, and nutrient availability [61, 62].

Many empirical studies have assessed the looming threats that face Arctic communities under developing climatic regimes [63–65]. Ideally these assessments would involve information about all trophic levels: long-term datasets of multiple population attributes across multiple species [66–69]. In terrestrial ecosystems, Arctic vegetation exhibit various responses to warming in space and time (i.e. through changes in phenology) as well as species-specific sensitivity to warming [70, 71]; in all cases there is an increase in primary production. Warmer temperatures and earlier snowmelt may also impact the phenology of Arctic wildlife, such as the nesting cycle of birds [72] or small rodent population dynamics [73]. Although, one study in the Canadian high-Arctic found little evidence to support changes in phenology, abundance, or productivity in many vertebrate species despite large increases in above-ground biomass due to warming [69]. Furthermore, trophic mismatch, i.e. a lack of synchrony between the phenology of consumers and their resources, can negatively affect the fitness of Arctic herbivores [74]. When considering the response of ecological communities as a whole, the net effect of climate change may be modified by indirect interactions [75]. But in Arctic communities dominated by vertebrates, herbivore-mediated cascading effects of climate on plants tend to lag behind the direct effects of climate warming, especially when key herbivores are long-distance migrants [76]. It has been suggested that allochthonous inputs from more productive ecosystems can amplify or dampen the destabilizing effects of a changing climate on different trophic levels in the Arctic tundra [69, 77, 78].

I.4.2 Hypotheses on drivers of food web stability in seasonal systems

Different types of organismal movements such as dormancy, migration, and flexible foraging may promote stable trophic interactions by allowing species to exploit abundant resources and decouple from declining ones [79]. According to McMeans et al. [79], this mechanism may ensure the maintenance of consumer populations and guarantee that no single resource becomes dominant (by consumers using abundant resources) or rare (through release of predation pressure). Changing environmental conditions may allow some species to prosper while others may suffer overall buffering top carnivores to climatic variability, such as communities found in the Serengeti [77]. On the other hand, in simple predator-prey communities involving small rodent populations like those found in the high Arctic, different climatic scenarios increase the length of population cycles and decrease their amplitudes. These effects are detrimental to predator populations which depend on years of high prey abundance to drive reproductive strategies [80]. Direct effects on species from climate may thus complicate the hypothesized stabilization from indirect effects from predator-prey interactions for systems with migration.

I.4.3 Gap in our knowledge

A drawback of many studies on Arctic ecosystems is that data is only available for the growing season, given the unique difficulties of sampling in winter conditions [81]. However, winter is a critically important season for these ecosystems [82, 83]. During winter, generalist carnivores feed exclusively on resident herbivores which remain active under snow or ice cover. These interactions lay the foundation for spring when there is a dramatic shift in community structure due to migrating species [84]. Despite strong seasonality driving species, very few studies have explicitly modelled multi-seasonal Arctic community dynamics and even fewer quantify their stability to a changing climate [80, 85]. A particular manifestation of seasonal food webs which lacks a theoretical basis is migrating species. Including migrants in food webs means that the paradigm of equilibrium dynamics no longer holds; when migrants arrive/leave resident communities they alter food web topology and modify community dynamics. A basic requirement of any model of trophic interactions including migrations is multiple equilibria, one for each season. Furthermore, due to switching between food web topologies, communities are usually far from their equilibria; consequently, local stability theory does not hold. In the case where migrations can be modelled as fast dynamics and predator-prey interactions as slow dynamics, a hybrid dynamical systems (HDS) framework may be appropriate as it can incorporate these different timescales.

I.4.4 General approach to address this gap

A dynamical system is a system evolves in time and/or space [86]. They can be modelled by a set of differential (continuous) or difference (discrete) equations for the system state. A classical example of a dynamical system in ecology is the classical Lotka-Volterra predator-prey equations [87, 88] which describe how a predator and prey evolve in time. This model has been applied to a variety of communities such as the Canada lynx and snowshoe hare [89]. Suppose $P(t)$ is the predator state (i.e. how its population changes with time) and $N(t)$

the prey state, then the Lotka-Volterra model has the form

$$\frac{dN(t)}{dt} = rN(t) - \beta N(t)P(t) \quad \text{(prey equation)} \tag{1}$$
$$\frac{dP(t)}{dt} = \gamma N(t)P(t) - dP(t) \quad \text{(predator equation).} \tag{2}$$

These equations say that in the absence of predators the prey population increases exponentially and in the absence of prey the predator population decreases exponentially. The cross-terms describe the interaction between the predator and prey. It assumes a type I functional response in the prey equation which means that there is a linear relationship between size of the prey population and the number of prey killed. In the predator equation, the numerical response is linear: the increase in the size of the predator population depends linearly on the prey population. The solutions to these equations are periodic with the predator population oscillation lagging behind the prey oscillation. This model has a plethora of generalizations and extensions in the literature too many of which to mention here.

A hybrid dynamical system (HDS) is an indexed collection of dynamical systems with a map which indicates how to jump between them; the jump may involve switching between dynamical systems or resetting the state [90]. The jump is triggered when the state satisfies particular conditions. According to Branicky 1997 [90], HDS thus stitch together dynamical systems with jumps that generally reset the initial state of possibly different dynamical systems when a final state is reached. Another way of looking at a HDS is that it models systems which have both fast (jumps) and slow dynamics and so involve both continuous and discrete variables. An "automaton" is a structure which defines the allowable switches in the HDS with nodes corresponding to specific dynamical systems and arrows corresponding to jumps. An early example of a hybrid system in the ecology literature is found in Koch 1974 [91]. Koch demonstrated that stable coexistence between two competing species, M an N, which grow at different rates in different seasons over many years. In spring, growth is unrestricted with one species outperforming the other beginning at small populations so that nonlinear terms can be ignored. In summer, growth becomes limited by the availability of a resource and competition ensues where N is the better competitor. Spring and summer dynamics are governed by Lotka-Volterra competition equations. Then in the fall and winter, there is a fold reduction in the populations (i.e. 40-fold) due to some adverse environmental conditions. For parameter values that maintain the initial state, stable cycles can be maintained as long as the season length is not too long or too short that growth is always in the density independent phase. The automaton and time-series for these dynamics is shown in Fig. 1. A stable cycle is reached after many seasons.

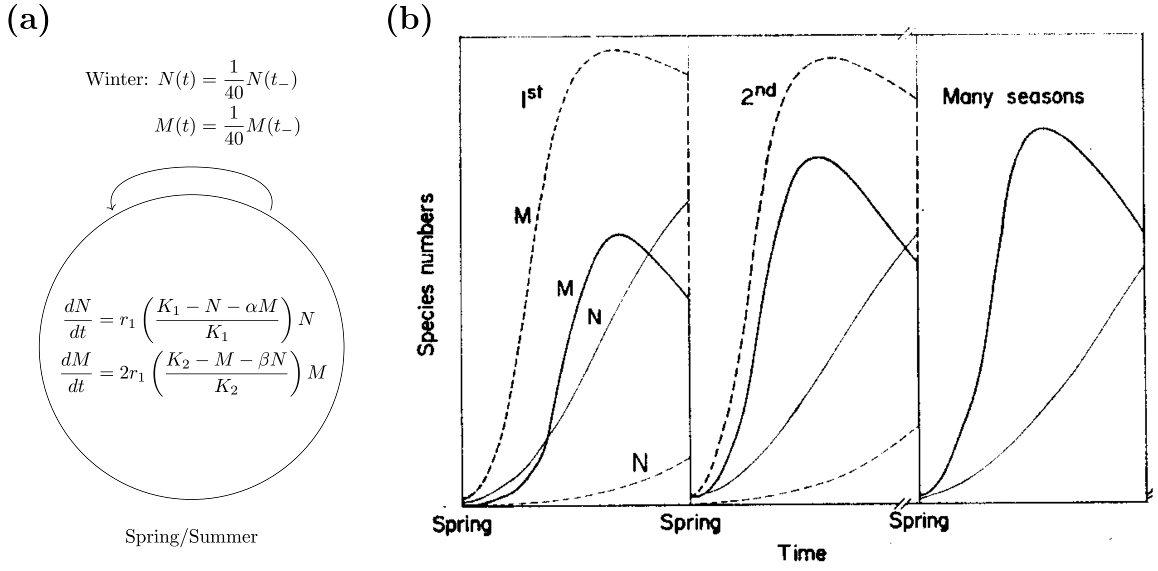
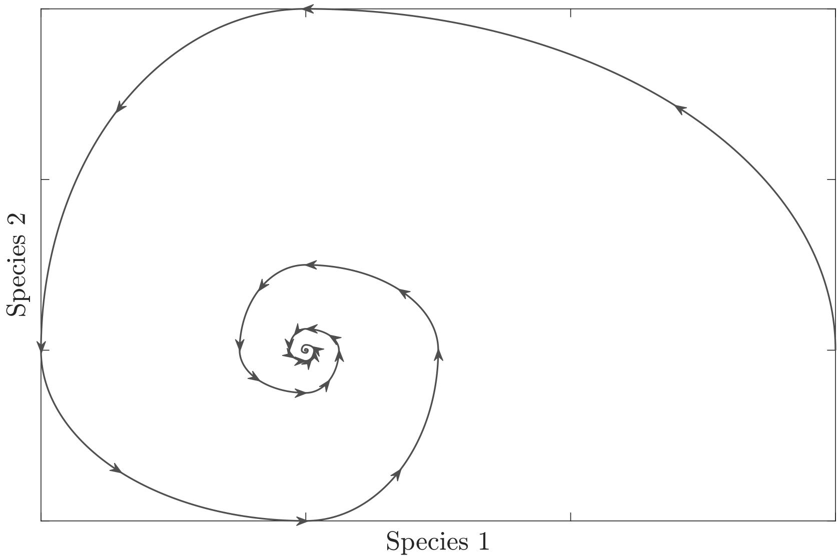


Figure I.1 (a) Interpretation of Koch 1974 model with an automaton and (b) time-series from [91]. The solid and dashed lines correspond to different initial conditions. The HDS reaches a stable cycle after many seasons.

The concept of a HDS shows up in many subsequent ecological studies. In particular, this framework has been used to study the population dynamics of migratory bird species [92, 93]; to quantify the effects of predation by generalists and specialist predators on a migrating prey population [94]; to study the qualitative behaviour of prey populations when the functional response of a generalist predator changes according to changes in prey availability by season [95]; and to model community dynamics of a small rodent population under seasonally varying predation pressure [80, 85]. The optimal control application of HDS has even been used to analyze the effect of switching of harvesting strategies on interacting fish populations [96]. Collectively, a HDS is a good model for these studies because there are both fast and slow dynamics. There are many other models that can be employed to study seasonal systems; to name a few, semi-discrete methods, periodic matrices, Floquet theory [97]. Semi-discrete methods are a simple hybrid dynamical system [98] which is, in fact, the example of Koch 1974. They have continuous dynamics with a (discrete) impulse; for example, seasonal reproduction which represents an instantaneous increase to population size. One class of periodically-forced matrix models has been used to separate within season breeding from between season demography [99]. The timescales may be different: during the reproductive season, time may be measured by a day while across seasons time may be over several months. Floquet theory is a tool for studying periodic, linear switched systems; Floquet's theorem can be used to understand the stability of fixed points and limit cycles [100].

HDS have interesting stability properties which may have important implications for ecological systems. When switching is unconstrained, it may be possible to destabilize the hybrid system *even though each component system is stable.* Furthermore, it may be possible to constrain switching in such a way that the switched system is stable *even though each component system is unstable* [101]. The classical stability theory of HDS is based on Lyapunov stability theory. Suppose that we have the same equilibrium point for each component (although it will be exploited in this thesis that HDS can handle situations with multiple equilibria). Lyapunov stability theory assumes that there exists a function, known as a Lyapunov function, which has three properties: it is positive, is zero only at the equilibrium point, and it is strictly decreasing along the system trajectory. (In the case when the Lyapunov function is decreasing but not strictly decreasing, the LaSalle invariance principle can be used to show stability.) This function can give information about stability because it is always decreasing and because it has a minimum point at the equilibrium, the system trajectory must asymptotically approach this point. The Lyapunov function will be an important concept in this thesis, in particular the third chapter, and has a precise ecological interpretation when the dynamical systems are from a general class of predator-prey models [102].

(a)



(b)

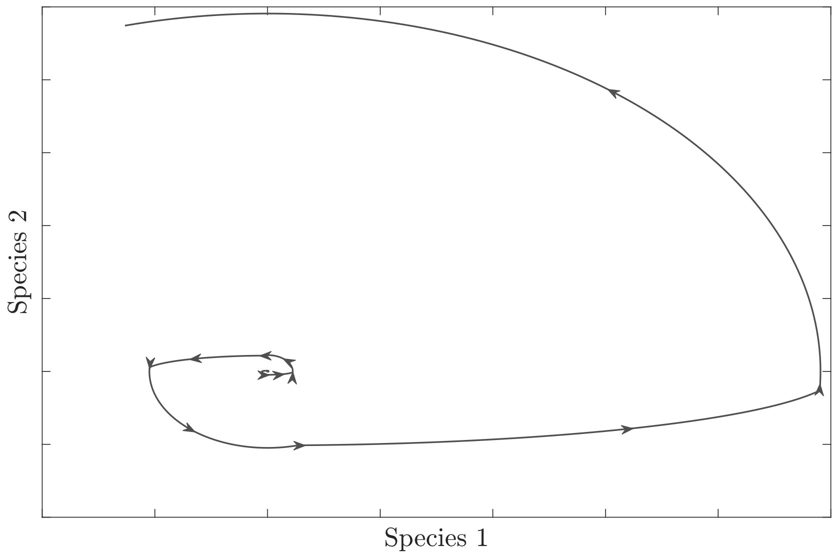


Figure I.2 (a) Stable and (b) unstable hybrid systems with two component systems. It is assumed that each of the component systems are stable. There are kinks when the system switches between components.

I.5 Structure of thesis

This is a manuscript based thesis with three chapters, each chapter corresponding to an article and author contributions appearing at the end of each chapter. The first chapter deals with the detection of stress response to extreme climate events in ca. 15 year tropical planted forest experiment along diversity gradients. Extreme climate events are characterized by the standardized precipitation-evapotranspiration index following the procedure of Isbell et al. [41]. We use the basal area increment summed over trees in a plot as a measure of plot-level performance. To test out hypotheses we construct two different null models: a growth model and a mortality model, which represent our null expectation for each diversity treatment if climate is not driving year to year differences in performance. Null distributions are generated via a bootstrapping procedure whilst preserving the species identity in a given plot. An effect of climate is identified if effect sizes, which compare observed plot performance to the null expectation, are significant. We then test the hypothesis about the loss of resilience, or a transition to massive die off, using two generally accepted indicators: temporal autocorrelation (TAC) at lag-1 and the power spectrum. TAC at lag-1 should approach one for monocultures under sustained stress as consecutive states in time are closer to one another due to a flattened basin of attraction before a transition. The power spectrum indicates how similar states are at higher lags and should exhibit spectral reddening for monocultures if close to a transition.

The second chapter lays the foundation for studying stability of systems with seasonal food webs by building a multi-season model for a simplified Arctic tundra food web (lemming-fox-goose-owl). The main objective of this chapter is to demonstrate that multi-season models capture essential information about species interactions which is missed in static models or when focusing on a single season (i.e. the growing season). I first construct a static predator-prey model for this food web by translating parameters in a mass-balance model to Lotka-Volterra predator-prey equations. Then, I construct a multi-season model using a hybrid dynamical systems framework. Such a framework allows for the inclusion of both fast (i.e.

migration) and slow (i.e. predator-prey) interactions. I generate simulated long-term time-series from the model by constraining the model using summer data on species interactions and population dynamics. I show that our model can reproduce observed behaviours in biomass fluctuations; in particular, multi-periodicity in lemming cycling. I use convergent cross mapping (CCM) on long-term time-series to infer causal relationships between species in the form of trophic control regimes and indirect interactions for the static model, our multi-season model, and a model where only summer time-series are used.

The last chapter of the thesis uses the multi-season model constructed in the second chapter to study how migrating species affect the resilience of community dynamics under climate change. I develop a conceptual framework for the model based on Lyapunov stability theory for hybrid dynamical systems with multiple equilibria. I interpret the ecological meaning of Lyapunov functions in the context of migrations as the biomass available for consumption and develop a novel partitioning of contributions of migrant and resident species. Using this partitioning I derive an analytical expression for the temporal flow of biomass from migrating species between seasons. I introduce a new definition of resilience for systems with multiple equilibria. Using climate change scenarios to estimate possible changes in summer season length, I study how these durations change the flow of biomass and alter predictability as well as resilience in strongly seasonal food webs with migration.

I.6 References

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Chapter 1

Effect of diversity on growth, mortality, and loss of resilience to extreme climate events in a tropical planted forest experiment

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Abstract

A pressing question is whether biodiversity can buffer ecosystem functioning against extreme climate events. However, biodiversity loss is expected to occur due to climate change with severe impacts to tropical forests. Using data from a ca. 15 year-old tropical planted forest, we construct models based on a bootstrapping procedure to measure growth and mortality among different species richness treatments in response to extreme climate events. In contrast to higher richness mixtures, in one species plots we find growth is strongly regulated by climate events and we also find increasingly higher mortality during a consecutive three year dry event. Based on these results together with indicators of loss of resilience, we infer an effect of diversity on critical slowing down. Our work generates new methods, concepts, and applications for global change ecology and emphasizes the need for research in the area of biodiversity-ecosystem functioning along environmental stress gradients.

1.1 Introduction

Projections of future climate change include higher mean temperatures, water deficit intensity, and more intense El Niño-Southern Oscillation events [1]. How biological systems will respond to stress due to changes in temperature and moisture regimes is therefore paramount [2]. Forecasting the impact a changing climate will have on forest ecosystems is particularly important because they cover 30% of the land surface, support 80% of the world's terrestrial biodiversity, and perform essential ecosystem functions and services such as carbon sequestration [3, 4]. These impacts may include reduced growth and increases in mortality [5]. Several recent studies in forests have investigated the stability of ecosystem functioning, such as growth or productivity, in response to drought [6–13] and suggest that there may be a positive link to diversity.

Here we define stability as the ability of a community to defy change (i.e. resistance and resilience) [14]. The basis for positive diversity-stability relationships is the insurance hypothesis. First proposed by [15] and refined by [16–19], the insurance hypothesis posits that species richness can act as a buffer against fluctuations in the environment. A key mechanism underlying insurance is species asynchrony: species may independently have different responses to similar environmental conditions [20]. How these species respond to environmental conditions may be driven by biological traits [21] as well as demography [22]. Furthermore, there may be more relevant aspects of diversity from which to discern diversity-stability relationships [23]. In a recent study [24], the authors found empirical evidence for decreased stability in certain functions from an analysis of species abundances in five different functional groups (i.e. decomposition, carbon sequestration, pollination, pest control, and culture values) which they posit is due to a weakened insurance capacity. They claim that there is a higher risk of failure in these functions under future environmental perturbations, although they do not consider perturbations of higher frequency and magnitude. Incidentally, stress, defined as extreme environmental conditions which are detrimental to ecosystem functioning [25], is largely ignored, both empirically and theoretically, in biodiversity-ecosystem functioning (BEF) research [25, 26] although there are exceptions [27–32].

Multiple mechanisms may drive BEF relationships during stressful events [33]. Niche complementarity predicts that heterogeneous environments lead to higher mortality in monocultures than in mixtures because resources are used more efficiently in mixtures than in monocultures thus mediating the community-level response to stress intensity [34]. Complementary effects can also come from changes in the functional contribution of facilitative interactions among species. However, a stressful environment can also change the strength of per capita species interactions. Specifically, it is posited that the performance of more diverse communities improves relative to that of low diversity communities in stressful environments because of the emergence of interspecific facilitative interactions among individuals [35]. Both species-specific (complementarity) and per capita (stress gradient hypothesis) mechanisms suggest a stronger impact of stress events on monocultures than on mixture communities.

Detection of community-level stress response of a community has been inferred from measures of resistance and resilience to stress. Pimm [36] defined resistance as the magnitude of change in a response variable during a perturbation and resilience as how fast recovery occurs following a perturbation. Subsequently there have been many different mathematical interpretations of these measures. In particular, resistance and resilience have been interpreted as "components" of temporal stability [37] (and references therein). A recent study [38] further proposes a bivariate framework for resilience in terms of normalized resistance and recovery metrics based on the undisturbed state in order to have a comparable measure of resilience between different systems. When introducing the concept of stress, including extreme climate events and tree stress response, individual variation becomes important and a new detection problem emerges. Therefore, separating the background variation in functioning from the signal due to stress means developing an approach to measure stability accounting for this variation.

The ability of trees to recover may be dampened by periods of stress such as drought or extreme heat [39, 40]. This loss of resilience or critical slowing down can push forests to the boundary of massive die-off [41]. Recently it has been shown using satellite data from evergreen tropical forests in South America, Africa, and Asia/Australia that slowing down may be driven by low levels of precipitation (i.e. mean annual precipitation values which are less than $1{,}500$ mm yr^{-1}) [42]. There are many indicators which may infer slowing down [43, 44]. Such indicators are related to the resilience, and in particular the shape of the basin of attraction, of the current state. As environmental drivers push the current state to a tipping point, the slope of the basin of attraction decreases and, consequently, resilience to small perturbations decreases [23]. If one were to measure the temporal autocorrelation (TAC) at lag-1 of this state, it would approach 1 as consecutive states in time are closer to one another due to a flattened basin. However, lag-1 autocorrelation does not account for variation at higher lags; the power spectrum can show changes in the spectral properties of a time series before a transition. In other words, a power spectrum can determine how similar states are at higher lags by decomposing a time series into its component frequencies.

Systems closer to a transition may exhibit spectral reddening, i.e. most of the variation in the series occurs at lower frequencies, because states tend to change slowly in time about this flattened basin. A particularly important question which, to the best of our knowledge, has not yet been explored in the literature is how diversity might impact slowing down. TAC and spectral reddening have the potential to provide novel insights to slowing down following extreme climate events.

Here we focus on the detection of stress response in forest communities. As our case study, we consider a long-running tropical tree diversity experiment [45] and identify stressful events at the site from the standardized precipitation-evapotranspiration index [46] (SPEI). We study how growth and mortality along diversity gradients are impacted by extreme climate events based on bootstrapping of tree data to generate the statistics need to account for potentially large individual variability. We hypothesize that differences in growth along a gradient of species richness should manifest mostly during wet or dry extreme climate events. In other words, monocultures should have greater variability in their growth compared to higher richness mixtures during stress. We also predict that mortality will be higher in monocultures during intense spells of drought as a result of lower resilience than higher diversity treatments. To determine whether the hypothesized mortality for monocultures may indicate sudden massive die-off we compute the temporal autocorrelation at lag-1 and the spectral density of growth time series. To study the relationship between species richness and slowing down, we compare these indicators across diversity treatments. Specifically we expect monocultures to exhibit spectral reddening whereas the power spectrum should become more flat at higher richness. Our approach improves our understanding and our ability to quantify stability under stress for forest ecosystems, and gives momentum to the study of the relationship between diversity and slowing down.

1.2 Results

1.2.1 Climate events identified from the SPEI

Based on a 21 year period from 1995 to 2016, we identify extreme climate events occurring approximately 10% of the time, moderate dry and wet events each occurring 25-30% of the time, and normal conditions persisting 35%. Normal years are identified based on the climate data (i.e. rainfall and evapotranspiration) over a 21 year period; because of the way SPEI is computed there is an unavoidable shifting baseline which depends on the period chosen. Climate extremes defined only using data from the early (or late) 1900s, would probably have identified more (or fewer) extreme climate events [29].

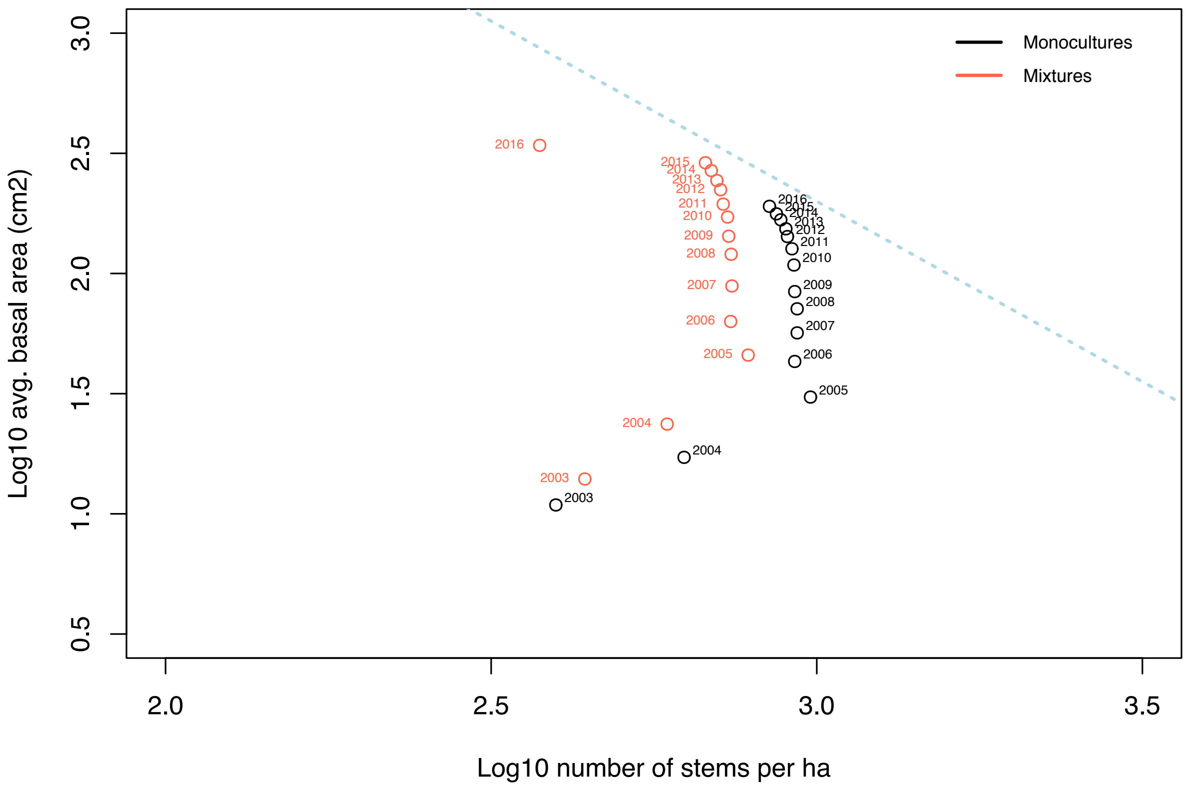

Figure 1.1 Development phase for the even-aged stands at Sardinilla. Two trajectories are shown for monocultures (black) and mixtures (red). As plot basal area increases the number of trees per hectare decreases over time starting in 2006, and the trajectory moves upwards and to the left as it converges to the self-thinning line with slope $-3/2$ (blue dotted line).

We chose the timeframe from 2006 to 2016 to construct our models and test our central hypotheses in order to control for stand development (Fig. 1.1). We see that from 2003 to 2005, the plots are in the establishment phase during which juveniles recruit into the size class in which diameter at breast height (DBH) can be measured (1.3m). By 2015, plots are just reaching the self-thinning line of slope $-3/2$. Along this line, mortality is mostly driven by strong competition between stems. By 2006, plots in both monocultures and mixtures are out of the early development phase and on a trajectory towards self-thinning, but have not reached it. Therefore, this appears to be the period over which climate may be the main

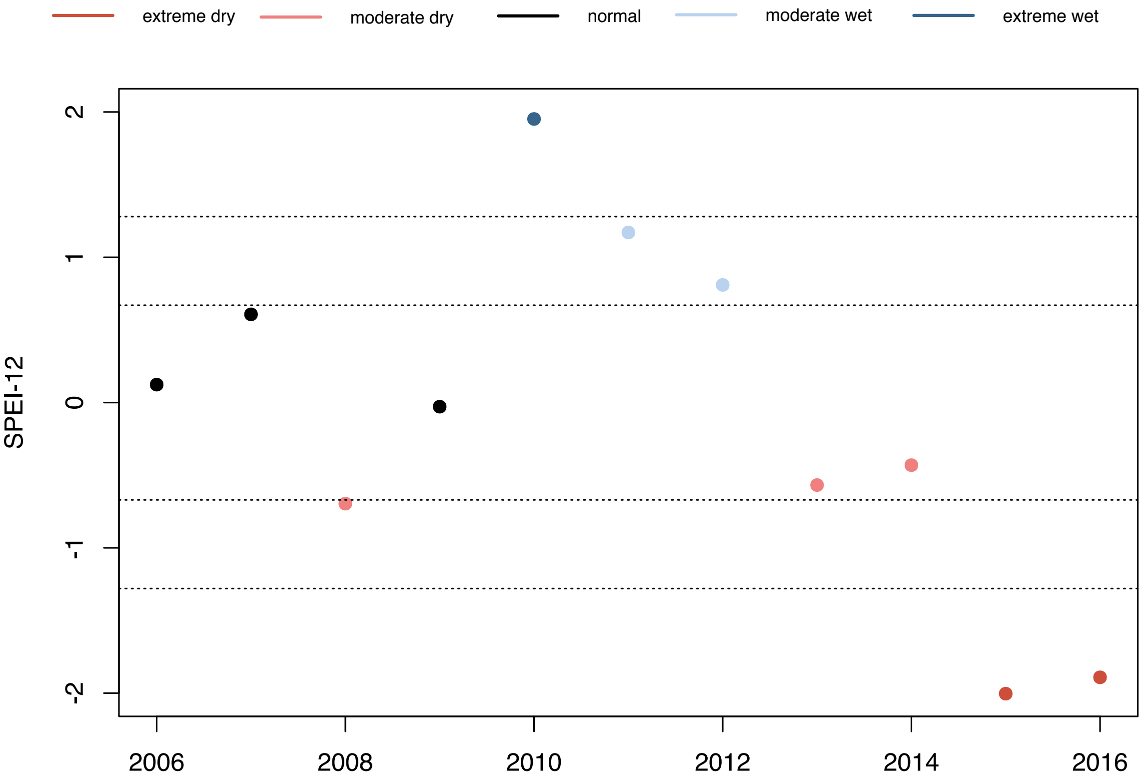

Figure 1.2 SPEI-12 (SPEI aggregated over twelve months) from December over 2006-2016. There is an extreme wet event in 2010 and an extreme dry spell from 2013 to 2016.

driver of growth and mortality [47].

In this timeframe, we find an extremely La Niña year in 2010 followed by two moderately wet years. Subsequently there is a series of dry years: 2013 and 2014 are moderately dry, and in 2015 there is a strong El Niño year with very dry conditions (Fig. 1.2).

1.2.2 Growth and mortality models

We built null models of growth and mortality assuming a time-independent distribution which would be the case if extreme climate events were not driving inter-annual variations in growth or mortality at a given diversity level (see Methods). The growth model shows that in 2010, the extremely wet year, monocultures grew significantly better than expected by the null hypothesis (Fig. 1.3a). In plots with species richness, the effect of the 2010 wet year is less pronounced; three- and five-species mixtures do no better than expected at random. During the drought episode, which lasts from 2013 through to 2015, we see that although all mixtures experience a decrease in growth, monocultures experience the largest decrease and five-species mixtures the smallest decrease (Fig. 1.3a). In the mortality model, we see that the number of dead trees is pushed further from the null expectation for monocultures during the continuous drought period from 2013 to 2015 (Fig. 1.3b). Mixtures show no significant difference from the null expectation in mortality during this period.

1.2.3 Indicators of critical slowing down

The effect of SPEI on TAC at lag-1 shows a positive trend as SPEI decreases for all diversity treatments with confidence bands overlapping (Fig. 1.4a). Consequently, the strongest effect of SPEI on TAC is seen during dry relative to wet years. The power spectrum (Fig. 1.4b) indicates that both the monocultures and two-species plots have most of their variance in tree growth at lower frequencies, while the three-species plots have their variance at intermediate frequencies, and the five-species treatments have their variance spread over all frequencies. The spectra for monocultures and SPEI strongly differ in their variance in the lower frequency spectrum.

1.3 Discussion

Because the concepts of resistance and resilience as proposed by Pimm [36] are very general, their expressions may be context dependent. For example, new standardized indices of resistance and resilience have been introduced to handle wet-dry cycles that are able to determine differences in stability between contrasting soils [48] . The effect sizes generated by our growth model are very similar to measures of resistance; however, our measure is adapted to studying stability in trees because we account for the large individual variation by adopting a bootstrapping procedure to compute both means and variances. Our results

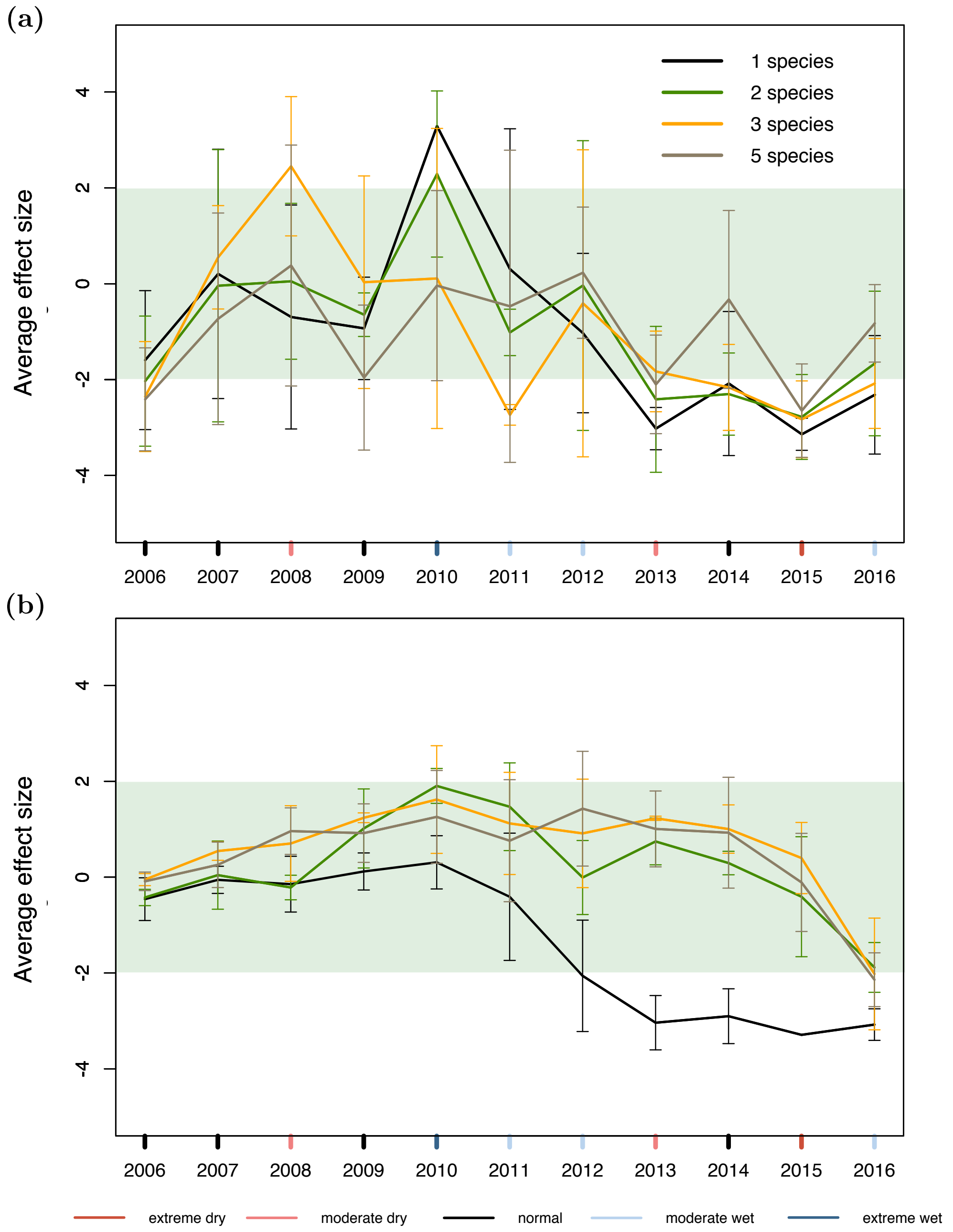

Figure 1.3 (**a**) Growth model and (**b**) mortality model. Average effect size over plots in monoculture, two-species mixtures, three-species mixtures, and five-species mixtures through time are shown. The error bars correspond to the mean ± the standard deviation for each year. SPEI-12 for a given year is indicated by the colour of the tick marks on the *x*-axis: normal is black, moderate wet is grey, moderate dry is coral, extreme wet is dark blue, and extreme dry is red. We find a clear distinction between growth and mortality between monocultures and higher species richness treatments compared to their null expectation which is represented by the honeydew band between $[-2.0, 2.0]$.

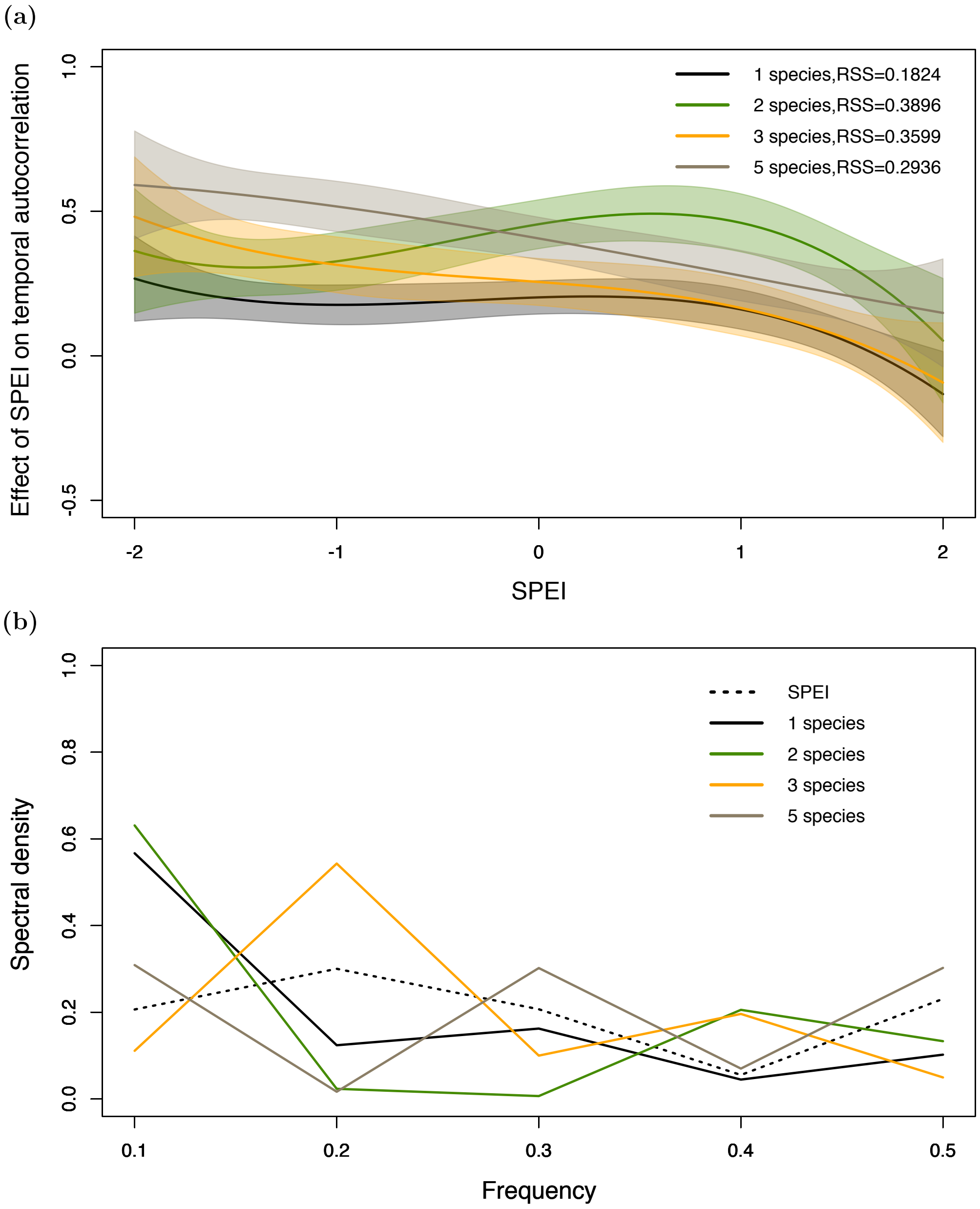

Figure 1.4 Indicators of critical slowing down. (**a**) Temporal autocorrelation at lag-1 of basal area increment time-series averaged over plots of the same species richness and (**b**) power spectrum of basal area increment time series averaged over plots of the same species richness and SPEI. We find that there is not a clear distinction between different species richness treatments and an increase in autocorrelation for dry conditions (i.e. increasingly negative SPEI). Monocultures and two-species mixtures have most of their variance in the lower frequency spectrum. This variance shifts to the right or to higher frequencies as richness increases.

show strong indications of a positive diversity-stability relationship through a species richness effect on growth/mortality response to stress. This suggests that background variation may be especially relevant when considering how stress affects stability of ecosystem functioning in forest ecosystems contributing to BEF literature.

We found that monocultures grow less than mixtures during a dry period from 2013 to 2015, culminating in 2015. Furthermore, mixtures experience less mortality than monocultures during these dry conditions. Higher growth and lower mortality in mixtures compared to monocultures is indicative of insurance effects [45]. Species complementarity in water uptake strategies is a possible mechanism for stress buffering in mixtures [11]. In fact, a series of studies conducted in Sardinilla between July 2007 and August 2008 found that complementary water uptake strategies between species was most pronounced during the dry season [49–51]. One of these studies [49] also proposed that one of the deep soil water exploiters, *Tabebuia rosea*, may facilitate other species through hydraulic redistribution of water resources. The stress gradient hypothesis also predicts that per capita changes in species interactions under stressful conditions can explain the stress buffering effect of mixtures [33]. However, we currently have no theory predicting the relative importance of complementarity and per capita interactions for stress buffering. Testing such predictions would most likely require that empirical BEF studies include the measurement of individual interaction strength during stress events [52].

Taken together, the results from the mortality model, temporal autocorrelation, and the power spectrum suggest that monocultures may exhibit greater sensitivity to extreme conditions than mixtures. We found that during the successive dry years from 2013 to 2015 there was increasingly higher mortality in monocultures compared to mixtures, which suggests that intraspecific competition is greater than interspecific competition during extreme climate events. Furthermore, in monocultures we found an increase in temporal autocorrelation as conditions become drier as well as most of its variation in tree growth in lower frequencies. These results suggest that the die-off present in monocultures may be indicative of slowing down, or a loss of resilience. In particular, the comparison of the spectral density of monocultures to SPEI suggests that they are not simply mirroring the environment. Our results and methods should facilitate the inference of a relationship between diversity and slowing down from experiments with a longer time series and with more extreme stresses. For example, massive mortality in some tropical forests have be observed for precipitation values less than $1,500$ mm yr^{-1} [42]. However, the precipitation at our site was never less than $1,900$ mm yr^{-1}. This suggests that perhaps there exists a threshold at which a distinction in slowing down between diversity treatments can be found under more extreme stress.

As more data becomes available from tree BEF experiments [53], we anticipate our work will set a benchmark to determine the impact of climate change on planted forests worldwide as our detection procedure is sensitive to the variation of individual trees. Furthermore our measure is based on standardized measures enabling comparisons of stability between sites in different forest types and climates can be made. Our study has shown that species richness buffers growth in response to strong drought episodes in agreement with theory on the relationship between abiotic stress, complementarity, and per capita interactions. We found that there was higher mortality in monocultures than mixtures, which increases when subjected to higher stress intensity. By accounting for mortality in the context of stability, we found evidence for slowing down in monocultures and posited a diversity-slowing down relationship. More mechanistic investigations are required to fully disentangle the relationship between stress and BEF. We anticipate that our work will add to the growing literature on BEF across environmental stress gradients, which have application across many ecological systems.

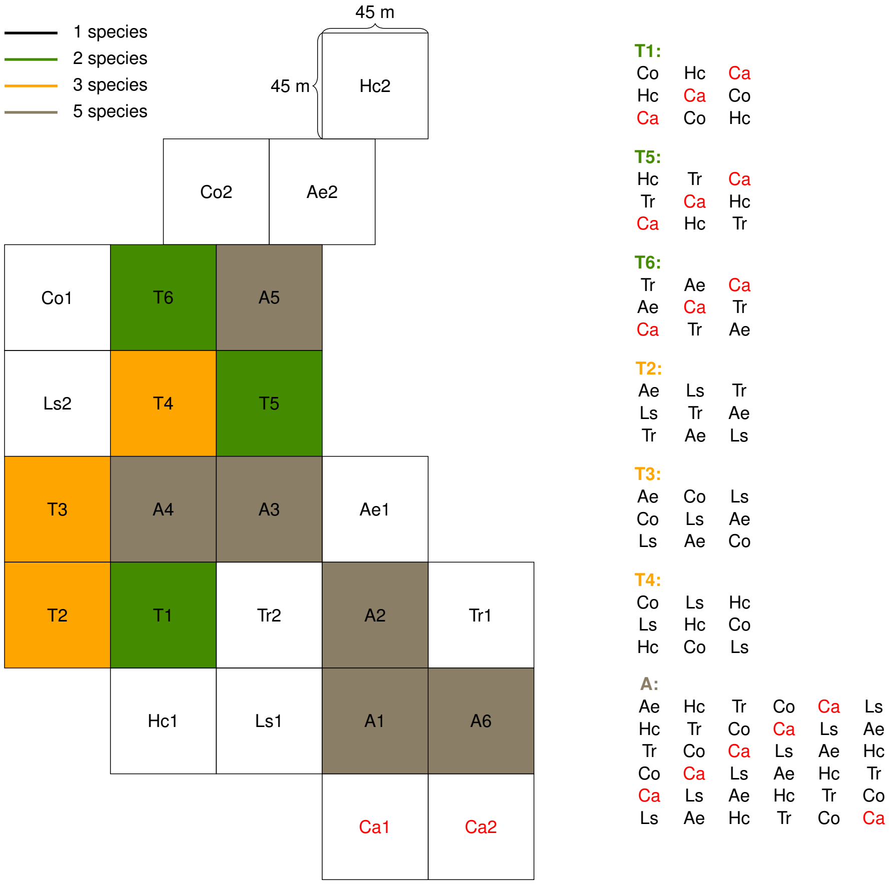

Figure 1.5 Schematic map of the Sardinilla planted forest. Diversity-levels and species neighbourhoods are shown. The species *Cordia alliodora* (Ca), which died in monoculture and in mixture, is excluded from this study and is indicated in red. The five remaining species are: *Anacardium excelsum* (Ae), *Cedrela odorata* (Co), *Hura crepitans* (Hc), *Luehea seemanni* (Ls), and *Tabebuia rosea* (Tr).

1.4 Methods

1.4.1 Study site and experimental design

Our case study is a ca. 15 year-old tropical planted forest in Sardinilla, Central Panama (9°19'N, 79°38'W) (Fig. 1.5). It was established in 2001 as part of a network of tree biodiversity-ecosystem functioning (BEF) experiments called TreeDivNet (`http://www.treedivnet.ugent.be/`). A total of 5,566 tree seedlings <6-months old were planted in 24 contiguous 45 m by 45 m plots in a pasture of ∼5 ha with mean 231.9 ± 8.93 seedlings per plot. Planting distances between individuals was 3 m following standard practices of reforestation in Panama. The planted forest has a substitutive randomized block design with species richness (monoculture, three-species, and six-species) and species combinations randomly allocated to allow quantification of biodiversity effects [54]. Six native tree species are represented based on their range of relative growth rates [55–57]. The fastest growing species are *Luehea seemanni* [Triana & Planch, Tiliaceae] and *Cordia alliodora* [(Ruiz & Pavon) Oken, Boraginaceae], the intermediate growing species are *Anacardium excelsum* [(Bertero & Balb. ex Kunth) Skeels, Anacardiaceae] and *Hura crepitans* [Linné, Euphorbiaceae], and the slow growing species are *Cedrela odorata* [Liné, Meliaceae] and *Tabebuia rosea* [(Bertol.) DC, Bignoniaceae]. *C. alliodora* suffered massive mortality in the monocultures and mixtures probably due to undrained and compact soil [58]. For this reason we do not include *C. alliodora* in our experiment. Consequently, we make comparisons using the actual diversity. At planting, there were 12 monocultures plots (two replicates of each of six species), 6 three-species plots, and 6 six-species plots. Using actual diversity removing *C. alliodora*, there are 10 monoculture plots (two replicates of each of five-species), 3 two-species plots, 3 three-species plots, and 6 five-species plots. The five-species plots were designed to have the same neighbourhoods whereas the two- and three-species plots all have different species compositions from each other. Undergrowth was manually cleared in the plantation three times per year to avoid competition with herbaceous vegetation. Measurements of tree height, diameter at breast height (∼1.4 m) or DBH, and basal diameter (10 cm from the ground) were made every year at the onset of the dry season (end of December, early January) starting in 2001.

1.4.2 Characterizing climate extremes

The region has a pronounced dry season from January to March [59]. Long-term meteorological data is available from nearby (≈ 30km) Barro Colorado Island (BCI) research station [60]. It has a humid tropical climate [61] with 25-50 mm per month during the dry season (January-March) and 250 mm per month wet season (May-November) [62]. The annual mean daily temperature is 33.1°C and minimum is 21.7°C [62]. We classify a year as being extremely dry/wet event, moderately dry/wet event or normal event by constructing the 12 month standardized precipitation-evapotranspiration index (SPEI-12 [46]) from rainfall and potential evapotranspiration data at BCI. SPEI has been used as a drought index to study BEF in many studies (e.g. [12, 29]). Unlike the standardized precipitation index (SPI [63]) the SPEI includes the effects of temperature; higher daily minimum temperature can increase water losses through evapotranspiration [64]. The SPEI is constructed as follows [46]. The D-series for month i is the difference between the precipitation, P_i, and potential evapotranspiration, PET_i: $D_i = P_i - PET_i$. D_i's can be aggregated at different timescales, i.e. one month, three months, six months, twelve months, etc. Selection of the most appropriate distribution to model the D-series was based on extreme values and found to be described by a log-logistic distribution, $F(x)$. Then, the SPEI is given by the standardized values of $F(x)$. The classical approximation is given by [65]

$$\mathrm{SPEI} = W - \frac{C_0 + C_1 W + C_2 W^2}{1 + d_1 W + d_2 W^2 + d_3 W^3} \tag{1.1}$$

where $W = \sqrt{-2\ln(P)}$ for $P \leq 0.5$ such that $P = 1 - F(x)$ is the probability of being greater than a given value of D. Note that if $P > 0.5$, P becomes $1 - P$ and the sign of the SPEI is reversed. The constants are given by $C_0 = 2.515517$, $C_1 = 0.802853$, $C_2 = 0.010328$, $d_1 =$

1.432788, $d_2 = 0.189269$, and $d_3 = 0.001308$. For our study, we chose to look at the D-series aggregated over twelve months, i.e. a yearly water balance. This is because it coincided with the yearly growth and mortality measurements at Sardinilla from which we can infer the relationship between climate and tree data.

1.4.3 Indicator of plot-level performance

Because tree growth and mortality are determinants of forest population dynamics [58, 66], they can be used to characterize its ecosystem state in response to extreme climate events when recruitment is controlled for. For each measurement period t from 2001 to 2017, we use DBH of each tree to construct its stem basal area increment and then sum all trees in a plot P. This basal area growth rate for plot P at time t, $\text{BAGR}_{P,t}$ is an indicator of plot-level performance:

$$\text{BAGR}_{P,t} = \frac{1}{\Delta t} \sum_{i=1}^{\text{No. trees in plot P}} \sum_{j=1}^{\text{No. of stems}} \left(\frac{\pi \text{DBH}_{i,j,t}^2}{4} - \frac{\pi \text{DBH}_{i,j,t-\Delta t}^2}{4} \right) \tag{1.2}$$

where Δt is the number of days between measurements, one sum is over the number of trees in a plot, and the other sum is over the number of stems of a tree is the plot. By performance, we mean that two biological processes act to change $\text{BAGR}_{P,t}$: growth and mortality [58]. In this case, *the first sum is done over both alive and dead trees.* If a tree has died we set the DBH at time t equal to the DBH at time $t - \Delta t$, so mortality acts by adding zero to $\text{BAGR}_{P,t}$ for a dead tree. Recruitment can also change $\text{BAGR}_{P,t}$; however, undergrowth (including seedlings) are manually cleared three times per year at the site so recruitment is assumed not to contribute to performance. [47] found that BAGR at the plot-level were positively and significantly correlated with climate, in particular rainfall and temperature, for permanent forest plots in a neotropical lowland Bolivia. Therefore, we expect that BAGR is an appropriate measure to use in order to study how performance changes across diversity-levels and climate events.

1.4.4 Models of growth and mortality

We hypothesized that differences in growth and mortality along a gradient of species richness should manifest mostly during extreme climate events. To test this hypothesis we construct two different null models: a growth model and a mortality model, which represent our null expectation for each diversity treatment if climate is not driving year to year differences in performance. For each null model, we use R statistical software version 3.4.3 (2017-11-30) to generate 1000 bootstrap samples for each plot by randomly sampling, with replacement, alive and dead trees with appropriate survival probabilities whilst preserving species identity in a given plot [58]. For the growth model, the pool is made of basal area increments for each tree in a plot over all years and we select a living tree with a probability of survival calculated for that year. We use a pool of increments from all years as a conservative choice which does not presuppose a relationship between plot-level growth and climate (Fig. 1.6). For the mortality model, the pool is made up of the basal area increments for the trees present in a given plot in a given year and we select a tree with a probability of survival which is constant year on year. Edge trees are removed from our analysis with the reasoning that those trees likely do not benefit from any full biodiversity effect. An effect size is computed to compare actual growth and mortality compared to the null expectation based on a probit-transformation of the one-tailed probability $0 < P < 1$ that the observed value is lower than expected [67–69]:

$$P = \frac{\#(null < obs) + \frac{\#(null = obs)}{2}}{1000}. \tag{1.3}$$

The probit-transform on P is implemented by using *qnorm* in the R statistical software version 3.4.3 (2017-11-30). The probit-transform accounts for skewness in data and is asymptotically equal to the standardized effect size introduced by [70]. We construct the average effect size by summing the effect sizes for each plot of a given richness.

We built our null models by assuming that growth or mortality are time-independent which would be the case if extreme climate events were not driving inter-annual variations in growth or mortality. For the growth model, we sampled from replacement a pool of BAGR from surviving trees in a given plot *over all years*. In this model, mortality is allowed to vary year on year. For the mortality model, mortality is similarly assumed *to be constant over the period of our analysis*. The instantaneous mortality rate m for each plot is then computed from $N_t = N_{t-\Delta t}e^{-Tm}$ where N_t is the number of surviving trees at time t and T is the number of years our analysis extends over. Growth is allowed to vary year on year. The estimated 95% confidence interval is given by $[-2.0, 2.0]$ [68]. We will thus consider that AES larger than 2.0 units indicates represents a significant effect of climate on growth/mortality at a given diversity level. AES that lie within the above interval are not significantly different from each other. We say that there is a biodiversity effect if differences between monocultures and mixtures manifest.

1.4.5 Indicators of stability and slowing down

We use the averaged standardized effect size as an indicator of stability to climate extremes. The larger the effect size, the less stable the system is to a perturbation due to drought or heavy rainfall. In the growth model, if the effect size is larger than 2.0 then growth is larger than expected by the null model and an effect size is less than -2.0 indicates less growth than expected. In the mortality model, if the effect size is larger than 2.0 then mortality is lower than expected and if the effect size is less than -2.0, mortality is greater than expected.

Temporal autocorrelation at lag-1 (TAC) can be measured in two equivalent ways [43]. The first way is to use

$$\rho_1 = \frac{\mathsf{E}[(z_t-\mu)(z_{t+1}-\mu)]}{\sigma_z^2} \tag{1.4}$$

where μ and σ_z are the mean and variance of the variable z_t. In our case z_t is the basal area increment over year t. Alternatively, an autoregressive model of order 1, a linear AR(1)-process, of the form

$$z_{t+1} = \alpha_1 z_t + \varepsilon_t \tag{1.5}$$

where ε_t represents Gaussian white noise. Here ρ_1 and the autoregressive coefficient α_1 are equivalent mathematically. We plot TAC against SPEI to determine whether there is an increase in autocorrelation with decreasing SPEI (i.e. more extreme drought conditions). We fit a single cubic spline to the data [42] and construct confidence bands. For polynomial regression, the confidence band is constructed in the same way as multiple linear regression because the standard deviation of the estimators of the regression coefficients has the same expression in terms of the model matrix.

We compute the power spectrum using the R-function spec.pgrm (`https://stat.ethz.ch/R-manual/R-devel/library/stats/html/spec.pgram.html`) and we normalize the spectral density to be between zero and one.

Data accessibility

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Author contributions

CH, DG, and CP conceived the project using the data from the study site where CP is principal investigator. CH developed the theory behind the manuscript and performed the data analyses. DG, FG, and CP had major input in technical discussions with CH. CH wrote the first draft of the manuscript, for which all authors contributed substantially to revisions.

Competing interests

The author(s) declare no competing interests.

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1.5 References

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1.6 Supplementary Information

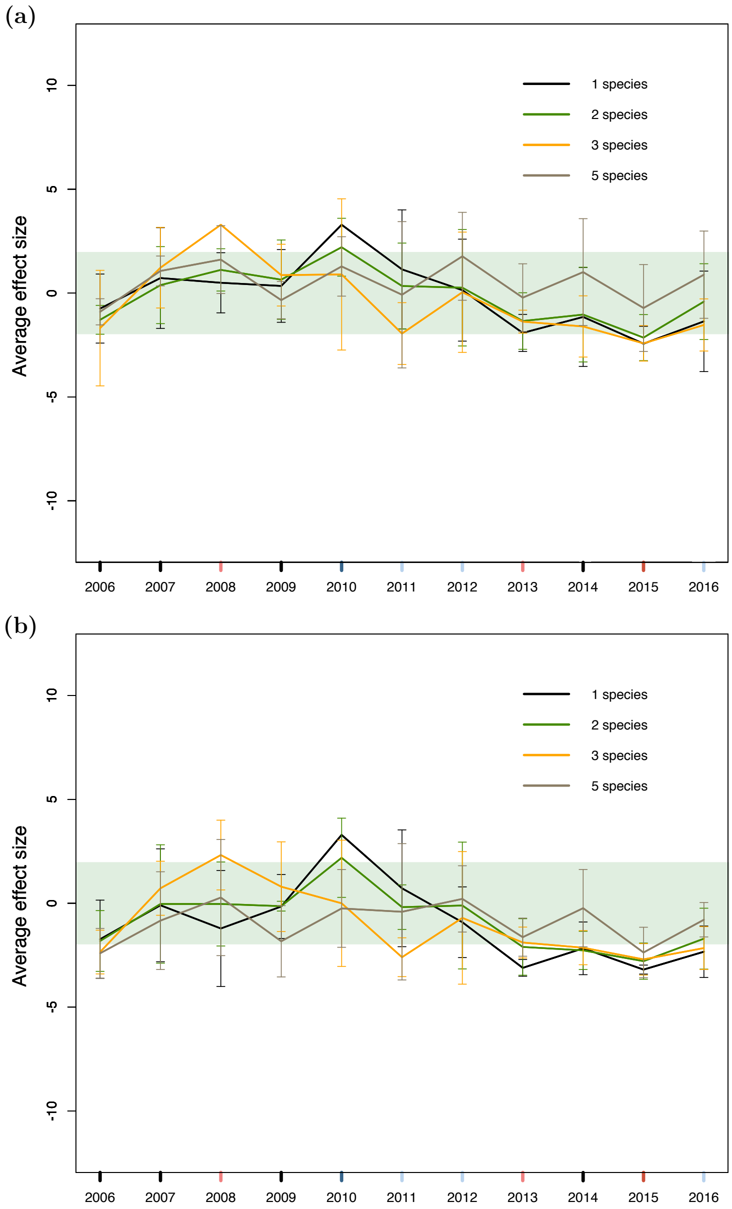

Figure 1.6 Sensitivity analysis including only (a) normal years (2006, 2007, and 2009) and (b) non-adjacent years in the pool for the growth model compared to all years as shown in the main text (Fig. 4). We find that our results are robust to changes in case (b). The effect of the consecutive dry spell from 2013-2016 is absent in case (a). One possibility is that growth which occurs in the three normal SPEI years of our study is not representative of the growth of the planted forest. It suggests that our choice of including all years in the pool for the growth model is conservative and unbiased.

Connecting statement

To address problems about yearly stress response in tree communities across a gradient of species richness, two types of statistical models may be used: parametric and nonparametric. In my first chapter, I show that a simple nonparametric model based on creating artificial plots through a bootstrap resampling procedure is an effective way of capturing "normal" behaviour in a highly complex system. In other complex communities, dynamical models, or models based on differential or difference equations, may be more appropriate. Seasonal predator-prey communities are an example of a system which is difficult to model because their dynamics can not be understood in terms of an equilibrium. Another specific example of this is systems with migrant species. Migrating species change the food web topology by coupling and decoupling from resident food webs in different seasons; they require, at least, a dynamic modelling framework which can accommodate multiple equilibria. Using data collected from the field, these multi-season models may be able to be parametrized in order to capture observed behaviours in time-series. In my second chapter, as in my first chapter, I aim to extract information about the system by doing transformations on time-series to infer the nature of species interactions. It is generally the case that diversity, such as species richness, modifies species interactions; however, it is less clear how diversity which changes with time, as is the case in seasonal communities, may alter interactions. The ability of migrants to modify species interactions, for example through trophic cascades by migrant predators, has lacked examination through a modelling framework and, thus, prevents a mechanistic understanding. Using long-term time-series generated from my multi-season model, I investigate the extent to which multi-season models can capture direct (i.e. trophic) and indirect (i.e. competition) interactions compared to models which do not incorporate seasonality.

Chapter 2

Seasonal food webs with migrations: Multi-season models reveal indirect species interactions in the Canadian Arctic tundra

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Keywords: multi-season model, species interactions, causality, arctic ecosystems, animal migration, climate change, tundra

Abstract

Models incorporating seasonality are necessary to fully assess the impact of global warming on arctic communities. Seasonal migrations are a key component of arctic food webs that still elude current theories predicting a single community equilibrium. We develop a multi-season model of predator-prey dynamics using a hybrid dynamical systems framework applied to a simplified tundra food web (lemming-fox-goose-owl). Hybrid systems models can accommodate multiple equilibria, which is a basic requirement for modelling food webs whose topology changes with season. We demonstrate that our model can generate multi-annual cycling in lemming dynamics, solely from a combined effect of seasonality and state-dependent behaviour. We compare our multi-season model to a static model of the predator-prey community dynamics and study the interactions between species. Interestingly, including seasonality reveals indirect interactions between migrants and residents not captured by the static model. Further, we find that the direction and magnitude of interactions between two species are not necessarily accurate using only summer time-series. Our study demonstrates the need for the development of multi-season models and provides the tools to analyse them. Integrating seasonality in food web modelling is a vital step to improve predictions about the impacts of climate change on ecosystem functioning.

2.1 Introduction

The Arctic is experiencing larger rises in surface air temperature compared to anywhere else on Earth, a phenomenon known as polar warming amplification [1]. An emergent feature of climate simulations is pronounced seasonality to polar warming amplification: winter warming is occurring four times faster than summer warming due to atmospheric processes such as dynamical feedbacks in energy transport [2–6]. Arctic ecosystems are expected to be profoundly impacted by these aspects of climate change, as biological and chemical processes are structured by seasonal shifts in temperature, snow, ice cover, and nutrient availability

[7, 8]. It is therefore paramount to develop accurate dynamical models based on field data, which capture the seasonality of arctic community dynamics, in order to make predictions about how warming might impact arctic ecosystems, including tundra, polar deserts, and the Arctic ocean.

Many empirical studies have assessed the looming threats that face arctic communities under various climatic regimes [9–11]. Ideally these assessments would involve information about all trophic levels: long-term datasets of multiple population attributes across multiple species [12–15]. In terrestrial ecosystems, arctic vegetation exhibit various responses to warming in space and time (e.g. through changes in phenology and productivity) as well as species-specific sensitivity to warming [16–18]; in many cases there is an increase in primary production [15]. Warmer temperatures and earlier snowmelt may also impact the phenology of arctic wildlife, such as the nesting cycle of birds [19] or small rodent population dynamics [20]. Furthermore, trophic mismatch, i.e. a lack of synchrony between the phenology of consumers and their resources, can negatively affect the fitness of arctic herbivores [21]. When considering the response of ecological communities as a whole, the net effect of climate change may be modified by indirect interactions [22]. But in arctic communities dominated by vertebrates, herbivore-mediated cascading effects of climate on plants tend to lag behind the direct effects of climate warming, especially when key herbivores are long-distance migrants [23]. It has been suggested that allochthonous subsidies from more productive ecosystems can amplify or dampen the effects of a changing climate on different trophic levels in the arctic tundra [24, 25].

A drawback of many studies on arctic ecosystems is that data tend to only be available for the growing season, given the unique difficulties of sampling in winter conditions [26]. However, winter is the longest season in the arctic and a critically important season for these ecosystems [20, 27, 28]. During winter, active generalist carnivores feed exclusively on resident herbivores, which remain active under snow or ice cover; carnivores may also exploit marine resources, above-snow carrion, and cached food. The dynamic behaviour when migrants arrive in the spring depends heavily on the populations of the resident species. Since these populations are in large part determined by winter dynamics, winter may be essential for the overall community dynamics [29]. Despite strong seasonality driving species interactions, very few studies have explicitly modelled multi-seasonal arctic community dynamics [30, 31].

Often the seasonality which is characteristic of some types of communities is not explicitly included in theoretical models, despite the acknowledgement of its importance by ecologists, likely due to the mathematical difficulties in handling large variability [32]. Efforts to incorporate seasonality into models reflects a trend in ecology away from modelling ecological systems with equilibrium dynamics (e.g. mass-balance models) [33]. There has been a growing number of studies using models which can incorporate the seasonality of these communities in a way that reflects the underlying ecology beyond simple time-varying parameters [33–37]. Food web dynamics with migrating species is an example where these more structured models are appropriate because the food web topologies differ among seasons when migrants are present or absent from resident communities at different times of the year. Basic models with migrating species thus require: 1) a dynamical system that can have multiple equilibria, 2) a set of coupled dynamical equations to capture species interactions for each season and 3) a way to switch between seasonal dynamics corresponding to the arrival or departure of migrating species. An appropriate framework to handle systems with both fast (discrete) and slow (continuous) dynamics is a hybrid dynamical system, which also has the capacity to deal with multiple distinct equilibria. The fast dynamics correspond to discrete changes such as migration, a fast-topological change in the food web structure due to the arrival or departure of migrating species. Slow dynamics might correspond better to predator-prey interactions that occur in each season. A hybrid systems framework allows classical, continuous differential equations to be applied to each season without having to resort to discontinuities in dynamical equations via a time-varying parameters approach. Furthermore, hybrid systems can accommodate time-dependent switches such as seasonal changes in predator functional responses [36] in addition to state-dependent behaviours such as a choice of breeding locations by predators in response to prey density.

Our objective is to investigate the relative advantage of using multi-season models to expose essential information about pairwise species interactions compared to non-seasonal models. We build a multi-season dynamical model for predator-prey interactions in a simplified tundra food web (lemmings-foxes-geese-owls). The seasonality in this model is introduced by a switch in dynamics caused by presence/absence of two species: the snow goose [*Chen caerulescens atlantica*] as a migrant prey and the predatory snowy owl [*Bubo scandiaca*] which is functionally absent in the winter. Our model is based on a hybrid dynamical systems framework where migration is modelled as fast dynamics and represents a discrete change in the food web topology, thus leading to a system with multiple distinct equilibria. Slow dynamics corresponds to Lotka-Volterra predator-prey interactions for each season. State-dependent behaviour is implemented for the snowy owl which are present in the summer only when the spring brown lemming densities are high. We attempt to include key processes of the underlying dynamics in order to generate representative, long-term time-series for each species over all seasons. We achieve this by constraining the model parameters using summer data on species interactions and population dynamics to generate possible time-series. We show that our model is able to reproduce the multi-annual cycling of lemmings and their amplitudes. We rely on convergent cross mapping [38], which uses time-series to infer causal interaction networks, in order to study direct and indirect interactions between species (i.e. can the population dynamics of a prey be inferred from the predator time-series?). We compare the pairwise species interactions that would be inferred from three modelling scenarios: i) a static model (no seasonality), 2) a multi-season model, and 3) summer snapshots from the multi-season model.

2.2 Methods

Predator-prey interactions play an important role in the tundra food web of Bylot Island, Nunavut, Canada (73°N, 80°W) and have been parameterised using data from long-term studies of population abundance and diet at this site [39]. In this system, the snow goose [*Chen caerulescens atlantica*] is a migratory bird species and the dominant herbivore (88% of herbivore biomass on average) during the summer. Two lemming species are present, the brown [*Lemmus trimucronatus*] and collared [*Dicrostonyx groenlandicus*] lemming, which constitute 2% and 25% of biomass during years of low and peak abundance, respectively. Both lemming species exhibit synchronous multi-annual cycles, but the amplitude of peaks are far greater in brown than in collared lemmings [15]. The main predator of the snow goose and lemmings are arctic foxes [*Vulpes lagopus*]. In peak years of brown lemming abundance, snowy owls can also be found on Bylot and represent a significant proportion of carnivore biomass. Although other predators are present in this system [25], these five species were chosen to construct (simplified) food webs in our multi-season model because they are the most abundant and are representative of each key functional group in the system (prey, predator, resident and migrant). The resident food web consists of the arctic fox and two sympatric lemming species. During summer, migrating snow geese are present and are an important alternative prey for the fox. Depending on the lemming biomass in spring, snowy owls can enter the system as an additional predator on all prey species in addition to the arctic fox in summer with $\sim 85\%$ of their diet coming from both species of lemmings [39].

2.2.1 Data on biomass, diet, consumption, and production

We use the same approach as described in Legagneux et al. [39] to conduct field work, compile field data, and obtain values for Ecopath model parameters for the period 1993-2009 to extend the dataset to 2010-2018 using more recent field data. Similar diet matrices are used. For both lemming species, we use mean lemming abundance for the months of July and August. Trapping occurred in both mesic and wet habitats. The percentages of wetland and mesic habitats in the study area (15% and 85%, respectively) are taken into account to calculate the overall lemming biomasses [40]. For the snow goose population, the exact same protocols are followed over the period 1993-2018 and provide comparable metrics of snow goose abundance over time [3]. The snowy owl nesting density is calculated over a searching area that varied over time but remained similar since 2007. We consider a constant arctic fox population over time as the number of reproductive and non-reproductive adults has been found to be stable between seasons using satellite tracking [41]. Furthermore, most juveniles produced during years of high lemming abundance disperse out of the system long after they are weaned; therefore, they are not significantly adding to the local population (D. Berteaux, unpublished satellite tracking data about juvenile dispersal). We use the similar density provided in [39]: 0.08 dry kg km^{-2}. Lemming density estimates obtained from 1993-2003 using snap traps are back-calculated based on new relationships obtained between snap and live trap comparisons [42]. The 2004-2018 dataset is obtained with the same live trapping protocol (see [43] for methodological details).

2.2.2 Translating mass-balance model parameters to a static, predator-prey model

Mass-balance models use the principle that the energy input has to balance the energy output for each species in the model [44]. The Ecopath approach to mass-balancing describes trophic flows within a food web assuming the system is at its stationary point [45–47]. Legagneux et al. [39] use the following master equation, which has been successfully applied to Bylot:

$$\frac{dB_i}{dt} = \left(\frac{P}{m}\right)_i B_i - \sum_i \left[DC_{ij}\left(\frac{Q}{m}\right)_j B_j\right] \tag{2.1}$$

where B_i is the biomass (in dry kg km^{-2}) of species i, $(P/m)_i$ is the production rate (per year) of species i per unit of biomass, DC_{ij} is the proportion of species i in the diet of predator j, $(Q/m)_j$ is the consumption rate (per year) of predator j per unit biomass. At its stationary point, dB_i/dt is zero and we get a balanced set of inputs and outputs. The Ecopath master equation can be translated into a general Lotka-Volterra model of the form

$$\frac{dB_i}{dt} = b_i B_i + \sum_{i \neq j} \alpha_{ij} B_i B_j \tag{2.2}$$

where b_i is the intrinsic growth rate of species i and the interaction coefficient between prey species i and predator j is given by

$$\alpha_{ij} = -\left(\frac{Q}{m}\right)_j \frac{DC_{ij}}{\bar{B}_i}. \tag{2.3}$$

where $\bar{B}_i$ is the long-term average biomass of species i. The interaction coefficient between species j and i is

$$\alpha_{ji} = e_{ij} \alpha_{ij} \tag{2.4}$$

where $e_{ij} = (P/m)_j/(Q/m)_j$ is the efficiency in the conversion of biomass for predator j. The long-term average for Lotka-Volterra is equal to its stationary point and can be used to determine the intrinsic growth rates. The static model assumes three prey (brown lemming, collared lemming, and snow goose) and two predators (arctic fox, snowy owl). We use a weighted average diet matrix of peak and low years as well as allometric values of production and consumption rates found in Legagneux et al. [39] to compute intrinsic growth rates and interaction coefficients for the static model. Allometric rather than empirical values are used for the static model to represent a suitable null model with which to compare to a multi-season model.

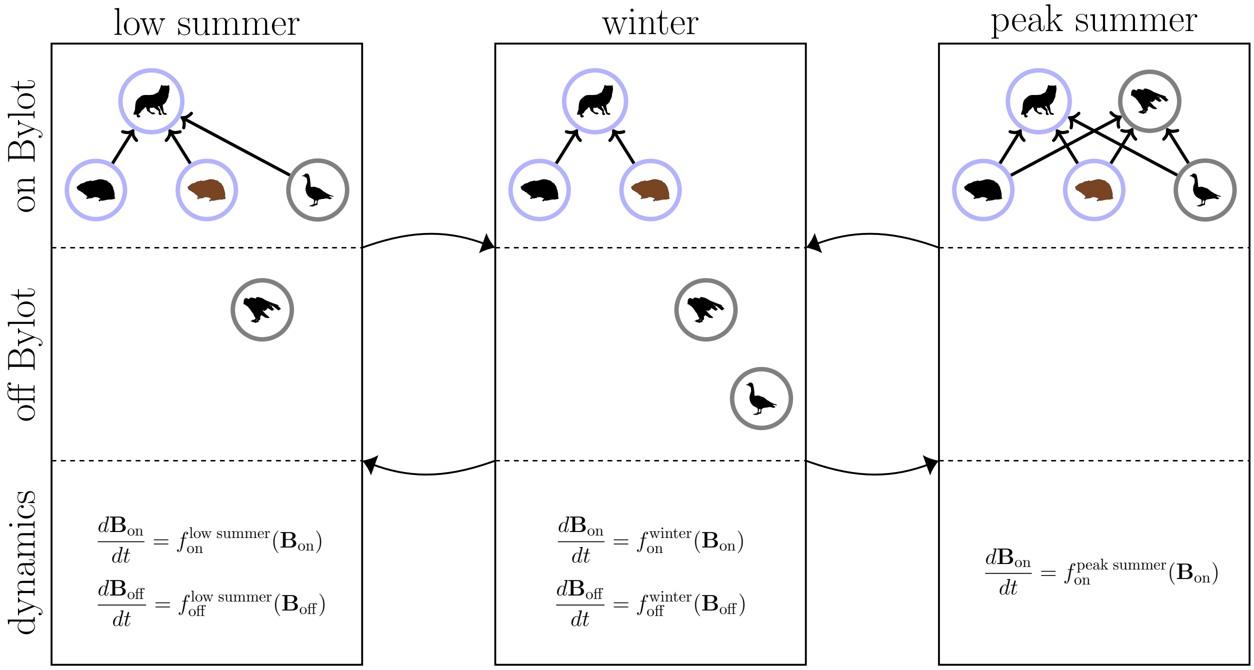


Figure 2.1 Hybrid automaton describing the multi-season model for a simple high-Arctic tundra food web. The species represented in the seasonal food webs are: brown and collared lemmings, arctic foxes, snow geese and snowy owls. Their biomasses are labelled by $\mathbf{B}_{\text{on}}$ for the biomass on Bylot and $\mathbf{B}_{\text{off}}$ for the biomass off Bylot. The resident species are lemmings and foxes. The winter dynamics occurs for 10 months and the summer for 2 months. Allowed transitions are from winter-to-low summer (and vice versa) and from winter-to-peak summer (and vice versa). Peak summers occur with a probability that depends on the brown lemming density at the end of winter. Lotka-Volterra predator-prey dynamics are used for the species on Bylot and logistic growth is used for species off Bylot. Silhouettes of species are from `http://phylopic.org`.

2.2.3 Using a hybrid dynamical system to model arctic community dynamics with migration

The hybrid system (i.e. automaton) corresponding to our multi-season model (Fig. 2.1) derives its structure from the Cartesian product of discrete and continuous-valued states. Our model has three discrete states corresponding to each possible seasonal food web, each represented by a separate box which we denote by winter, low summer, and peak summer. A low summer is a summer when owls are absent, and a peak summer is when they are present in the food web. Whether they are present depends probabilistically on the biomass of the brown lemming being above 2.50 dry kg km^{-2} which is the average biomass of brown lemmings from the summer data when owls were absent. Winter is taken to occur for 10 months and summer 2 months (i.e. from mid-June to mid-August) corresponding to the minimum length of the breeding cycle of the snow goose (laying to median end of moult) when arctic foxes are preying on their eggs and young. The allowable transitions are represented by the arrows connecting the boxes in the automaton in Fig. 2.1; winter-to-low summer, low summer-to-winter, winter-to-peak summer, and peak summer-to-winter.

For each season, we illustrate the food web on Bylot and off Bylot. In both cases, all species (even the non-interacting species) are assumed to have dynamics. Gilg et al. [30] develops a model for a community of collared lemmings and their predators in eastern Greenland and has both dynamic and non-dynamic predators. Because our goal is to infer causal relationships such as trophic control regimes using time-series, it is essential that we include the dynamics of all predator species. Each discrete component of the model (i.e. "season") is associated with continuous dynamics of five state variables, representing changes in species biomasses from either predator-prey interactions or density-dependent growth. Predator-prey dynamics are assumed to be of Lotka-Volterra type with linear functional responses and intraspecific density dependence for all species (see Supplementary Information). For the prey, lemmings and snow geese, intraspecific density-dependence is implemented by a carrying capacity. The existence of an upper limit, or carrying capacity, on brown lemming populations may be imposed as it more accurately reflects their observed population dynamics [48]. We assume that the snow goose dynamics also has a carrying capacity for similar reasons [40]. Arctic foxes and snowy owls are self-regulated because of territoriality (Berteaux & Clermont, unpublished, [49]). Intraspecific interaction terms are estimated simultaneously with the model parameters for winter (see (d) and further details in Supplementary Information). Including intraspecific terms in our model has the added benefit that the dynamics within a season has a stable equilibrium and, as a result, our multi-season model is one with multiple distinct equilibria satisfying the basic requirement of seasonal models. The general form of the dynamics for the biomass of each species, B_i (in units of dry $\mathrm{kg}\cdot\mathrm{km}^{-2}$) in each season is given by

$$\frac{dB_i}{dt} = b_i^{(q)} B_i - \eta_i^{(q)} B_i^2 + \sum_{i \neq j} \alpha_{ij}^{(q)} B_i B_j \tag{2.5}$$

where $i = \{\text{brown lemming, collared lemming, arctic fox, snow goose, snowy owl}\}$ labels the species and $q = \{\text{winter, low summer, peak summer}\}$ labels the season. Here, b_i is the intrinsic growth rate (rate of increase for prey and mortality for predators), η_i are the carrying capacity terms for the prey or self-regulation terms for the predators (described above), and α_{ij} the interaction strength coefficient corresponding to the per capita effect of species j on the growth rate of species i. Geese and owls are assumed to follow logistic growth to their carrying capacity η_i when they are uncoupled from the food web on Bylot.

Choosing the model to be of Lotka-Volterra type with linear, predator-prey functional responses means that we can employ quantities from mass-balance models previously constructed for the system on Bylot [39] to set the parameters in the low and peak summer. Using this information, we can infer parameter values for the winter dynamics of our hybrid system using the method described below.

2.2.4 Unknown parameter guesses for multi-season model

We require a procedure to guess unknown parameter values from Eq.(2.5) (i.e. $b_i^{(q)}$,$\eta_i^{(q)}$,$\alpha_{ij}^{(winter)}$) to generate time-series for our multi-season model with which to study species interactions. The difficulty lies in the fact that direct parameter estimates are only available for the summer, but we also require estimates for the winter period as well as estimates for the intrinsic growth rates and intraspecific terms. Summer interaction strengths $\alpha_{ij}^{(1)}$ and $\alpha_{ij}^{(2)}$ are fixed using data estimates for consumption and production rates as well as diet proportions [39]. They can be found by translating parameters from a mass-balance model following standard approaches to Lotka-Volterra [14, 50]:

$$\alpha_{ij}^{(q)} = -\left(\frac{Q}{m}\right)_j^{(q)} \frac{DC_{ij}^{(q)}}{\bar{B}_i^{(q)}} \tag{2.6}$$

where terms have the same interpretations as in (b); however, the superscript q indicates their value in season q.

To estimate unknown parameters (i.e. $b_i^{(q)}$,$\eta_i^{(q)}$,$\alpha_{ij}^{(winter)}$) we develop an algorithm to help refine guesses for their values by comparing the multi-season model biomass output, obtained by inserting these guesses into the dynamics of the hybrid system, to the available summer biomass data. We do not constrain the fox dynamics to be constant as observed in the data, instead we allow for fluctuations. Because other resident mammalian predators in this system could actually fluctuate over time, we allowed fox population to fluctuate to account for this process in our system given that we consider foxes to be representative of this functional group. The idea behind this algorithm is to incrementally improve the qualitative aspects of the model output (i.e. reproducing lemming peaks and crashes) by slowly adding more time-points, in this case 3 years at a time up to 26 years which is the entire timespan over which data is available, to make a more informed guess about what the unknown parameters may be. The assumption is that as more data are added in, the "difference" between successive guesses (represented as a vector), $\{\mathbf{b}_i, \mathbf{b}_{i+1}\}$ decreases, where

$\mathbf{b}_i$ is the parameter set estimated from the time-series over 1993 to $1993+3\times i$ and $\mathbf{b}_{i+1}$ the set over 1993 to $1993+3\times(i+1)$. We calculate the difference between successive guesses as:

$$\text{difference} = \frac{|\mathbf{b}_{i+1}-\mathbf{b}_i|}{(|\mathbf{b}_{i+1}|+|\mathbf{b}_i|)/2} \tag{2.7}$$

and then take the root-mean-square (RMS) by squaring each of the components, taking the mean of the result, and then taking the square root. Further details are provided in the Supplementary Information.

2.2.5 Identifying multi-annual cycling in lemming time-series

If the generated time-series shows multi-annual lemming cycling then we expect to see some regular frequencies in the data corresponding to, for example, 3-4 years (year=1/frequency). If there is no multi-annual cycling, then frequencies tend to exhibit noise. To test for the presence of frequencies we take the Fast Fourier Transform (FFT) of the time-series; the absolute value of the FFT output is how much of each frequency is present in the time-series. To test for multi-annual cycles, we use only the summer points in the time-series which corresponds to how these cycles are identified in data. If multi-annual cycling is present, we expect to see a range of values in the FFT output above the low amplitude noise. The spread of these values will tell us the range of cycling frequencies which are present and the highest peak will tell us the median cycle length. This is similar to the test conducted by Predavec et. al. [51] on binary time-series. This test is unbiased, and quite robust, as it does not depend on an arbitrary threshold value in order to define a peak or a low summer.

2.2.6 Inferring species interactions from causal structure

To test the necessity of using multi-season modelling in temporally-forced food webs, we consider the structure of inferred indirect interactions between species using the static model, the multi-season model, and summer snapshots extracted from merging part of the time-series generated from the multi-season model which corresponds to summer. To do this, we examine the inferred causal relationships between species using convergent cross mapping (CCM). CCM has been shown to give information about trophic control regimes (i.e. top-down vs. bottom-up control in predator-prey systems) and about interspecific relationships (i.e. interspecific competition; amensalism, commensalism, and mutualism) [38]. CCM is designed for testing the presence of these (causal) relationships specifically for ecological time-series, or systems which may be related through nonlinear dynamical equations. If we have two time-series, say $N(t)$ for a prey and $P(t)$ for a predator, CCM measures the extent that the history of $N(t)$, specified as a collection of lags $N(t-1)$, $N(t-2)$, etc., can estimate $P(t)$ (and vice versa). Pearson's correlation coefficient, ρ, is computed between $P(t)$ itself and $P(t)$ predicted from the history of $N(t)$. This estimate must improve (i.e. converge) with longer time-series in order to infer a causal relationship. We know that $P(t)$ causes $N(t)$ if ρ is positive, significant, and converges because it means that information about $N(t)$ can be used to learn more about $P(t)$. In other words, $P(t)$ leaves a footprint on $N(t)$. This procedure can be carried out between any two time-series (i.e. between prey, between predators, between a prey and a predator) to infer causal structure. There is also the aspect of bidirectional vs. unidirectional relationships. If the cross mapping in both directions converge we say that there is a bidirectional relationship. Otherwise, if one of these relationships is non-significant, then the relationship is unidirectional. Unidirectional relationships may indicate that there is an amensal, commensal, or mutual interaction occurring (but which one cannot be determined from the CCM on its own). More details about CCM can be found in the Supplementary Information. We conduct a CCM between each pair of species using a 500-year time-series generated from our model. First, taking one point per month to capture the seasonality for the static and multi-season model and, second, taking only months corresponding to summer. We compare the causal information between these cases.

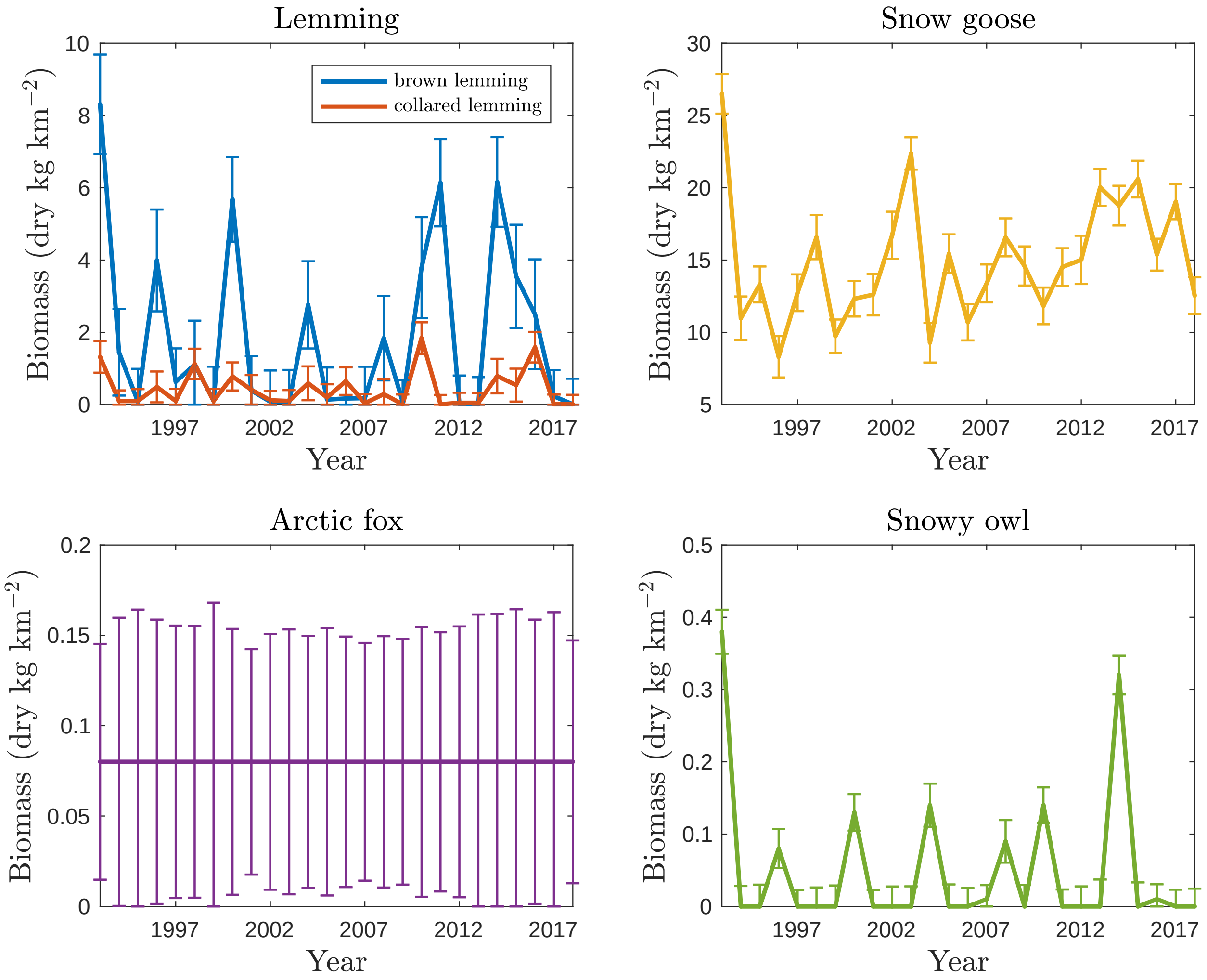


Figure 2.2 Summer biomasses for the five species based on data collected on Bylot from 1993-2018. Error bars are based on the 95% confidence intervals identified in [39].

2.3 Results

Data from wildlife monitoring on Bylot Island from 1993-2018 shows strong, cyclic fluctuations in summer lemming biomass (Fig. 2.2). In the brown lemming time-series, there are 7 peaks defined as a year of high density which is preceded by a year of increasing density and followed by a year of decreasing density: 1993, 1996, 2000, 2004, 2008, 2011, and 2014. Thus, there are three cycles of 3 years (1993-1996, 2008-2011, 2011-2014) and three cycles of 4 years (1996-2000, 2000-2004, 2004-2008) in the data. On average, the cycle lengths are 3.5 years long. There are 4 years which have biomass peaks greater than 5 dry kg km^{-2}. Collared lemmings exhibit peaks roughly synchronous with the brown lemmings (in particular, when brown lemming peaks are high) with 4 years between 1-2 dry kg km^{-2}. Snow geese biomass range from 10-25 dry kg km^{-2}. The biomass of adult territorial arctic fox does not fluctuate significantly between years due to the stability of the number of breeding pairs [39] even though foxes reproduce only during peaks; offspring disperse outside the system. Snowy owl peaks almost always coincide with peaks in brown lemmings.

Using these data as a basis to guess unknown parameter values in our multi-season model (specifically, winter model parameters), we find that the root-mean-square (RMS) difference in successive parameter refinements Eq.(2.7) decreases between 1993-2002 and 2008-2018 but increases between 2002-2008 (Fig. 2.3). This suggests parameters may be non-stationary, dividing the data time-series into three segments. This is because as we add in more data, we expect a better refinement of our parameter estimates and thus a decreasing RMS. If the RMS difference becomes larger, it may suggest that the underlying parameters may have changed so we are no longer converging to the parameters describing the dynamics at that time. Thus, from our parameter refinement we find three segments with different parameter values and need to choose between them to generate model time-series. We use the statistics of the brown lemming cycle lengths from the data as this is a key characteristic of the dynamics on Bylot. The first segment between 1993-2002 has an average cycle length

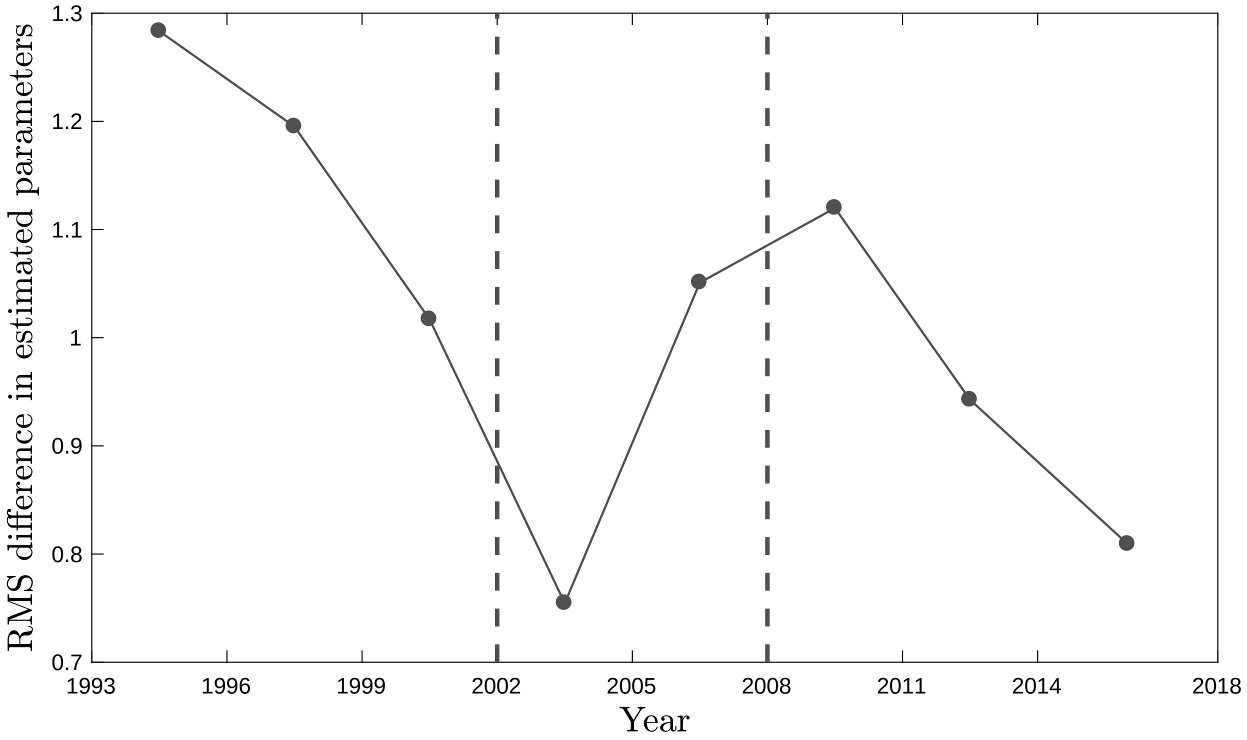


Figure 2.3 Computation of root-mean-square (RMS) differences between successive parameter guesses. For example, the point in the middle of 1996 and 1999 represents the RMS difference Eq.(2.7) between the parameters describing the data from 1993-1996 and the parameters describing the data from 1993-1999. 2002 is the last year for which the RMS difference is decreasing. In 2005, it is increasing. We take the first parameter segment to be from 1993-2002. Afterwards, the RMS difference decreases and, consequently, we define another parameter segment from 2008-2018. This suggests that there may be three different parameter regimes in the time-series.

for the brown lemming density of 3.5 years (one cycle of 3 years and one cycle of 4 years); the second segment from 2002-2008 has an average cycle length of 4 years; and the segment from 2008-2018 has an average cycle length of 3 years. We therefore believe that choosing the parameter set from the first segment over 1993-2002 is justified in that it more closely represents the overall cyclic dynamics found in the data.

A 50 year time-series simulation is shown in Fig. 2.4b. Time-series resulting from the static model does not reproduce at all the dynamics seen in the data (Fig. 2.4a). In contrast, the time-series from the multi-season model (Fig. 2.4b) shows qualitatively similar behaviour to the data. In particular, we find that brown lemmings have large population fluctuations but with variable amplitudes with peaks of the collared lemming roughly coinciding with brown lemming, but of much smaller amplitude. Also, the fluctuations in snow goose biomass have a similar range than the data. In Fig. 2.5, we can see from the power spectrum that there is a peak at a frequency of 0.33 year^{-1} corresponding to a period of approximately 3 years. This peak has a spread which runs between 2.5-3.6 years. This is consistent with the cycle lengths observed from the data time-series and the cycling values reported in the literature. This result, in conjunction with the simulated time-series in Fig. 2.4b indicates the presence of multi-annual cycling in the brown lemming population.

Our multi-season model captures essential season-to-season causal relationships between species: between residents, between migrants, between migrant and resident predator-prey, and intraguild relationships between prey and between predators. This is illustrated in Figs. 2.6-2.8 with cross map plots (Pearson's correlation coefficient, ρ, vs. length of time-series) along with the causal network structures for the three models considered: static, multi-season, and summer model. The cross map plots for the static and summer models are shown in the Supplementary Information Fig. 3 and 4, respectively.

The multi-season cross mapping analysis between residents reveals strong bidirectional relationships between brown and collared lemmings, brown lemmings and arctic foxes, and collared lemmings and arctic foxes (Fig. 2.6c). The predator-prey relationships show both

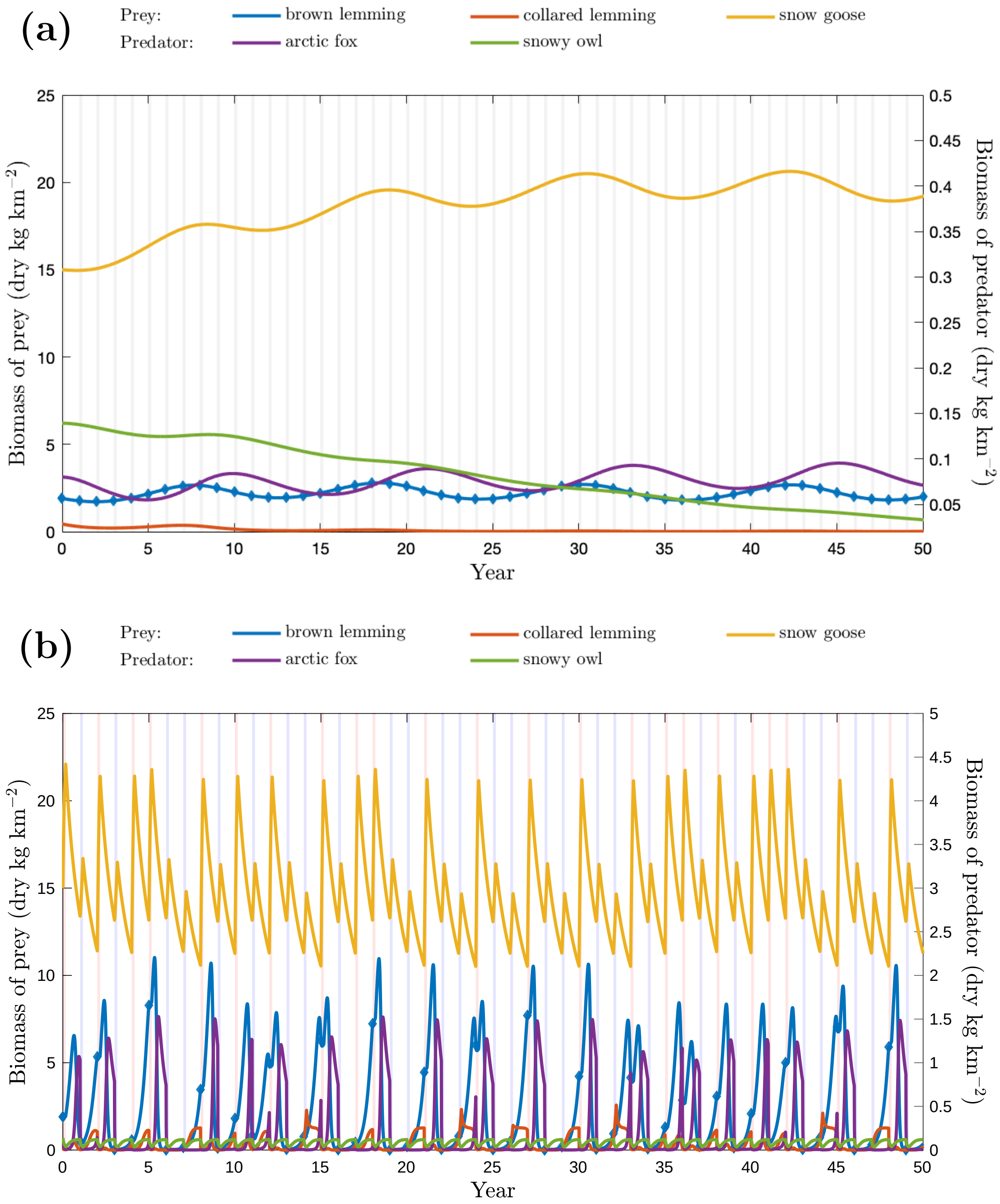


Figure 2.4 (a) Long-time series from the static model. Dark grey bars represent the time periods where summer would be. (b) Long-term time series (50 years) generated using parameters identified for the period 1993-2002. A threshold of 2.50 dry kg km^{-2} is used to set the probability that a peak summer occurs. Blue bars represent the period over which a low summer happens and red bars where a peak summer happens.

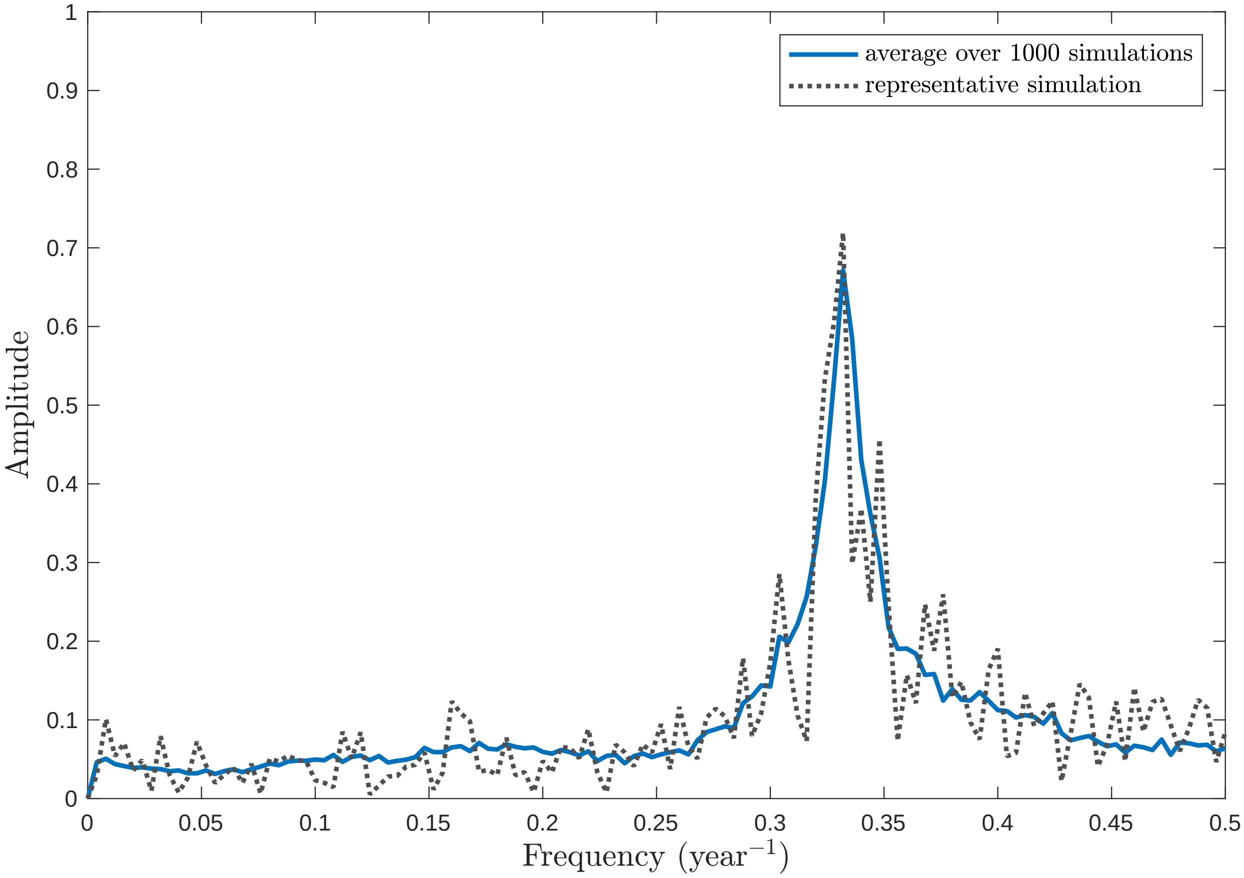


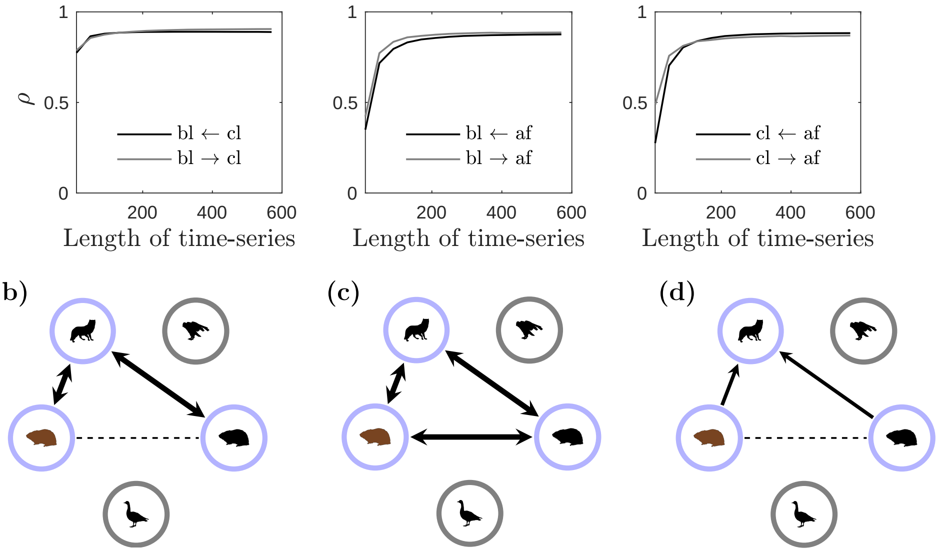
Figure 2.5 Power spectrum averaged over 1,000 simulated brown lemming time-series using the densities at the end of winter (diamonds in 2.4b). Each frequency is associated with a period of time (year=1/frequency).

top-down and bottom-up control. In other words, the predator drives population fluctuations of its prey and vice versa. When comparing the multi-season causal structure with the one obtained just looking at the multi-season model time-series over summers (i.e. summer snapshots), we find weaker causal relationships and rather bottom-up control in the brown lemming-arctic fox interaction (Fig. 2.6d). In other words, the prey fluctuates and this drives fluctuations in predator populations. Doing the same exercise with the static model (Fig. 2.6b) also shows both top-down and bottom-up control similar to the multi-season model but no indirect interaction between the lemming species can be inferred due to a lack of convergence of the cross map likely due to their time-series being strongly correlated. The multi-season cross mapping between migrants (i.e. the snow goose and snowy owl) (Fig. 2.6e) shows bidirectional predator-prey relationships (Fig. 2.6g) but much weaker ones likely due to the shorter time period over which they interact.

The intraguild multi-season cross mapping reveals that the migrants are causally influencing the residents in their respective guild; that is, the goose influences both lemming species and the snowy owl influences the arctic fox (Fig. 2.7a). Comparing the multi-season causal structure (Fig. 2.7c) with the summer one (Fig. 2.7d), we see that the direction of strongest causal influence changes between the brown lemming and the snow goose. No indirect interactions can be inferred from the static model (Fig. 2.7b) and the cross mapping only reveals that there are correlations, the value of the correlation being indicated by the magnitude of ρ.

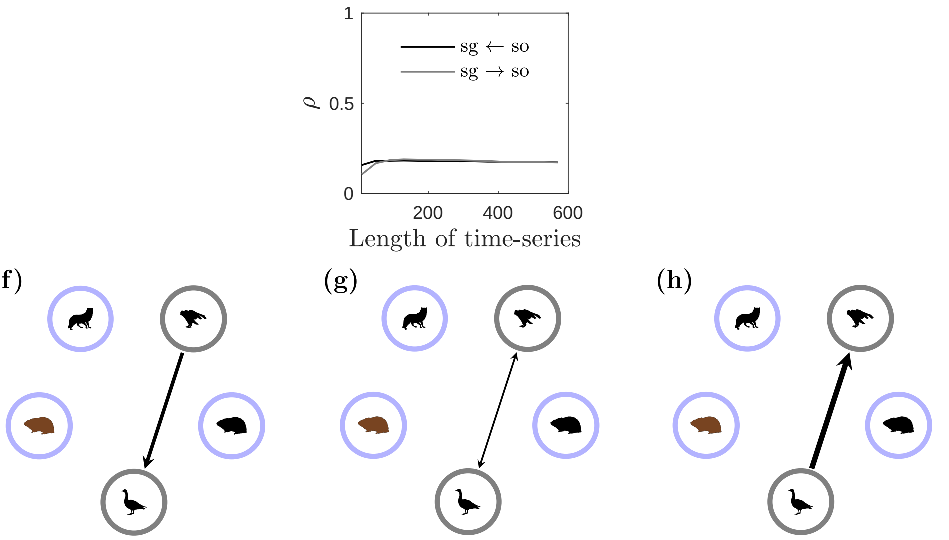
Lastly, we consider the multi-season cross mapping between migrant predator and resident prey, and vice versa (Fig. 2.8a). We find evidence for top-down control between all pairs; that is, between the arctic fox and snow goose (relatively strong), and between the snowy owl and lemmings (weak). Looking at the summer causal structure, we find that the relationship between the owl and the brown lemming turns into a bottom-up one (Fig. 2.8d). In the static model, both top-down control and bottom-up control is detected (Fig. 2.8b).

(a) Multi-season cross mapping (residents)



Static causal structure Multi-season causal structure Summer causal structure

(e) Multi-season cross mapping (migrants)



Static causal structure Multi-season causal structure Summer causal structure

Figure 2.6 (a) Cross maps averaged over 50 simulations for the multi-season model between resident species. Cross maps for the static and summer models can be found in Supplementary Fig. 3 and 4, respectively. Only correlation coefficients, ρ, which are significantly different from zero ($P < 0.05$) are shown (see Supplementary Information section 3). A causal relationship is indicated if ρ increases as the length of the time-series increases and if ρ converges to a fixed value. Species 1 ← species 2 means that species 2 causes species 1 if the above criteria are met. Here bl=brown lemming, cl=collared lemming, af=arctic fox, sg=snow goose, and so=snowy owl. If a causal relationship is not present, then ρ can be taken to represent the degree of correlation between the variables. (b-d) Represent the strongest causal direction in the cross map for the three different models. A stippled line in the network indicates a causal relationship could not be determined due to an absence of convergence. The thickness of the lines represent the magnitude of ρ. A thicker line means a larger ρ. (e) Cross map for the multi-season model between migrant species. (f-h) Causal interaction networks between migrant species for the three models considered.

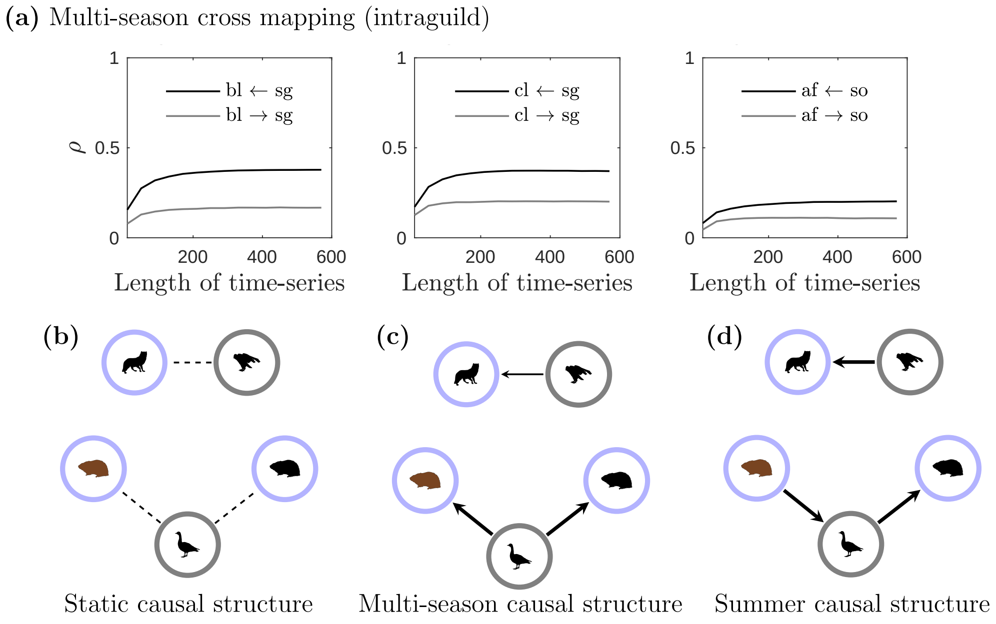


Figure 2.7 (a) Cross maps averaged over 50 simulations for the multi-season model between resident and migrant predator species and resident and migrant prey species. Cross maps for the static and summer models can be found in Supplementary Fig. 3 and 4, respectively. Only correlation coefficients, ρ, which are significantly different from zero ($P < 0.05$) are shown (see Supplementary Information section 3). A causal relationship is indicated if ρ increases as the length of the time-series increases and if ρ converges to a fixed value. Species 1 ← species 2 means that species 2 causes species 1 if the above criteria are met. Here bl=brown lemming, cl=collared lemming, af=arctic fox, sg=snow goose, and so=snowy owl. If a causal relationship is not present, then ρ can be taken to represent the degree of correlation between the variables. (b-d) Represent the strongest causal direction in the cross map for the three different models. A stippled line in the network indicates a causal relationship could not be determined due to an absence of convergence. The thickness of the lines represent the magnitude of ρ. A thicker line means a larger ρ.

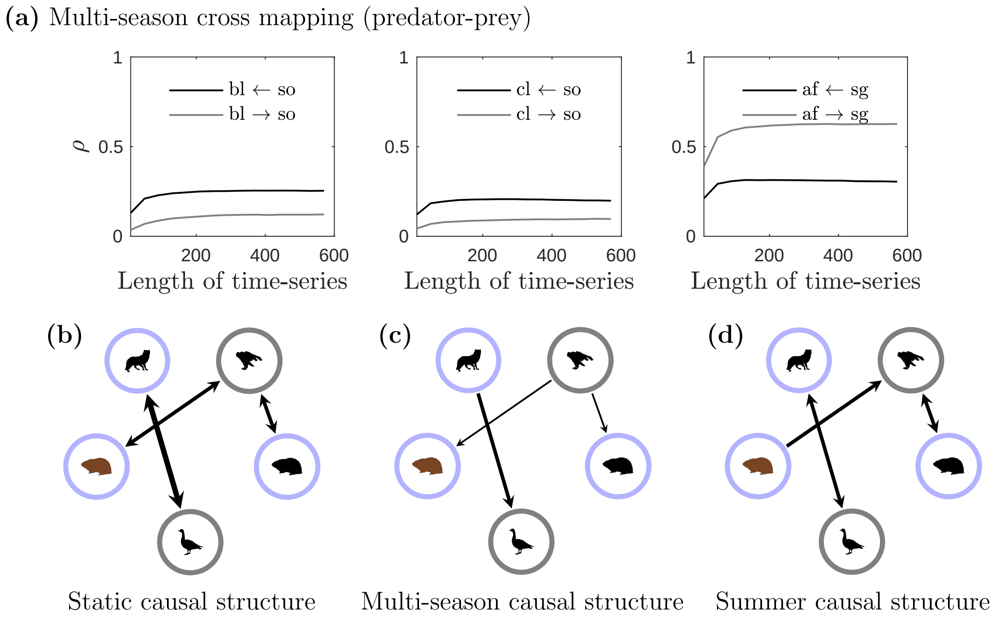


Figure 2.8 (a) Cross maps averaged over 50 simulations for the multi-season model between predator-prey species. Cross maps for the static and summer models can be found in Supplementary Fig. 3 and 4, respectively. Only correlation coefficients, ρ, which are significantly different from zero ($P < 0.05$) are shown (see Supplementary Information section 3). A causal relationship is indicated if ρ increases as the length of the time-series increases and if ρ converges to a fixed value. Species 1 ← species 2 means that species 2 causes species 1 if the above criteria are met. Here bl=brown lemming, cl=collared lemming, af=arctic fox, sg=snow goose, and so=snowy owl. If a causal relationship is not present, then ρ can be taken to represent the degree of correlation between the variables. (b-d) Represent the strongest causal direction in the cross map for the three different models. The thickness of the lines represent the magnitude of ρ. A thicker line means a larger ρ.

2.4 Discussion

Many communities experience strong seasonal variation in their biotic and abiotic environments, particularly at high latitudes. In a strongly seasonal environment like the Arctic, there are very few studies which have modelled, at the food web level, seasonal predator-prey interactions [30, 31]. Our study advances existing literature by providing a comprehensive framework (i.e. hybrid dynamical systems) to include migrants as a dynamical part of the community through fast-topological changes in the food web. With our multi-season framework we find two important features. The first is that multi-annual cycles of small rodent populations can be driven by seasonal changes in species interactions and by state-dependent behaviour governing some predator responses to small rodent densities. This result lends support for the model when compared with what is known about the drivers of multi-annual cycles in the literature. Secondly, and most importantly, our model captures indirect interactions between resident and migrant species in the community which non-seasonal models miss. These interactions may be essential to any model which aims to understand these temporally-forced communities and, especially, the impact of climate change on these communities.

2.4.1 Hybrid dynamical systems capture dynamics of changing food web structure due to migration

We have constructed a multi-season model for a simplified arctic tundra food web (lemmings-arctic fox-snow goose-snowy owl) using a hybrid dynamical systems framework where migration is modelled as fast dynamics and predator-prey interactions as slow dynamics. Our model consists of three distinct equilibria, one for each possible seasonal food web: winter, a low lemming summer (snowy owls absent), and a peak lemming summer (owls present). The existence of multiple equilibria is a basic requirement for any model of seasonal food webs and hence represents a coherent way to look at communities that have a fast-topological change in their structure. Furthermore, a hybrid system also allows us to incorporate state-dependent behaviours; for example, in our model presence of snowy owls during summers of peak lemming abundance occurs with a probability that depends on how high the brown lemming biomass is at the end of winter. Being able to incorporate species behaviour into seasonal models is a strength of hybrid models. Gilg et al. [30] built a seasonal model for the collared lemming and its four predators in eastern Greenland: in the summer when lemmings are abundant, there is predation by migratory or partially nomadic species. Tyson & Lutscher [36] also studied predators that switch from being generalists to specialists according to seasonally varying prey densities, such as in the case of the great horned owl and the snowshoe hare. Our study illustrates another way that this state-dependent behaviour is exhibited.

2.4.2 Seasonality and state-dependency as potential drivers of multi-annual lemming cycles

Seasonality and state-dependent behaviour are known to be important for the generation of multi-annual cycles in small rodent populations, such as lemmings. Generating cycles in our model is necessary to make meaningful comparisons of causal interactions between our model and non-seasonal models. The underlying drivers of multi-annual cycling in small rodent populations have been the cause of much debate in the scientific community [48, 52]. Of particular importance to rodent cycles in Fennoscandia are seasonality as well as community composition and dynamics of predators and prey [53]. Although it is likely that different processes may come into play for different rodent populations in different geographical locations [54], these two components are common in many studies modelling cycles [30, 55–58] including our model. In these models, seasonality is generated by having different parameters in winter and summer or having constantly varying parameters in time, and state-dependent behaviour is incorporated by having a delayed numerical response of predators (typically a one-year lag) to lemming peaks.

Our model output can reproduce observed behaviours; in particular, the multi-annual cycling of the lemming populations in summer as well as the spread in their amplitudes (i.e. peak vs. low densities). We generate seasonal behaviour by assuming there is a topological change in the food web structure in each season and state-dependent behaviour arises from the owl coupling to the summer dynamics (brown lemming-collared lemming-arctic fox-snow goose) when the density of brown lemmings is high enough at the end of winter. Our approach to including seasonality and state-dependency is likely more appropriate to the type of community seen on Bylot Island and probably the Canadian Arctic in general as opposed to that seen by [58] due to the presence of (often avian) species at specific locations at different times of the year. In Fennoscandia; however, both types of models with seasonality/state-dependency can generate cycles in their respective small rodent populations. Delayed density-dependence has been identified as an important component of small rodent cycles [59]. Here, it may be that seasonality becomes a functional analogue of a delayed response by allowing prey to build up in winter when the impact of predation is lower than in summer thereby generating a time delay, which is known to be destabilising. This mechanism is somewhat analogous to that found in Barraquand et al. [60] where overcompensating density dependence, together with phase-dependency (e.g. an increasing phase has a different density-dependent structure than a decreasing phase of a population cycle), can explain common vole population cycles in western France. The randomness in the owl coupling expands the potential for multi-annual cycling in the lemming populations. These results suggest that seasonality and state-dependency may be universal determinants of small rodent multi-annual cycles when predation behaviour is the underlying mechanism.

2.4.3 Multi-season models can capture causal information about indirect interactions

Our multi-season model exposes indirect interactions between migrant and resident prey, which static models do not. Indirect interactions require the presence of an intermediary species and unlike direct effects, do not require a physical interaction between two species [61]. They can arise from two general mechanisms: an interaction chain, such as exploitative competition, or an interaction modification, which occurs when one species affects the interaction between two other species. In our static model, the causal signature between intraguild species (e.g. between lemming species, geese and lemmings, foxes and owls) is overshadowed by correlations in their time-series. Due to mediation by a common predator or prey over a part of the year, in our multi-season model we expect to see indirect competition between migrant and resident prey and similarly for predators. Indeed, we find that these types of causal links emerge from our multi-season model; seasonality may expose these causal relationships by disrupting persistent correlations in time-series. In models with multi-seasonality, the mechanism driving the indirect interaction may be that the snow goose "modifies" the interaction between the resident lemming and fox and thus leaves a causal signature on the lemming [62, 63]. However, it is not clear from the analysis which mechanism underlies the causal relationship. Furthermore, non-seasonal models appear to be unable to distinguish between resident-migrant, predator-prey relationships and resident predator-prey relationships (i.e. direct interactions). We anticipate that a multi-season perspective should provide a better estimation about real pairwise species interactions.

A further goal for quantifying pairwise species interactions in dynamical models may be to determine the sign as well as magnitude of these indirect interactions to understand phenomena such as trophic cascades. In equilibrium systems, community matrix methods are used to quantify indirect interactions. Extensions of these methods have been developed for smooth non-equilibrium systems [64]. These methods rely on numerically computing the community matrix at each state rather than having a single community matrix defined at the equilibrium. However, our multi-season model is a system which abruptly switches its dynamics between seasons. A given state can thus have more than one possible future depending on the current season. This means that each state can be associated with multiple community matrices which means that these extensions fail. New methods to determine the sign of indirect interactions need to be developed for multi-season models as contemporary methods currently available do not suffice. As a first step to address this challenge, pairwise interactions could be computed on a season-by-season basis. However, there may be discontinuities in the sign and magnitude of the indirect interactions which would require deeper investigation.

Our study demonstrates the need for seasonality in modelling food web dynamics and also the need for collecting data throughout all seasons, not just the growing season. Exclusion of these aspects in food web studies means that important information about trophic interactions and indirect interactions between species in general is lost. In addition to developing multi-season models, new theory needs to be developed to analyse community interactions. This enterprise is even more urgent for arctic ecosystems which are poised to experience unprecedented changes in community structure and dynamics from a changing climate due to the arrival of new species. We can not assess the impact of climate change on ecosystems, in particular on strongly seasonal systems like the Arctic, without seasonality: seasonal changes in abiotic and biotic processes is fundamental to ecosystem structure and functioning in these systems, which may in some instances amplify and in other instances dampen the effects of climate change. We believe that moving towards an ecology of seasonality, by developing theoretical models which can handle this type of variation and also by spreading data collection over multiple seasons, is crucial to fully assess ecological responses to a changing climate.

Ethics

Field techniques were approved by Université du Québec à Rimouski Animal Care Committee and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada.

Data Accessibility

Most data is available in the electronic appendices of Legagneux et al. (2012) in Ecology (compiled data used for modelling). More recent raw data for lemming and geese are available on line at:

Gauthier, G. 2018. Lemming monitoring on Bylot Island, Nunavut, Canada, v. 1.1 (1994-2017). Nordicana D22, doi: 10.5885/45400AW-9891BD76704C4CE2
Gauthier, G., Cadieux, M.-C. 2020. Monitoring of Greater Snow Goose reproduction on Bylot Island, Nunavut, Canada, v. 1.1 (1989-2019). Nordicana D41, doi: 10.5885/45570CE-2D00DCA728074FA7

Raw data on arctic foxes and snowy owls are available at:

Berteaux, B. 2019. Monitoring of arctic and red fox reproduction on Bylot Island, Nunavut, Canada, v. 1.0 (1993-2017). Nordicana D49, doi: 10.5885/45594CE-A69880E653314887
Gauthier, G., Cadieux, M.-C. 2019. Monitoring of avian predator reproduction on Bylot Island, Nunavut, Canada, v. 1.0 (2004-2018). Nordicana D50, doi: 10.5885/45591AW-F9B906CC647948E0

Author Contributions

CH created the model and performed the modelling with significant input from FG and DG. GG, JB, DB, DF, and PL collected data. CH wrote the manuscript with input from all co-authors.

Competing Interests

We have no competing interests

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2.6 Supplementary Information

2.6.1 Continuous dynamics for the hybrid model

The continuous dynamics of the hybrid dynamical system employed for the multi-season model assumes Lotka-Volterra, predator-prey interactions for species on Bylot and logistic growth for species off Bylot. There are three "seasons" in the model: $q = 0$ is winter, $q = 1$ is a low summer, and $q = 2$ is a peak summer. Let $\mathbf{B}$ be a vector of species biomasses where the component B_1 is the biomass of the brown lemming, B_2 is the biomass of the collared lemming, B_3 is the biomass of the snow goose, B_4 is the biomass of the arctic fox, and B_5 is the biomass of the snowy owl. Allowing the dot symbol (i.e. $\dot{B}_i$) to be the time derivative, the dynamics for winter are given by the interactions between the resident species (brown lemming, collared lemming, and arctic fox):

$$\begin{aligned}
\dot{B}_1 &= b_1^{(0)} B_1 \left(1 - \frac{B_1}{K_1^{(0)}}\right) - \alpha_{14}^{(0)} B_1 B_4 \\
\dot{B}_2 &= b_2^{(0)} B_2 \left(1 - \frac{B_2}{K_2^{(0)}}\right) - \alpha_{24}^{(0)} B_2 B_4 \\
\dot{B}_3 &= b_3^{(0)} B_3 \left(1 - \frac{B_3}{K_3^{(0)}}\right) \\
\dot{B}_4 &= B_4(-b_4^{(0)} + \alpha_{41}^{(0)} B_1 + \alpha_{42}^{(0)} B_2) - \eta_4^{(0)} B_4^2 \\
\dot{B}_5 &= -b_5^{(0)} B_5 - \eta_5^{(0)} B_5^2,
\end{aligned} \tag{2.8}$$

For the low summer dynamics, the predator-prey equations involve the resident species as well as the snow goose:

$$\begin{aligned}
\dot{B}_1 &= b_1^{(1)} B_1 \left(1 - \frac{B_1}{K_1^{(1)}}\right) - \alpha_{14}^{(1)} B_1 B_4 \\
\dot{B}_2 &= b_2^{(1)} B_2 \left(1 - \frac{B_2}{K_2^{(1)}}\right) - \alpha_{24}^{(1)} B_2 B_4 \\
\dot{B}_3 &= b_3^{(1)} B_2 \left(1 - \frac{B_3}{K_3^{(1)}}\right) - \alpha_{34}^{(1)} B_3 B_4 \\
\dot{B}_4 &= B_4(-b_4^{(1)} + \alpha_{41}^{(1)} B_1 + \alpha_{42}^{(1)} B_2 + \alpha_{43}^{(1)} B_3) - \eta_4^{(1)} B_4^2 \\
\dot{B}_5 &= -b_5^{(1)} B_5 - \eta_5^{(1)} B_5^2,
\end{aligned} \tag{2.9}$$

and for the peak summer all species, including the snowy owl, are involved in Lotka-Volterra dynamics:

$$\begin{aligned}
\dot{B}_1 &= b_1^{(2)} B_1 \left(1 - \frac{B_1}{K_1^{(2)}}\right) - \alpha_{14}^{(2)} B_1 B_4 - \alpha_{15}^{(2)} B_1 B_5 \\
\dot{B}_2 &= b_2^{(2)} B_2 \left(1 - \frac{B_2}{K_2^{(2)}}\right) - \alpha_{24}^{(2)} B_2 B_4 - \alpha_{25}^{(2)} B_2 B_5 \\
\dot{B}_3 &= b_3^{(2)} B_2 \left(1 - \frac{B_3}{K_3^{(2)}}\right) - \alpha_{34}^{(2)} B_3 B_4 - \alpha_{35}^{(2)} B_3 B_5 \\
\dot{B}_4 &= B_4(-b_4^{(2)} + \alpha_{41}^{(2)} B_1 + \alpha_{42}^{(2)} B_2 + \alpha_{43}^{(2)} B_3) - \eta_4^{(2)} B_4^2 \\
\dot{B}_5 &= B_5(-b_5^{(2)} + \alpha_{51}^{(2)} B_1 + \alpha_{52}^{(2)} B_2 + \alpha_{53}^{(2)} B_3) - \eta_5^{(2)} B_5^2
\end{aligned} \tag{2.10}$$

2.6.2 Algorithm for parameter estimation refinement

We develop an optimisation scheme to help refine parameter estimates for unknown parameters (i.e. intrinsic growth rates, intraspecific terms, and winter model parameters) by comparing the model output to the yearly (summer) biomass data. For dynamical systems which are sensitive to parameters, small differences in values can cause large changes in out-

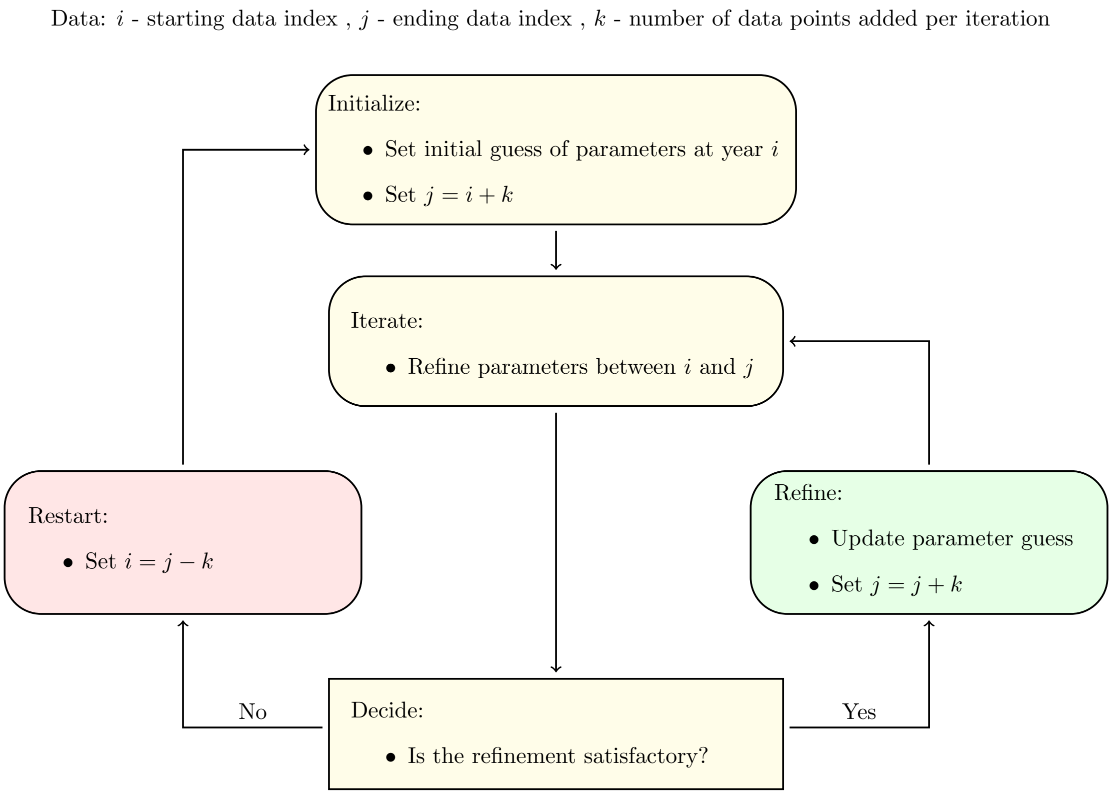

Figure 2.9 Flow chart of the refinement algorithm to set unknown parameter values for our hybrid system model using the yearly data available for summer biomasses. In our implementation of this algorithm, we assume that $k = 3$ or we are aggregating the time-series in three-year segments.

put. The algorithm we develop allows us to incrementally improve parameter estimates by slowly adding more time-points such that we always have a good guess to start the refinement procedure. Fig. 2.9 details the steps of the algorithm: initialise, iterate, decide, refine or restart.

Initialise: An initial guess is chosen, which should be the best guess we have at any point. To begin, we estimate the intrinsic growth rates using Legagneux et al. [1], which assumes that the equilibrium biomass is equal to the long-term average. We create a local distribution of initial guesses around the best guess and execute the next step for all guesses.

Iterate: MATLAB fmincon function is used to minimise a cost function, thus, refining and improving parameter estimates constrained by suitable upper and lower bounds. Data between years i and j is used. The cost function has two parts:

(i) Weighted least squares: brown lemmings have the highest weight in an effort to capture multi-annual cycles. Foxes have the least weight to allow for temporal fluctuations.

(ii) Equilibrium cost: We only look for estimates which have positive equilibria in each season.

Decide: After every iteration a decision must be made. As it is an incremental parameter refinement, a refinement is rejected as being further from the "optimal" parameters if: a) the cost is too large or the distance between subsequent parameter estimates is increasing (i.e. we are not converging to a parameter set) and b) the qualitative dynamics are poor (i.e. the parameters are such that there is no variation in the lemming biomasses).

Refine: If a parameter refinement is accepted, more data is added in units of three years and another refinement is performed.

Restart: If a parameter refinement is rejected, a new set of parameters are generated and refined from the best guess that exists so far. In this case, the cost is no longer computed using data which was used for the previous set of parameters. This step helps to improve the parameter estimates overall.

This algorithm generates three segments from the biomass data available for the Bylot Island community. These are shown in Fig. 2.10.

It is possible that the non-stationarity of parameters in the model are driven by such environmental factors such as spring snow cover. The set of parameters used in this study are from the first segment (i.e. 1993-2002). The reason for this choice is threefold: 1) they seem to represent "historical" brown lemming cycling, 2) they have the lowest cost of the three segments, and 3) they capture important qualitative features desired in the model. For this segment, the intrinsic growth rates are given by

$$b^{(0)} = (3.7588, 8.7888, 0.1394, -0.8003, 6.8620) \tag{2.11}$$

$$b^{(1)} = (0.9068, 9.9698.2.1270, -9.9993, 3.1959) \tag{2.12}$$

$$b^{(2)} = (0.4576, 9.9690, 16.1250, -9.9982, -3.5495). \tag{2.13}$$

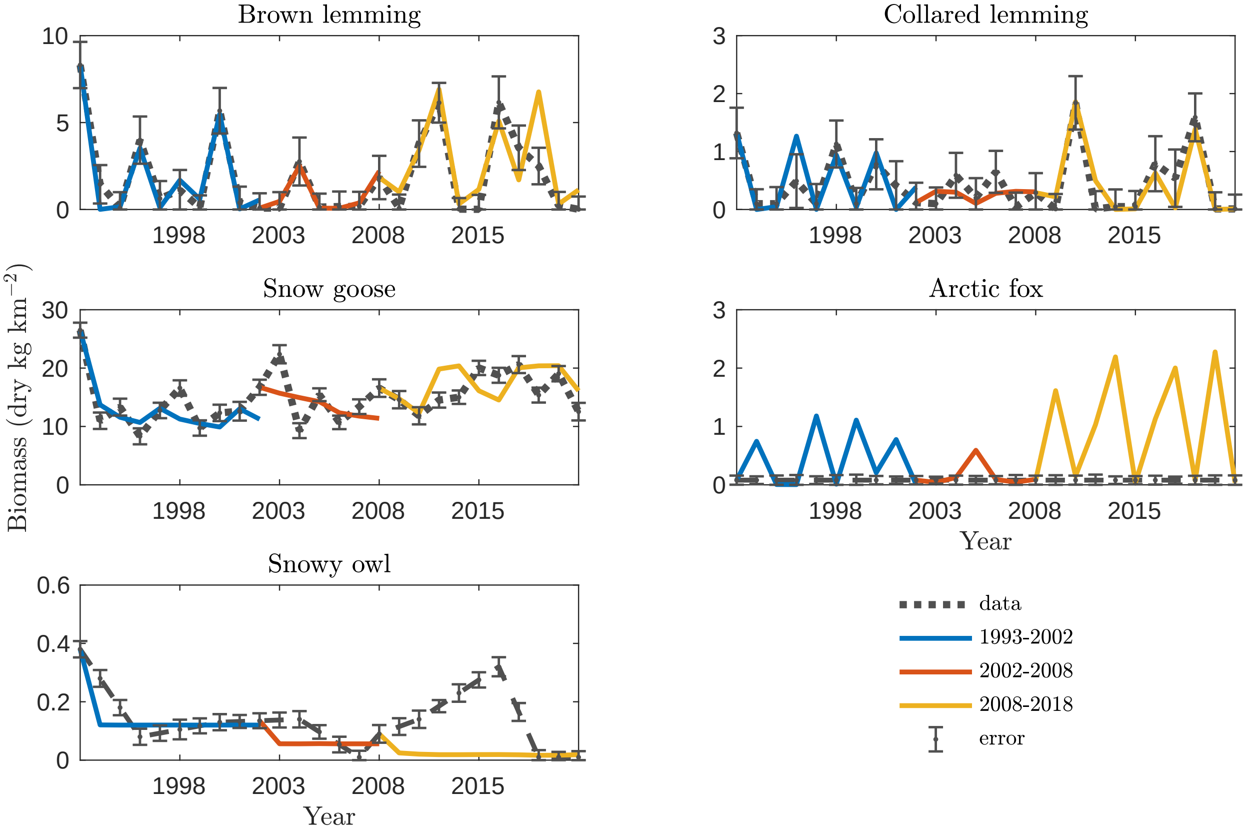

Figure 2.10 Model output using parameter estimation scheme. Three segments are inferred. The blue segment (1993-2002) is used for this study.

The winter interaction coefficients are given by

$$\alpha^{(0)} = \begin{bmatrix} -0.1481 & 0 & 0 & -13.5012 & 0 \\ 0 & -6.8874 & 0 & -19.9908 & 0 \\ 0 & 0 & -0.0437 & 0 & 0 \\ 1.7848 & 0.2341 & 0 & -1.0430 & 0 \\ 0 & 0 & 0 & 0 & -56.6439 \end{bmatrix} \tag{2.14}$$

the low summer coefficients are

$$\alpha^{(1)} = \begin{bmatrix} -0.0006 & 0 & 0 & -29.8506 & 0 \\ 0 & -1.1080 & 0 & -83.7546 & 0 \\ 0 & 0 & -0.0413 & -2.6821 & 0 \\ 0.7939 & 2.2275 & 0.0713 & -278.5454 & 0 \\ 0 & 0 & 0 & 0 & -187.4275 \end{bmatrix} \tag{2.15}$$

, and for a peak summer

$$\alpha^{(2)} = \begin{bmatrix} -0.0001 & 0 & 0 & -7.3207 & -1.2696 \\ 0 & -694.9786 & 0 & -8.4118 & -8.1196 \\ 0 & 0 & -0.7034 & -0.9229 & -0.1563 \\ 0.1947 & 0.2237 & 0.0245 & -176.5767 & 0 \\ 0.1123 & 0.7183 & 0.0138 & 0 & -65.6308. \end{bmatrix} \tag{2.16}$$

The diagonal components are proportional to the intraspecific competition terms (i.e. carrying capacities). We do not expect these to correspond to independently measured quantities (i.e. in the field).

2.6.3 Convergent cross mapping (CCM)

Interpreting CCM

To conduct a CCM, two manipulations need to be done to the time series [2]. First, the time-series for each species needs to be normalised to allow comparison between them. This is accomplished by subtracting from it the mean and dividing by the variance. Second, the time-series must exhibit stationarity; that is, the mean and variance are time independent. We check for stationarity by inspection, choosing only simulations which best satisfy this constraint.

rEDM (Empirical Dynamic Modelling) is an R package which computes cross map skill based on these time-series as Pearson's correlation coefficient, ρ [3]. The CCM function requires several inputs in addition to the time series of the target and the causal variables. One of these inputs is the optimal embedding dimension for each species is the number of lagged coordinates for that species needed to best reconstruct the state space attractor (it may not be the same as the dimensionality of the corresponding dynamical system). We use rEDM simplex projection to identify the embedding dimension for each species. The second input depends on a splitting of the time-series into two halves: a ”library” set, which is used to create reconstructions, and a prediction set, which is used to make forecasts on. We chose to take time-data once per month as this is the most common method for collecting data. We compute the averaged cross map skill as the average ρ over 100 simulated runs (which differ from each other due to the inherent randomness of owls coupling to the summer dynamics) with invalid time-series removed (i.e. those which had cross maps with NA).

The cross map for the time-series generated from the multi-season model is shown in the main text. Below we show the results of the cross mapping for the static model in Fig. 2.11 and every 2 months of summer are taken from the time-series and concatenated in Fig. 2.12.

Significance testing

Suppose that we want to determine whether the converged value of Pearson's correlation coefficient, ρ, associated with the causal link $x \rightarrow y$ is significantly different than zero. We use the method developed by Aftab et al. [4]. Since ρ is obtained from using a sample of points in the state space attractor of x, it has a distribution which we can transform via Fisher's z-transformation to a normally distributed variable or z-score:

$$z = \frac{1}{2} \ln \left(\frac{1+\rho}{1-\rho} \right). \tag{2.17}$$

We then standardize to the unit normal,

$$Z^* = \frac{z}{\sqrt{\frac{1}{N-3}}}. \tag{2.18}$$

For a $Z^* = 1.96$ indicating a p-value of 0.05 and a library size of $N = 600$ (multi-season and summer models) $\rho > 0.080$ for the causation to be significant. For a library size of $N = 3000$ (static model), $\rho > 0.036$ for the causation to be significant.

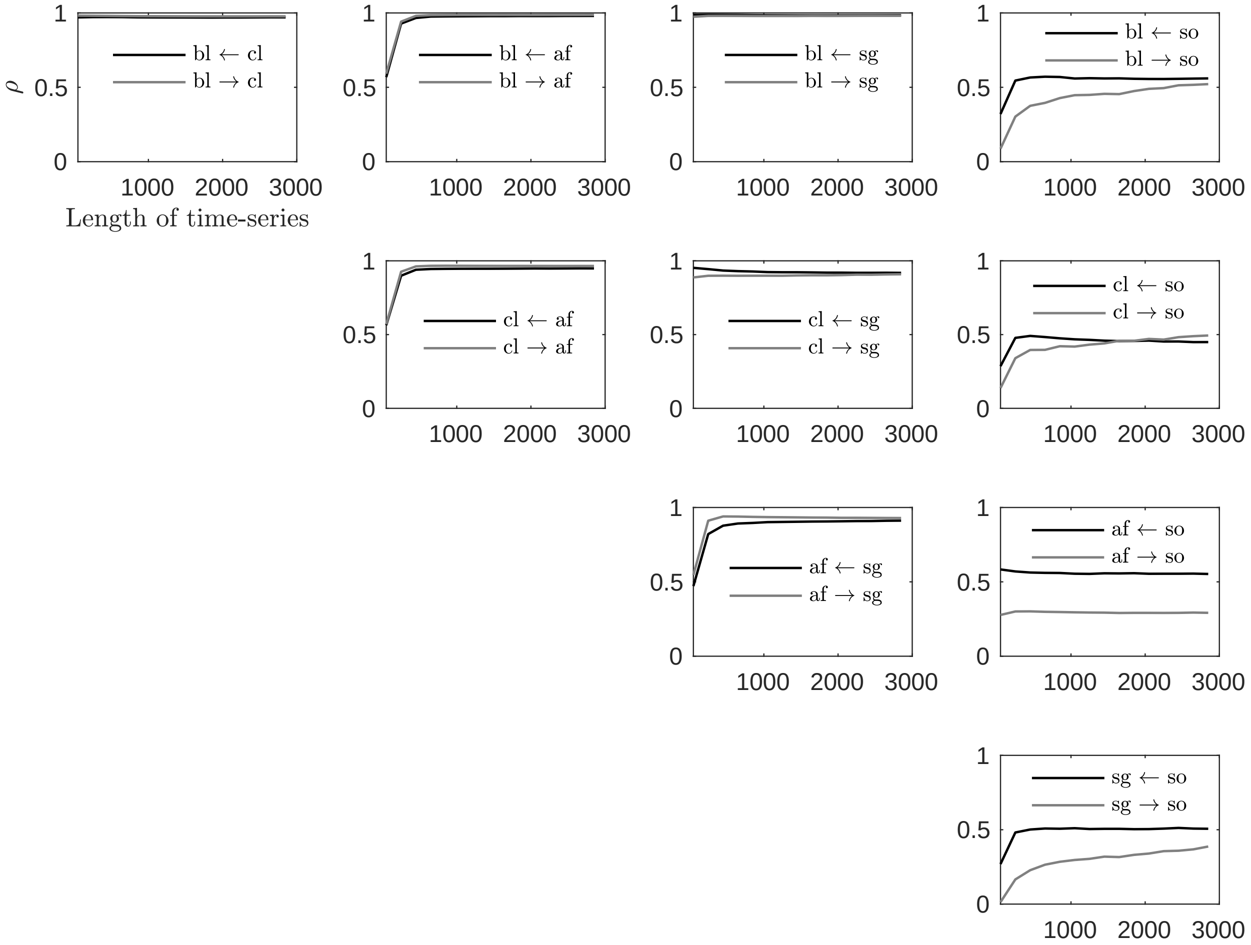

Figure 2.11 Cross maps for the static model which assumes three prey (brown lemming, collared lemming, and snow goose) and two predators (arctic fox and snowy owl). Only correlation coefficients, ρ, which are significantly different from zero ($P < 0.05$) are shown (see Supplementary Information section 3). A causal relationship is indicated if ρ increases as the length of the time-series increases and if ρ converges to a fixed value. Species 1 $\leftarrow$ species 2 means that species 2 causes species 1 if the above criteria are met. Here bl=brown lemming, cl=collared lemming, af=arctic fox, sg=snow goose, and so=snowy owl. If a causal relationship is not present, then ρ can be taken to represent the degree of correlation between the variables.

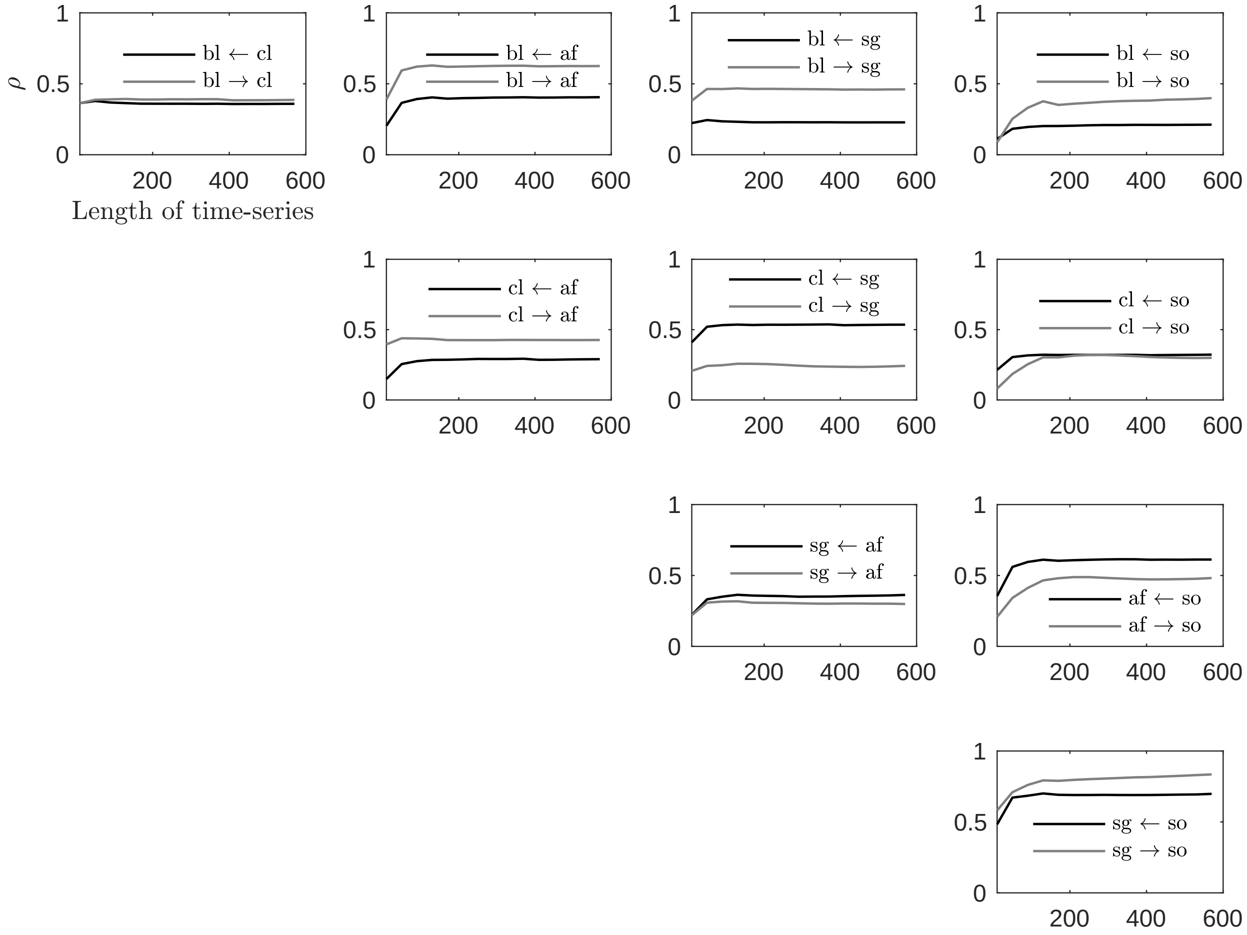

Figure 2.12 Cross maps for the summer snapshot model obtained from concatenating the time-series in the multi-season model which correspond to summer months. Only correlation coefficients, ρ, which are significantly different from zero ($P < 0.05$) are shown (see Supplementary Information section 3). A causal relationship is indicated if ρ increases as the length of the time-series increases and if ρ converges to a fixed value. Species 1 ← species 2 means that species 2 causes species 1 if the above criteria are met. Here bl=brown lemming, cl=collared lemming, af=arctic fox, sg=snow goose, and so=snowy owl. If a causal relationship is not present, then ρ can be taken to represent the degree of correlation between the variables.

2.6.4 References

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Connecting statement

In communities with seasonal food webs, ecological dynamics may often only be understood in the context of multi-season models. For systems which have fast and slow dynamics, such as those with migrant species, a hybrid dynamical system (HDS) may be a suitable framework with which to study seasonal predator-prey community dynamics. These models are better able to capture the types of direct and indirect relationships between species which interact with each other during different parts of the year compared to models which do not incorporate seasonality or only include temporal snapshots. My second chapter focuses exclusively on the plausibility of HDS and heavily depends on numerical analysis of time-series. The next chapter of my thesis probes deeper into what multi-season models can tell us about the role of migrants in seasonal communities, in particular how they alter stability. Not only is this problem interesting from the perspective of resident-migrant interactions, it is also extremely relevant for understanding how climate change impacts seasonal communities. HDS have a long and rich body of literature establishing the theoretical underpinnings of stability. The nontrivial dynamical structure of HDS is best demonstrated by the fact that even though component systems may be stable, the hybrid system may be unstable. It may also be the case that a hybrid system is stable even though its component systems are unstable. Thus, making use of the theoretical machinery developed to capture the mechanisms through which these dynamical systems and their components interact with one another is a fantastic opportunity to explore long-standing hypotheses about the trophic effects of migrant species. Furthermore, the idea of how long each component system is active is a deeply ingrained notion in HDS theory and may provide a way to systematically explore how climate change, by altering the length of seasons and, therefore, species interactions with migrants, may drive a loss of stability.

Chapter 3

Migrating species lead to less resilient community dynamics under climate change

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Keywords: climate extremes, forest, diversity, stress, growth, mortality, resistance, resilience, critical slowing down, complementarity

Abstract

Migratory species are hypothesized to strongly mediate diversity and stability of resident communities of which they are seasonally part. The interaction between mediation due to migrants and changes in the timing and magnitude of abiotic and biotic cues due to a changing climate have rarely been explored but urgently needed especially for strongly seasonal systems. The objective of this study is to investigate how seasonal communities with migrating species may be impacted by longer summers associated with different climate scenarios. We use a multi-season model for a simple Arctic tundra food web framed as a hybrid dynamical system with multiple equilibria to model fast (i.e. changes in topology due to migrating species) and slow (predator-prey interactions) dynamics. Using the stability theory of hybrid systems put in an ecological context, we develop a novel partitioning between migrants and residents of the transference of biomass stock between seasons and a new measure of resilience for systems with multiple equilibria. For longer summers predicted by high emissions scenarios, we find that migrants may not get close to their winter equilibria leading to larger local stocks in summer. Furthermore, we find that greater distances between equilibria and longer season lengths each contribute to a decrease in resilience in seasonal communities. Our study demonstrates that migrating species may be crucial in determining the stability of local communities to climate change and, moreover, that the development of theoretical models to handle seasonal communities is a fundamental step in understanding the mechanisms driving stability.

3.1 Introduction

Climate change is directly altering the temporal fabric governing species interactions through mismatches in the timing of life-history events [1], through extending growing seasons [2], and through reducing amplitude of seasonal differences leading to so-called "eternal summers" [3]. However, many species, such as those found in seasonal environments, depend on the regularly timed co-occurrence of potential prey, competitors, and predators [4]. Alterations in timing and magnitude of abiotic and biotic cues may have serious consequences for the structure and dynamics of seasonal food webs [5]. A current lack of empirical and theoretical studies which incorporate the seasonality of ecological dynamics means that assessments of the threat that climate change might have, especially on strongly seasonal communities such as the Arctic, are limited. Of paramount importance is incorporating migration into seasonal food web models as they can connect distant communities, thus having the potential to alter ecological networks globally. In particular, an earlier arrival in spring and a later departure in autumn due to more favourable climatic conditions [6] may permanently alter prevailing local dynamics.

Seasonal migrations are regularly pulsed flows involving a mass movement of organisms across biogeographical scales [7]. Migrating species can change food web topology as they embed themselves in resident communities and input (usually large) amounts of biomass with consequences to food web stability. Migrants can have different roles in the communities of which they are seasonally part through herbivory, serving as predators and/or alternative prey [8]. Herbivorous migrants can alter nutrient cycling, primary productivity, and biomass of plant communities where they graze, by exploiting vegetation in plentiful seasons and, in some cases, coexisting with dominant resident species ([9]). Migratory predators can regulate prey in resident communities in the spatially separated localities which they connect, thus acting as a stabilizing mechanism by circumventing spatial and temporal variation in prey abundance [10]. When migrants serve as prey, their effect on resident prey species depends on the tension between offering resident prey with a temporal refuge from predation and driving predator population increases due to their often high abundances.

In addition to altering trophic structure, migrating species input a massive amount of biomass into resident communities; in the case of some migratory birds, on the order of several million tons [11]. Although animal inputs from migration can in general include the deposition of nutrients, energy and other substances such as parasites, here we consider their input as being the biomass of a migrant population in order to study flows between seasonal food webs. Theoretical studies show that the quantity, quality, timing, and duration of animal inputs can impact food web stability [12]. For example, larger inputs can promote longer transient dynamics and, therefore, loss of resilience [13]. Developing theory which can translate between biomass inputs and resilience are crucial models of community dynamics with migration.

The model we seek has a multi-season structure to account for the effects of migrants on resident dynamics. Constructing a multi-season model requires a departure from the paradigm of equilibrium dynamics. Because migrants are discretely changing the food web topology, models over multiple seasons must at least have multiple equilibria, one for each season. In systems with a single equilibrium, resilience is defined as the time required to return to equilibrium following a perturbation [14]. To characterize resilience in multi-season models, a new concept emerges: how close to an equilibrium does the system get if it is within a certain distance of the equilibrium in the previous season? To develop these ideas more fully, a hybrid dynamical systems (HDS) framework is used. We assume that migration (or seasonal shifts in food web topology due to migrating species) is instantaneous. A hybrid system allows us to model both fast (i.e. migration) and comparatively slow (i.e. predator-prey) dynamics. We can use the theory of hybrid systems to: 1) define important quantities that characterize seasonal dynamics and give them ecological interpretations, 2) use these quantities to develop a novel partitioning of the contributions of resident and migrant species to the temporal flow of biomass between seasons, and 3) use this partitioning to study resilience of local community dynamics to longer season lengths. With these tools we can then assess the impact that climate change might have on seasonal communities by altering the length of time migrants interact with resident species.

There are only a few multi-season dynamical models in the literature, elements of which can be translated into community models for dynamics with migrating species. Gilg et al. ([15], [16]) build a seasonal, predator-prey model for the collared lemming and its predators (stoat, snowy owl, long-tailed skua, and arctic fox) in eastern Greenland. The collared lemming and stoat have coupled dynamics for winter and summer while the remaining predators are described by non-dynamic equations based on lemming density. [17] assess the effects of non-dynamical predation by generalists and specialists in a single season on a migrating prey population using a time-dependent switching system to divide the annual cycle into segments. A drawback of these studies is that although they employ a type of "switched" system, they lack sufficient tractability, which means that it is difficult to identify mechanisms and coherent patterns arising from the multi-seasonality. We propose to frame our model in terms of the quantities upon which HDS theory is built, namely Lyapunov stability theory, making them useful by giving these quantities ecological interpretations.

The structure of our study is as follows. First, in the section "Conceptual framework" we convey through schematic diagrams key mathematical concepts, and their ecological interpretations, which are needed to understand the results of the paper. Differences between multi-season models and classical food web models are examined, the basic requirement of a multi-season model being the existence of multiple distinct equilibria. For each season we can define a Lyapunov function, a fundamental quantity in HDS theory, and show that it can be interpreted as surplus biomass available for consumption ("surplus stock") beyond what is required to maintain the equilibrium state. This is used in the development of methodology to partition contributions from migrants and residents to community dynamics. Lastly, we develop a measure of resilience based on how close to equilibrium the system gets in each season. In Methods, we develop 1) a simple multi-season model based on a high-Arctic tundra food web (brown lemming-collared lemming-arctic fox-snow goose-snowy owl) with winter and summer dynamics, 2) an algebra which shows how to determine the surplus stock in season-to-season transitions, and 3) a measure of resilience based on the stock between seasons. We then use representative concentration pathway (RCP) climate change scenarios to study the impact on stability of increasing the length of summer. Our study demonstrates that multi-season models can give ecologists completely new insights and tools to understand the community dynamics in systems with migration. By developing these models further, they may allow us to find coherent patterns of change in communities with multiple equilibria and more accurately assess the impacts that a changing climate may have on seasonal ecosystems.

3.2 Conceptual framework

3.2.1 Comparison of classical and multi-season dynamical models: Systems with multiple equilibria and other defining characteristics

When developing a multi-season model, several important features distinguish it from classical dynamical models with some new features emerging (Fig. 3.1). Suppose we have a classical dynamical system with an attracting region such as a stable equilibrium (Fig. 3.1a, red region). An example of a system is Lotka-Volterra predator-prey models with density-dependence. A basic requirement of any multi-season model is that there are at least two equilibria (Fig. 3.1b, red regions). In our example, this can occur in systems with migrating species as the food web topology is changed by the arrival and departure of migrants.

In classical models, the system tends towards an attractor and the rate of decrease becomes slower the closer it gets to the equilibrium, approaching it asymptotically (Fig. 3.1a inset 1). However, in a multi-season model, the system can enter and leave an attracting region during a transition between seasons (Fig. 3.1b inset 1). A consequence of this is that, in seasonal systems, movement between equilibria means that linearized stability theory no longer holds. This feature demands a theory of stability which can be used to study stability far from equilibrium points or attracting regions. This theory is known as Lyapunov (or, more generally, LaSalle) stability theory.

Another prominent feature of multi-season models is that each state can have multiple possible futures (Fig. 3.2b inset 2) compared to one possible future for classical models

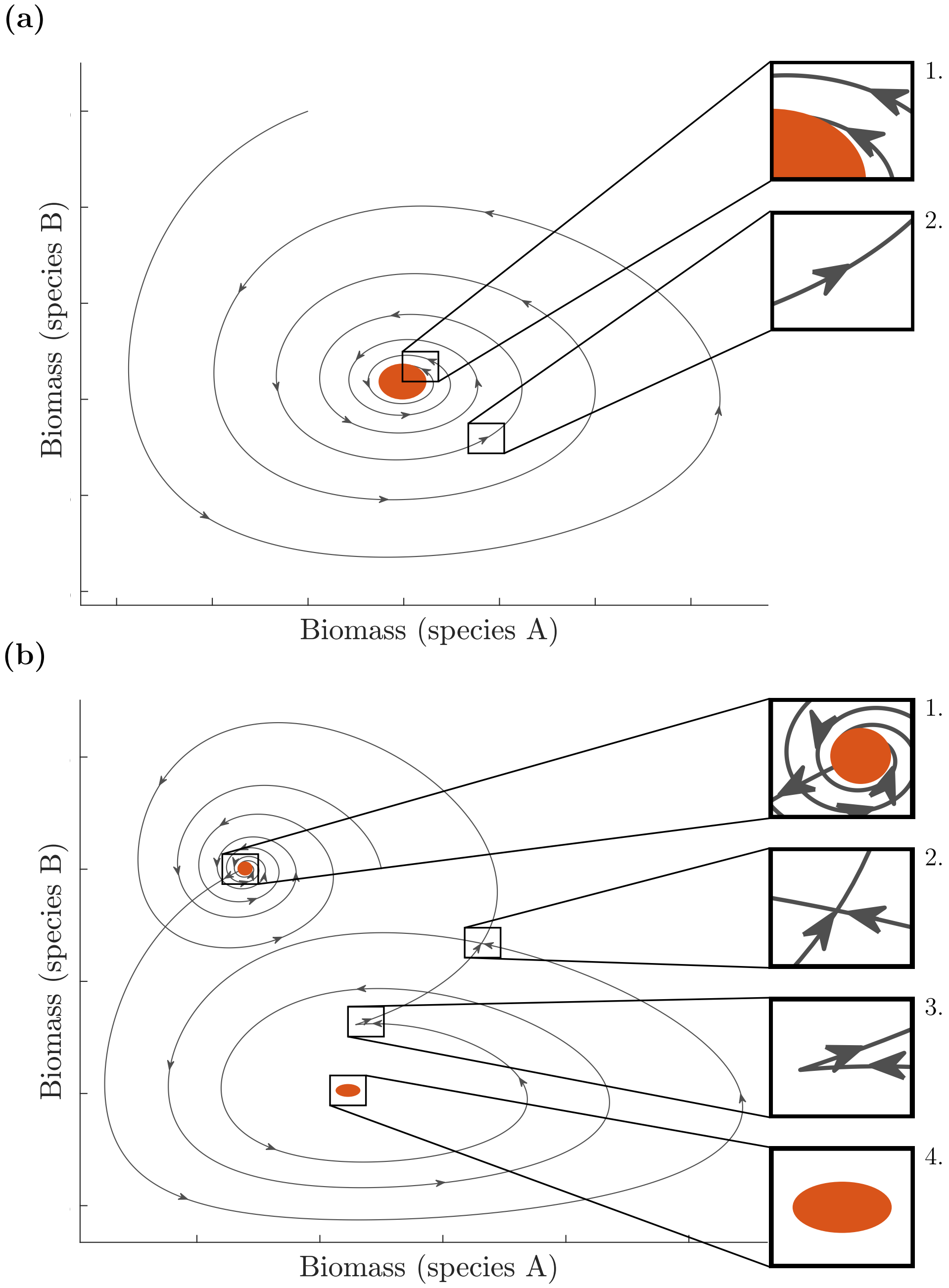

Figure 3.1 Comparison between (a) a classical dynamical models (b) and a multi-season model in the space of predator-prey interactions. The prey is on the *x*-axis and the predator on the *y*-axis.

(Fig. 3.2a inset 2). This is represented by the system crossing itself. This means that where the system ends up depends upon whether the the the season is in winter or in summer, for example. In higher dimensions with many species, it is possible not to have crossings; however, the idea is that crossings do not happen in systems that are not switching between attractors.

There are also features of multi-season systems which do not emerge in classical ones. Fig. 3.1b (inset 3) shows that it is possible to have kinks/discontinuities where the state transitions between seasons. It is also possible for the system to never get "close" to the dynamical equilibrium of any of its components within each season. This is not true as classically asymptotically stable system which always get arbitrarily close to its equilibrium. This feature is illustrated in Fig. 3.1b (inset 4).

Taken together, these features give a basic characterization of multi-season models. In what follows, we assume that each season is associated with an asymptotically stable equilibrium which depends on the parameters of the dynamics. We use these features in the context of a generalized Lyapunov (hybrid) stability framework to show how the objects in this theory can be given meaningful ecological interpretations in the context of seasonal dynamics.

3.2.2 Lyapunov's functions in an ecological context

The last section motivated the need for a generalized hybrid Lyapunov stability theory to analyze the behaviour of systems operating far from their equilibrium points. A (Lyapunov) stable equilibrium means that there exists a *Lyapunov function*, which is a positive scalar function that depends on the system state only, and which always decreases in time [18]. It is zero only at the stable equilibrium. A trial Lyapunov function for a general class of predator-prey interactions is [19]:

$$V(\mathbf{B}(t)) = \sum_i A_i \left(B_i(t) - B_i(t)^* - B_i(t)^* \ln \left(\frac{B_i(t)}{B_i(t)^*} \right) \right) \tag{3.1}$$

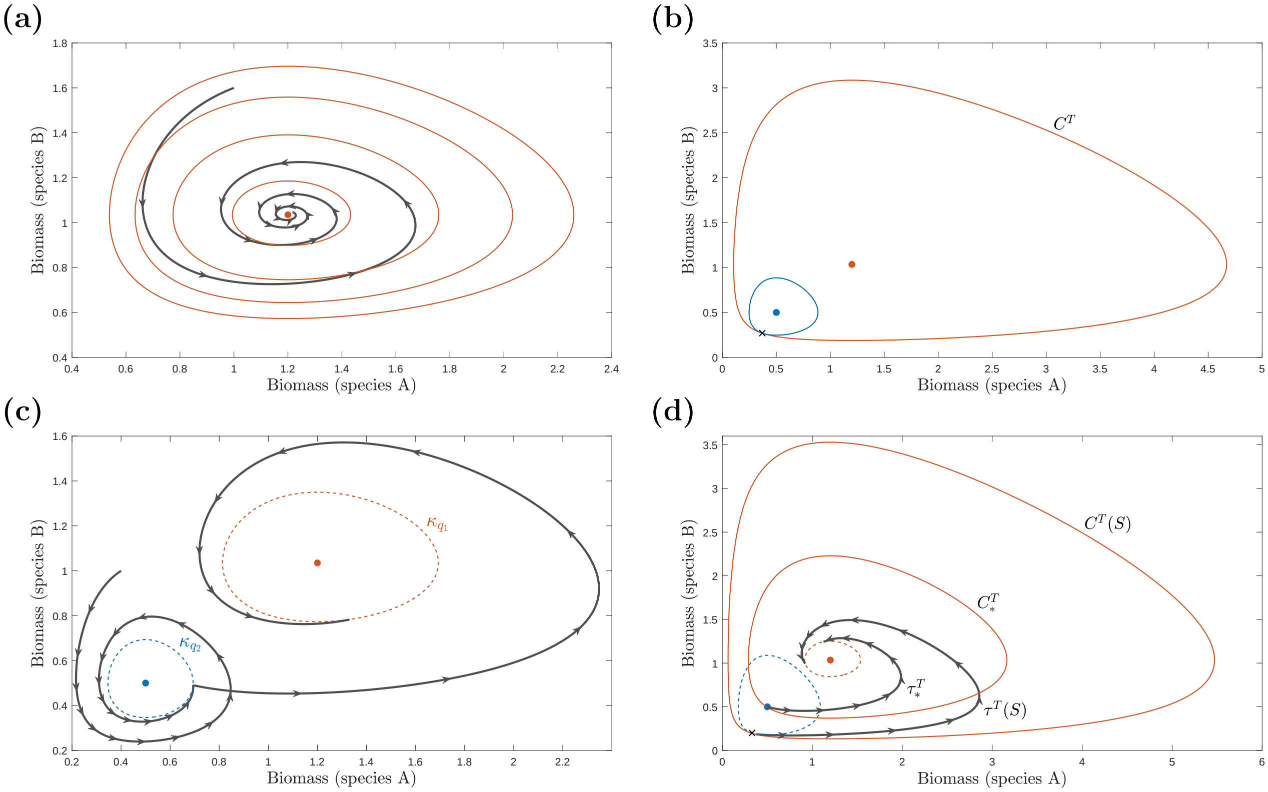

Figure 3.2 Conceptual framework for our study. (a) Illustrates the concept of a Lyapunov function (red curve) as the prey biomass available for consumption (i.e. “surplus stock) with dynamics (grey line). (b) Supposes there are two equilibria one for each season, say, season q_2 (blue) and season q_1 (red). The × indicates the state when a transition between seasons happens and the surplus stock that corresponds to each equilibrium at this point. (c) Establishes the concept of how “close” to an equilibrium the predator-prey dynamical system can get at the end of a season. The value of the Lyapunov function at this time is denoted by κ_{q_2} for the blue equilibrium and κ_{q_1} for the red equilibrium. (d) Captures the concept of resilience introduced in this study. The further the system is from the blue equilibrium at a transition, the longer it takes to get within κ_{q_1} in the next season.

where i labels each species (i.e. prey and predators), B_i is the biomass of species i, A_i are conversion factors which depend on the parameters of the interactions. We show in section 3.3.1 of the Methods what the conditions are on the A_i are for V to be a Lyapunov function of our system. Fig. 3.2a shows curves of constant V (red) when species 1 is prey biomass and species 2 is the biomass of a predator (linear functional responses are assumed as well as density-dependence for both species). The ecological meaning of these curves can be interpreted as the maximum prey biomass available for consumption by a predator beyond the prey biomass required to keep the system at its equilibrium: a surplus stock. This interpretation is to be essential in quantifying flows of biomass by migrants and residents.

Note that this interpretation is only valid between species that are interacting in a predator-prey relationship. In our multi-season model, a migrant species, m, is not always interacting with other species (i.e. migrants in winter). If a migrant prey, say has a self-regulation term (i.e. a carrying capacity, K), a possible Lyapunov function for it is

$$V(B_m(t)) = \frac{1}{K}(B_m(t) - K)^2 \tag{3.2}$$

and so is a measure of how far the prey biomass is from its carrying capacity (i.e. the equilibrium in this case). However, similar to the predator-prey discussion, it is in a sense a measure of surplus stock. In the context of a multi-season model, it may be possible to view this surplus stock as being *latent* in that it will contribute to the summer stock during a winter-to-summer transition. In general, the total Lyapunov function will be the sum of terms like Eq.(3.1) and Eq.(3.2).

Over time, because the time derivative of $V(\mathbf{B}(t))$ is negative, $\dot{V} < 0$ (see Methods), the surplus stock is used by the predators. At the equilibrium, $\mathbf{B}^*$, $V(\mathbf{B}^*) = 0$ and there is no surplus. This is represented by the grey curve tending towards the equilibrium over time. In fact, for the dynamics considered here, we have the stronger condition that

$$V(t) < e^{-\varepsilon t} V(0) \tag{3.3}$$

for some ε. This inequality can be used to define a notion of resilience for seasonal systems (see section 3.2.5).

3.2.3 Transitioning between seasons changes the surplus stock

Fig. 2b shows what happens to the surplus stock when transitioning between seasons in the predator-prey space. Suppose the blue dot represents the equilibrium during season q_2 and the red during season q_1. If the system is in the q_2 dynamics (blue curve), suppose that the transition happens at the point labelled by ×. The starting surplus stock for the q_1 dynamics, $C^T(S)$ where T denotes it is from a transition, say, from season q_2 to season q_1, is obtained by finding the level set of the q_1 equilibrium that passes through this point. Here, S is the duration of season q_2. Because in Eq.(3.1) is additive, we can decompose C^T into the contribution from residents (r) and the contribution from migrants (m) by grouping together the appropriate species:

$$C^T(S) = C_r^T(S) + C_m^T(S). \tag{3.4}$$

It is important to note that we can not compare the *values* of the surplus stock between seasons. They are each defined relative to their own equilibrium point (but see Supplementary Information for a discussion). More or less surplus stock is available in a season depending on the parameters defining the dynamics in each season and the state at which the transition occurs. Because we are interested in finding bounds on surplus stock (and also the time to get close to equilibria), we always assume that the state at which a transition occurs is the state on a level set which is furthest away from the equilibrium of the season to which the system is transitioning (i.e. the worst-case scenario). In Fig. 3.2b, this state corresponds to the × and we will refer to it as the worst-case or WC point.

3.2.4 Quantifying how close to an equilibrium the system gets in a season

Surplus stock decreases over time as it is being consumed and reaches its smallest value at the end of a season. We denote this stock at the end of a season by κ; it indicates how close to equilibrium the system gets just before a transition. This is the sense in which we use the word "close" throughout the paper. Fig. 3.2c shows, for example if the system is transitions between season q_2 to season q_1, possible κ_{q_2} and κ_{q_1} as blue and red dashed lines, respectively. We expect that the longer the system stays in a season, the closer to the equilibrium it gets and the smaller κ is; in other words, $\kappa_q(S)$ depends on the time spent in season q, S. A reasonable hypothesis for the effect of climate change as it increases the length of the summer is that κ will increase for winter and decrease for summer.

3.2.5 A measure of resilience for systems with multiple equilibria

In a multi-season model, the existence of multiple distinct equilibria means that the usual definition of resilience as proposed by [14], as the time it takes to recover towards the equilibrium after a perturbation, is not general enough. In particular, seasonality perturbs the system between multiple equilibria. Suppose the system switches from season q_2 to season q_1. To build a definition of resilience for a multi-season model, we define a time τ^T which measures how long it takes to get close to the q_1 equilibrium after a transition which is labelled by the dashed red line in Fig. 3.2d. This time depends on the time spent in season q_2, S. We call this time $\tau^T(S)$ and it relates the two timescales in the system: the season length (S) and the underlying dynamics τ. In the limit that the system stays infinitely long in season q_2 before a transition, it reaches the q_2 equilibrium. The time it takes to reach the dashed red line is thus given by the time τ^T_* which is always less than $\tau^T(S)$ for finite S. This can be seen through the length of the grey lines in Fig. 3.2d. The larger the difference $\Delta\tau^T(S) = \tau^T(S) - \tau^T_*$ the less resilient the system is because it takes a longer time to recover after the seasonal perturbation. When finding $\tau^T(S)$ we assume that the switch happens at the WC point in the q_2 dynamics.

We can find a geometric bound on $\Delta\tau^T(S)$ using the surplus stocks, C^T, because of the relationship Eq.(3.3). In fact, an upper bound can be given by

$$\frac{1}{\Delta\tau^T_{ref}}\Delta\tau^T(S) \leq \frac{1}{C^T_{ref}}\ln\left(\frac{C^T(S)}{C^T_*}\right) \tag{3.5}$$

where $\Delta\tau^T_{ref}$ and C^T_{ref} are scaling factors. If we compute this bound, for a given S, between all possible season-to-season transitions, then the largest one sets the bound and we denote this bound by $\Omega(S)$. We expect that under extreme climate scenarios for which the length of summer is largest, the winter-to-summer transitions will get the upper bound since it will spend less time in winter and so make the $C^T(S)$ larger. (Note that it is actually the case that $C^T(S)$ can be more finely decomposed into $C^T(\kappa_{q_2}(S))$ using the definition of κ in 3.2.4). We will make this definition more precise in the methods.)

3.3 Methods

3.3.1 A multi-season model for a strongly seasonal Arctic food web

We build our model using a simplified high-Arctic tundra food web as a case study. Arctic ecosystems are an example of strongly seasonal systems, with an important migratory component, experiencing faster warming than the rest of the globe due to polar warming amplification [20]. The species in our model are two sympatric lemming species (brown and collared), the arctic fox as the resident predator, and two migrating species: the snow goose as a migrant prey and the snowy owl as a seasonal avian predator [21].

The multi-season model is illustrated in Fig. 3.3. There are three seasonal food webs in the model: winter, low summer, and peak summer. Winter dynamics occur for 10 months. At the end of winter, depending on the brown lemming density either the owls couple to the resident dynamics (peak summer) or they do not (low summer) for 2 months with a probability weighted by the density of lemmings. Snow geese always couple to resident dynamics in the

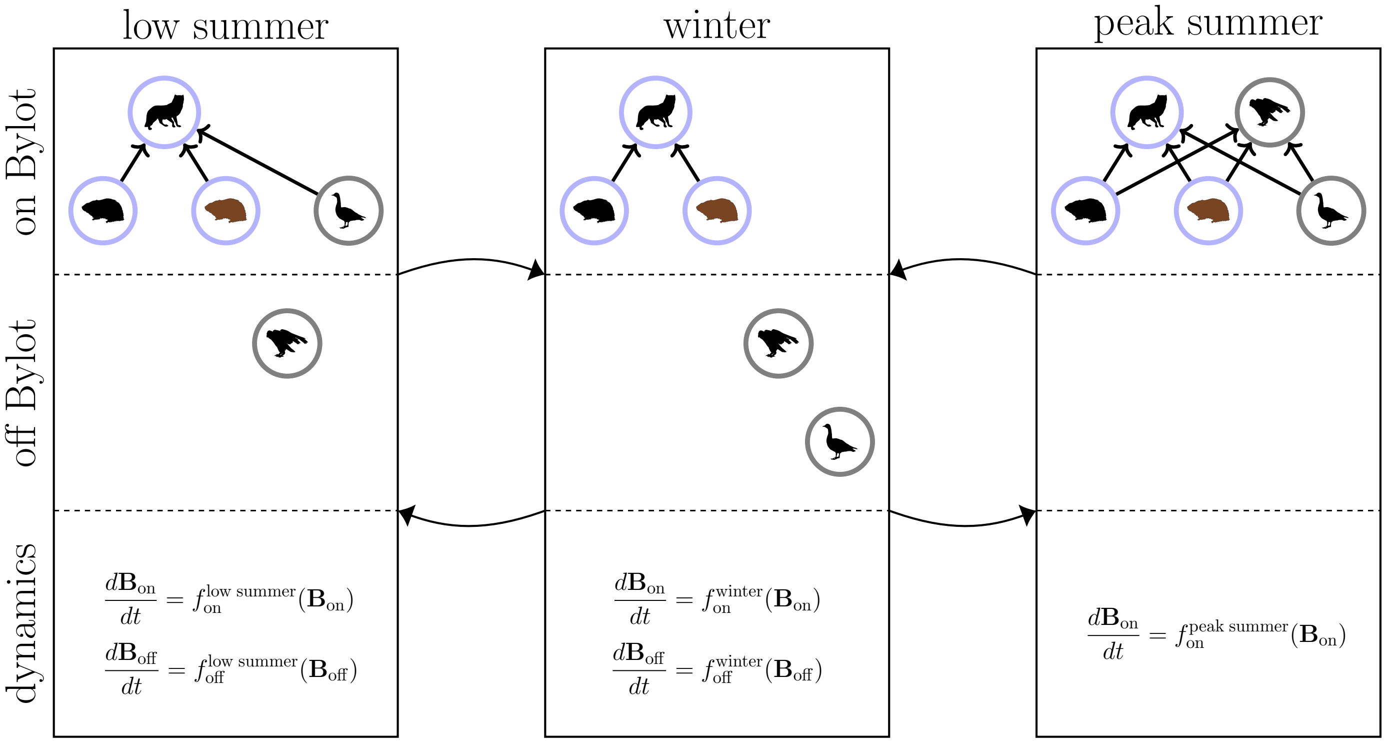

Figure 3.3 Multi-season model for a simple high-Arctic tundra food web (brown lemming-collared lemming-snow goose-arctic fox-snowy owl). In winter, only resident species are local (i.e. on Bylot). In a low summer, owls remain non-local because the brown lemming density at the end of winter is low. In a peak summer, owls become local because the brown lemming density at the end of winter is high. The dynamics are described by Lotka-Volterra predator-prey interactions with linear functional responses and density-dependence for all species. For non-local species, dynamics are simply density-dependent growth.

summer. A crucial component of our modelling approach is to partition species as local, in other words interacting with resident species, and non-local, not interacting with residents. Migrating species (i.e. snow goose and snowy owl) can shift from being non-local to local and vice versa depending on the winter-to-summer and summer-to-winter transitions. In our case, non-local species are also not interacting with other non-local species, but, in general, this does not have to be the case. Equivalently, we define local and non-local dynamical equations on species biomasses. The dynamics are chosen so that each season has associated with it a stable equilibrium where species biomasses are positive.

The continuous dynamics are assumed to be of a Lotka-Volterra type with linear functional responses and intraspecific competition terms for all species. In general, the set of differential equations can be written:

$$\frac{dB_i}{dt} := \dot{B}_i = b_i B_i + \sum_j \alpha_{ij} B_j B_i, \tag{3.6}$$

where the b_i are intrinsic growth rates and α_{ij} are the interaction coefficients (which include intraspecific terms). This can equivalently be written:

$$\frac{d\ln(B_i)}{dt} = b_i + \sum_j \alpha_{ij} B_j. \tag{3.7}$$

The equilibrium point, in the strictly positive part of the space, is defined by:

$$b_i + \sum_j \alpha_{ij} B_j^* = 0 \Rightarrow B_i^* = -\sum_j (\alpha^{-1})_{ij} b_j. \tag{3.8}$$

Substituting in for $b_i = -\sum_j \alpha_{ij} B_j^*$ we can write the dynamical equations as:

$$\frac{d\ln(B_i)}{dt} = \sum_j \alpha_{ij}(B_j - B_j^*). \tag{3.9}$$

Now, consider a trial Lyapunov function discussed in the "Conceptual framework" for predator-prey interactions:

$$V(\mathbf{B}) = \sum_i A_i \left(B_i - B_i^* - B_i^* \ln \left(\frac{B_i}{B_i^*} \right) \right). \tag{3.10}$$

Each term in the sum above is positive, and vanishes at $B_i = B_i^*$ (i.e. the equilibrium). Taking the time derivative gives:

$$\dot{V}(\mathbf{B}) = \sum_i A_i (B_i - B_i^*) \frac{\dot{B}_i}{B_i} = \sum_{i,j} A_i (B_i - B_i^*) \alpha_{ij} (B_j - B_j^*). \tag{3.11}$$

If we define the components of a matrix

$$\tilde{\alpha}_{ij} = A_i \alpha_{ij}, \tag{3.12}$$

then we have that:

$$\dot{V} = \sum_{i,j} (B_i - B_i^*) \tilde{\alpha}_{ij} (B_j - B_j^*). \tag{3.13}$$

If the matrix $\tilde{\alpha}$ is negative definite (i.e. has all strictly negative eigenvalues) then $\dot{V} < 0$, and the function as defined is indeed a Lyapunov function and so defines a surplus stock. In this case, the A_i are chosen so that the cross terms are in the same units (i.e. in the units of prey or in the units of predator). Suitable choices of A_i for the dynamical system Eq.(3.6) are given in the Supplementary Information. With the choices of A_i and α_{ij} using model parameters found in [22], the eigenvalues of $\tilde{\alpha}$ are given by (in the following order: brown lemming, collared lemming, snow goose, arctic fox, snowy owl):

$$\lambda^{(winter)} = (-541.7582, -176.5761, -18.4862, -0.0003, -0.2205), \tag{3.14}$$

$$\lambda^{(low)} = (-3849.0, -176.5761, -18.4862, -0.0002, -0.0187), \tag{3.15}$$

$$\lambda^{(peak)} = (-176.5745, -65.5023, -61.6086, -0.0009, -0.0622). \tag{3.16}$$

and so satisfy the negative definite constraint. The equilibria for each season using the model parameters are given by

$$\mathbf{B}^*_{winter} = (0.5440, 0.4853, 3.1902, 0.2724, 0.1211), \tag{3.17}$$

$$\mathbf{B}^*_{low} = (1.0033 \times 10^{-05}, 6.7017, 49.5234, 0.0304, 0.0171), \tag{3.18}$$

$$\mathbf{B}^*_{peak} = (88.2520, 0.0126, 22.8457, 0.0439, 0.1019). \tag{3.19}$$

3.3.2 The locality set algebra (LSA): Partitioning contributions of local and non-local species to surplus stock between seasons

To account for biomass influx and efflux from seasonal food webs on surplus stock, we introduce a new mathematical tool which we call the *locality set algebra* (LSA). This algebra is necessary because migrant species are not always coupled to the resident food web; therefore, using a single κ_q (here q denotes an arbitrary season) imposes a superficial coupling between interacting and non-interacting species. To that end, we first define a set of resident and a set of migrant species:

$$\sigma_m = \{\text{migrant species}\}, \quad \sigma_r = \{\text{resident species}\}. \tag{3.20}$$

These sets can be used to define what we refer to as *local* and *non-local* species. Local species refers to the set of species which, in the current dynamics, are interacting. Non-local species are species which are not interacting with any other species. The resident species are always local, but the migrant species can move between the two sets. It is possible for the set of non-local species to be empty if all migrants are interacting with the residents. So we have,

$$\sigma_l = \sigma_r \cup (\sigma_l \cap \sigma_m), \tag{3.21}$$

$$\sigma_{nl} = \sigma_{nl} \cap \sigma_m. \tag{3.22}$$

It follows that for each seasonal food web q we can write:

$$\sigma_l^{(q)} = \{\text{local species in seasonal food web } q\}, \tag{3.23}$$

$$\sigma_{nl}^{(q)} = \{\text{non-local species in seasonal food web } q\}. \tag{3.24}$$

The total surplus stock can be partitioned into two parts, which are equivalent,

$$V^{(q)} = V_{\sigma_l}^{(q)} + V_{\sigma_{nl}}^{(q)} = V_{\sigma_r}^{(q)} + V_{\sigma_m}^{(q)}. \tag{3.25}$$

After a transition, it is useful to know how much surplus stock is available to local species and how much to non-local species. Suppose we are transitioning from the food web labelled by q_2 to the food web labelled by q_1. The locality state of each species in the transition can be described by four transition sets

$$\sigma_{l,l}^T = \sigma_l^{(q_1)} \cap \sigma_l^{(q_2)}, \tag{3.26}$$

$$\sigma_{nl,l}^T = \sigma_{nl}^{(q_1)} \cap \sigma_l^{(q_2)}, \tag{3.27}$$

$$\sigma_{l,nl}^T = \sigma_l^{(q_1)} \cap \sigma_{nl}^{(q_2)}, \tag{3.28}$$

$$\sigma_{nl,nl}^T = \sigma_{nl}^{(q_1)} \cap \sigma_{nl}^{(q_2)}. \tag{3.29}$$

$\sigma_{l,l}^T$ reads as the set of species in q_2 which are local that remain local in q_1; $\sigma_{nl,l}^T$ reads the set of species in q_2 which are local that become non-local in q_1, etc. As an example, suppose we are transitioning from a peak summer to winter. Then $\sigma_{l,l}^T = \{$brown lemming, collard lemming, arctic fox$\}$, $\sigma_{nl,l}^T = \{$snow goose, snowy owl$\}$, and $\sigma_{l,nl}^T = \sigma_{nl,nl}^T = \{\ \}$. Therefore, the available stock to local and non-local species in q_1 after a transition from q_2 can be written as

$$C_l^T = \underbrace{\max_{\mathbf{B}_l}\left\{V^{(q_1)}_{\sigma_{l,l}} : V^{(q_2)}_{\sigma_{l,l}} < \kappa_{q_2,l}\right\}}_{C^T_{l,l}} + \underbrace{\max_{\mathbf{B}_l}\left\{V^{(q_1)}_{\sigma_{l,nl}} : V^{(q_2)}_{\sigma_{l,nl}} < \kappa_{q_2,nl}\right\}}_{C^T_{l,nl}}, \tag{3.30}$$

$$C_{nl}^T = \underbrace{\max_{\mathbf{B}_{nl}}\left\{V^{(q_1)}_{\sigma_{nl,l}} : V^{(q_2)}_{\sigma_{nl,l}} < \kappa_{q_2,l}\right\}}_{C^T_{nl,l}} + \underbrace{\max_{\mathbf{B}_{nl}}\left\{V^{(q_1)}_{\sigma_{nl,nl}} : V^{(q_2)}_{\sigma_{nl.nl}} < \kappa_{q_2,nl}\right\}}_{C^T_{nl,nl}}. \tag{3.31}$$

The bigger C_l^T is the more surplus stock is available to predator species which are considered local in the q_1 dynamics; in other words, the more biomass values are available to local species. Similarly for C_{nl} but for non-local species. In this sense, bigger C_l^T can be an indicator of less predictable dynamics for a given group (see Fig. 3.2c). These definitions assume the worst case (i.e. largest stock). In our study of Eq.(3.30) and Eq. (3.31) we only consider winter-to-low summer and winter-to-peak summer transitions. This is because it is possible to define the contribution that non-local species bring to local dynamics. The other way around (i.e. summer-to-winter) is more involved because it is not entirely clear “how much biomass” non-local species take with them as their dynamics is coupled to the local species. To do this properly a reference points needs to be defined in an ecologically sound way (see Supplementary Information for more discussion on this point).

3.3.3 Deriving resilience for local dynamics

Consider a transition from season q_2 to season q_1 and suppose that the system gets within κ_{q_2} of the equilibrium of q_2 just before the transition. We define a timescale, $\tau^T(\mathrm{S})$, where T denotes the transition from season q_2 to season q_1, as the time required for the system to get within κ_{q_1} of the q_1 equilibrium after spending a time S in q_1 just before another transition at time t_2. To arrive at a formula for this concept of resilience (for local interactions) we have the following inequality constraints of q_1:

$$V_{\sigma_l}^{(q_1)}(\mathbf{B}) \leq \kappa_{q_1,l}, \tag{3.32}$$

$$V_{\sigma_l}^{(q_1)}(\mathbf{B}) \leq C_l^T(\kappa_{q_2,l}) = C_{l,l}^T(\kappa_{q_2,l}) + C_{l,nl}^T(\kappa_{q_2,l}), \tag{3.33}$$

where we have used Eq.(3.30) in Eq.(3.33) assuming the worst case, and demand that Eq.(3.32) is true. We can use the fact that our Lyapunov function satisfies the decreasing condition Eq.(3.3), that is, $V^{(q)}(t) \leq e^{-\varepsilon_q t}V^{(q)}(0)$, for some non-zero, positive ε_q (for example, ε_q could be the smallest eigenvalue identified) and write

$$V_{\sigma_l}^{(q_1)}(\mathbf{B}(t_2)) \leq e^{-\varepsilon_{q_1}\tau_l^T(S)}(C_{l,l}^T(\kappa_{q_2,l}(S)) + C_{l,nl}^T(\kappa_{q_2,nl}(S))) \leq \kappa_{q_1,l}(S). \tag{3.34}$$

So, $\tau_l^T(S)$ for local species needs to satisfy

$$\tau_l^T(S) \leq \frac{1}{\varepsilon_{q_1}} \ln\left(\frac{C_{l,l}^T(\kappa_{q_2,l}(S)) + C_{l,nl}^T(\kappa_{q_2,nl}(S))}{\kappa_{q_1,l}(S)}\right). \tag{3.35}$$

Here we can see that $\tau_l^T(S)$ increases if the distance between the equilibria increases (numerator) for a given $\kappa_{q_1,l}$. Holding the numerator constant, it also increases if $\kappa_{q_1,l}$ decreases (i.e. demanding that the system get closer to the q_1 equilibrium). If ε_{q_1} is small, then the system approaches the equilibrium at a slower rate and, consequently, the time required to get within κ_{q_1} of the q_1 equilibrium is larger again.

We can eliminate $\kappa_{q_1,l}$ by subtracting from τ_l^T the time it takes to get close to the q_1 equilibrium from the q_2 equilibrium (which is always smaller than τ_l^T from Fig. 3.2d). So we have an expression for the difference, $\Delta\tau_l^T$, in terms of the surplus stock in the pre-transition season only:

$$\Delta\tau_l^T(S) \leq \frac{1}{\varepsilon_{q_1}} \ln\left(\frac{C_{l,l}^T(\kappa_{q_2,l}(S)) + C_{l,nl}^T(\kappa_{q_2,nl}(S))}{C_{l,l}^T(0) + C_{l,nl}^T(0)}\right), \tag{3.36}$$

where $\kappa = 0$ at the equilibrium. We define S as the length of the summer season in summer-to-winter transitions and $12 - S$ in winter-to-summer transitions. To remove the dependence on ε_{q_1} can divide $\Delta\tau_l^T(S)$ by $\Delta\tau_{ref}^T = \Delta\tau_l^T(S_0)$ for some reference season length S_0. In our analysis, we choose S_0 to be 2 as we vary the length of summer from 2 to 3.5 months (see section 3.3.4 below).

$$\frac{1}{\Delta\tau_{ref}^T}\Delta\tau_l^T(S) \leq \frac{1}{C_{ref}^T}\ln\left(\frac{C_{l,l}^T(\kappa_{q2,l}(S)) + C_{l,nl}^T(\kappa_{q2,nl}(S))}{C_{l,l}^T(0) + C_{l,nl}^T(0)}\right) \tag{3.37}$$

where $C_{ref}^T = \ln\Big((C_{l,l}^T(\kappa_{q2,l}(S_0)) + C_{l,nl}^T(\kappa_{q2,nl}(S_0)))/(C_{l,l}^T(0) + C_{l,nl}^T(0))\Big)$. $\Delta\tau_l^T(S)$ is the extra time it takes to get close to the q_1 equilibrium from the WC (worst-case) point compared to the time it takes to get close to the q_1 equilibrium from the q_2 equilibrium and we define this as our generalized measure of resilience. We expect the further in one season the system gets to its equilibrium, the larger this time can be in order to reach the equilibrium in the next season (this can be seen from Fig. 3.2d). We define the greatest bound on Eq.(3.37) as $\Omega(S)$ as it tells us the worst-case estimate on the resilience given a seasonal duration S.

3.3.4 Estimating κ from RCP climate change scenarios

Representative Concentration Pathways (RCP) describe four possible pathways including greenhouse gas emissions and atmospheric concentrations (among other factors) for the 21st century [23]. The term “representative” means that each RCP should represent a complete range of scenarios available and “concentration” instead of ”emissions” indicates that concentrations are used as the input to climate models [24]. We use the RCP scenarios from 2006 to 2100 presented by the Government of Canada. RCP 8.5 is a high global emissions scenario with warming of 3.2 to 5.4°C by 2090; RCP 4.5 is a medium emissions scenario corresponding with global warming of 1.7 to 3.2°C by 2090; lastly, RCP 2.6 is a low emissions scenario with 0.9 to 2.3°C warming by 2090. A historical pathway is also used as a baseline from 1900 to 2005. Each scenario is accompanied by a set of percentiles which represents the range of results for the climate model ensemble. We use the 25th percentile for snow depth which means that 25% of individual model results show the same or less snow cover.

Our goal is to obtain an estimate for the duration of summer, as captured by the amount of time that snow geese are interacting or local species on Bylot Island (i.e. roughly speaking, the breeding area residence time or BART), for each year of the different climate change scenarios. Snow melt and temperature at laying time have been shown to be important environmental constraints on the phenology of reproduction in snow geese (Bêty et al. 2003, Dickey et al. 2008). In particular, snow geese laying date, but not moult completion date, is correlated with the timing of snow melt [25]. To do this, we use data from 1992 to 2013 and compute the difference between the laying dates and moult completion dates of snow geese as a proxy for the duration of summer (i.e. time over which migrants are interacting with residents). We then use average snow depth measurements from 50 stations on Bylot Island during the months of May and June from 1992 to 2013 to find a polynomial fit between snow depth and duration of summer (coefficients: $\beta_0 = 4.118$, $\beta_1 = -2.152 \times 10^{-1}$, $\beta_2 = 8.010 \times 10^{-3}$, $\beta_3 = -1.180 \times 10^{-4}$, $\beta_4 = 5.988 \times 10^{-7}$; adjusted R-squared$= 0.4821$). To be able to get a relationship between the snow depth predictions from RCP and the duration of summer, we map the snow depth at the location of the RCP prediction (lon=-79.5°E, lat=72.5°N) to the observed snow depth to that of Bylot from 1995 to 2013 using a linear relationship as in Dickey et al. 2008 ($\beta_1 = 0.8431$; adjusted R-squared$= 0.7362$). Consequently, we can use these fits to predict the duration of summer from the snow depth from the RCP models using the value of quadratic fits at the end of the prediction range (2005 for historical and 2100 for RCP scenarios) if they are significant, otherwise the mean duration is used. This characteristic duration is then used as the length of time for the summer dynamics of our hybrid dynamical system. A distribution for κ_q can be generated for each of the seasonal food webs as the minimum stock over a full time series (106 years for historical and 95 years for each RCP scenario) for 10,000 simulations.

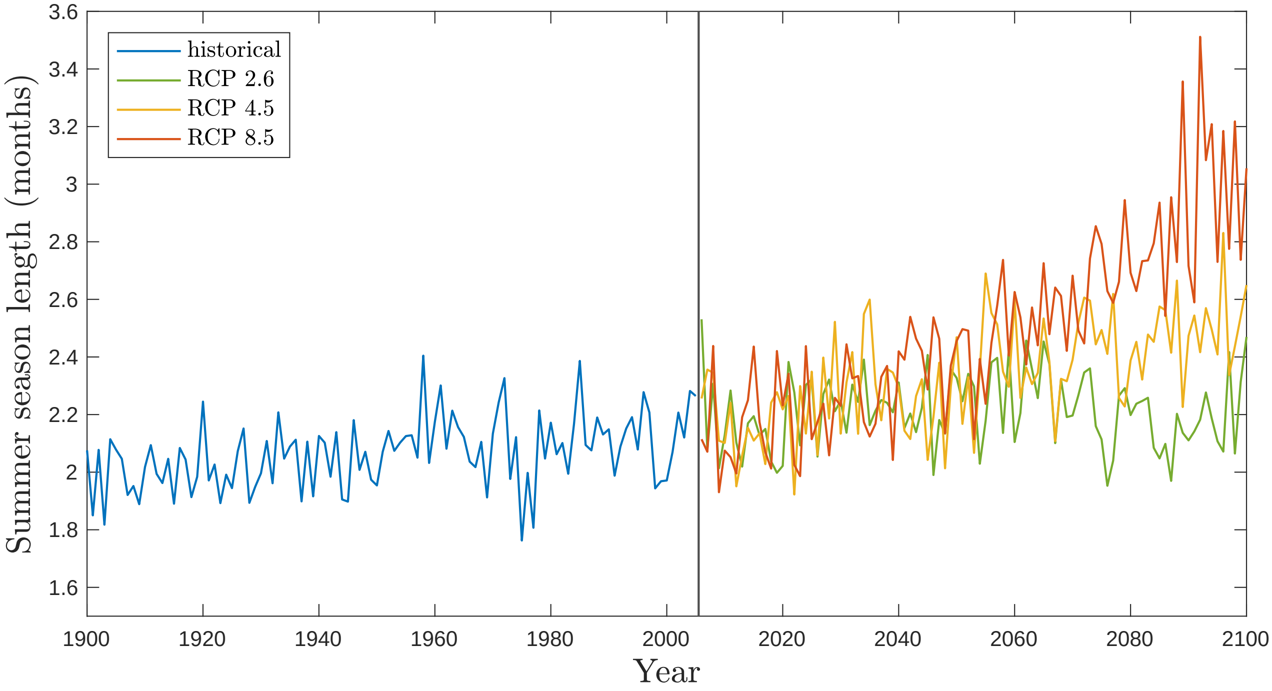

Figure 3.4 Historical and projections for the length of summer on Bylot baed on RCP climate change scenarios.

3.4 Results

3.4.1 Projections for summer season length

Fig. 3.4 shows predictions for the length of summer (in months) for each year from 2006 to 2100 in the RCP scenarios and in the historical baseline from 1900 to 2005. A characteristic of the length of summer for each case is either obtained from the mean or inputing the last year in a quadratic fit, if this fit is significant, to get a worst case estimate. Historical estimates for average snow depth in May and June infer, through an assumed relationship to the amount of time snow geese are considered local species, a summer length of 2.06 months between 1900 and 2005. The low emissions scenario, RCP 2.6, has associated with it a length of 2.17 months; RCP 4.5 has 2.34 months as a characteristic summer length; and RCP 8.5, the highest emissions scenario, is 3.06 months. A year is assumed to have 12 months so these values fix the length of winter.

3.4.2 RCP climate predictions for closest approach to seasonal equilibria

For these summer season lengths, the *local* $\kappa_{q,l}$ defined as the minimum surplus stock over a full time series (historical: 106 years; RCP: 95 years) for season q histogrammed over 10,000 simulations. We chose to histogram the local κ because it represents when resident and (at least one) migrant species are interacting. Fig. 3.5a shows that the median $\kappa_{winter,l}$ is shifting to larger values for more extreme scenarios. This is conceptually reasonable because as the length of summer increases from 2.06 months (historical) to 3.06 months (RCP 8.5), the length of time that the dynamics are occurring in the winter decreases and so less time to reach the winter equilibrium. The inset shows the median value of $\kappa_{winter,l}$ for a range of summer lengths, which increases in an approximately linear way. The $\kappa_{low,l}$ distributions are shown for the low summer, a summer when owls are non-local, in Fig. 3.5b. Here, the distribution is bimodal because there is a dependence on whether the previous summer was a peak summer, a summer when owls are local, or low summer (see Supplementary Fig. 3.9). We see the opposite trend from historical to progressively higher emissions scenarios compared to the $\kappa_{winter,l}$. Both peaks are shifted towards smaller values, again supported by the inset. Lastly, Fig. 3.5c shows $\kappa_{peak,l}$ distributions for a peak summer, a summer when owls are local, exhibit a similar but not as extreme bimodal distribution. While there is a shift towards closer approaches to its equilibrium, the RCP 8.5 scenario demonstrates a complete flattening of its distribution which indicates that its minimum surplus stock is unpredictable. The median $\kappa_{peak,l}$ in the inset is similar to the $\kappa_{low,l}$, but less linear.

3.4.3 Surplus stock from local and non-local species after transitions

We can partition the largest surplus stock to each group of species, local and non-local, after a transition. We refer to these surplus stocks as C_l^T and C_{nl}^T, respectively, where T

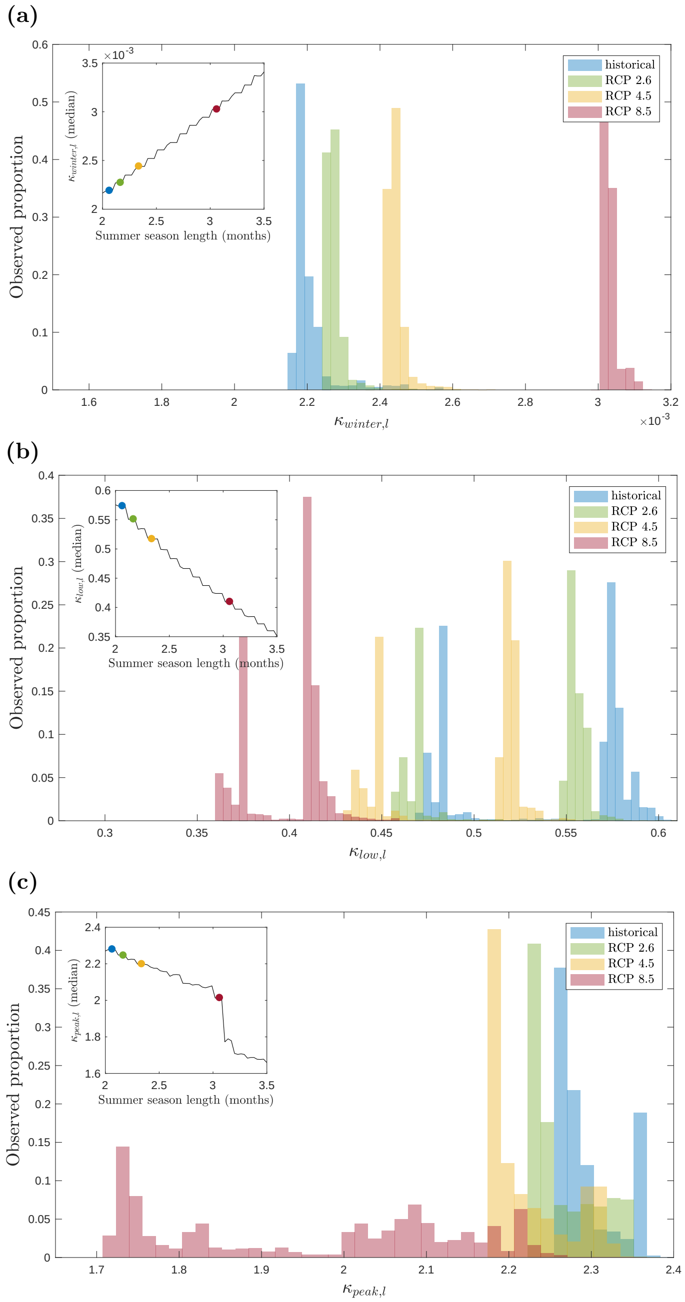

Figure 3.5 Closest approach to the equilibrium as measured by the smallest value of the surplus stock or Lyapunov function for local species attained for each season under each RCP scenario. 10,000 different time-series generated from the multi-season model are used to generate the distributions to account for the randomness in the owl's locality. (a) Closest approach to the winter equilibrium during winter dynamics, (b) closest approach to the low summer equilibrium (i.e. when owls are non-local) during summer dynamics, and (c) closest approach to the peak summer equilibrium (i.e. when owls are local) during summer dynamics.

denotes that it comes from a transition. Transitions associated with C^T_{nl} are addressed in the Supplementary Information. Suppose we are transitioning from winter to a low summer. The transition sets from the locality set algebra (LSA), which describe how a species changes its locality during a transition, for a winter-to-low-summer transition are given by

$$\sigma^T_{l,l} = \{\text{brown lemming}, \text{collared lemming}, \text{arctic fox}\} \tag{3.38}$$

$$\sigma^T_{nl,l} = \{\ \} \tag{3.39}$$

$$\sigma^T_{l,nl} = \{\text{snow goose}\} \tag{3.40}$$

$$\sigma^T_{nl,nl} = \{\text{snowy owl}\}. \tag{3.41}$$

Recall that $\sigma^T_{l,l}$ is the group of species that are local in winter and stay local in a low summer and similarly for the remaining sets. C^T_l is the largest surplus stock available to the local species in a low summer (brown lemming, collared lemming, arctic fox, and snow goose).

The magnitude of C^T_l for a winter-to-low summer transition depends on the "closest" the winter dynamics got to its equilibrium (Fig. 3.2b); namely, $\kappa_{winter,l}$ through $\sigma^T_{l,l}$ and $\kappa_{winter,nl}$ through $\sigma^T_{l,nl}$ (see Methods). Fig. 3.6a is a heat map for C^T_l; the surplus stock available to local species in a low summer depends on both $\kappa_{winter,l}$ and $\kappa_{winter,nl}$. For a fixed $\kappa_{winter,l}$, Fig. 3.6a shows that if $\kappa_{winter,nl}$ is small then C^T_l is smaller in a low summer, but if $\kappa_{winter,nl}$ is large then the largest stock available to local species in a low summer is larger. For a winter-to-low summer transition, $\kappa_{winter,nl}$ is provided by the snow goose, which suggests that if the snow goose does not get "close" to its winter equilibrium (i.e. its carrying capacity) then they may contribute to a larger surplus stock in the low summer.

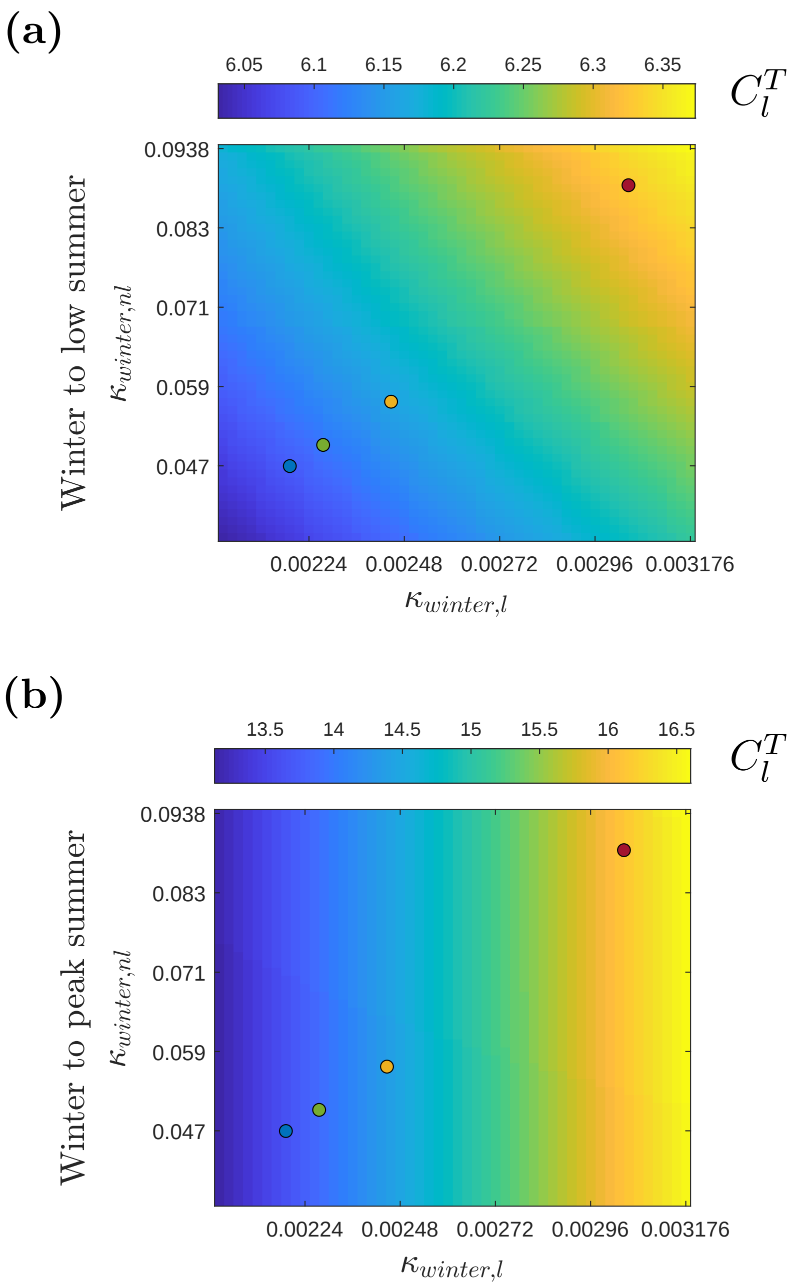

Figure 3.6 Estimates of surplus stock in a (a) low summer after a winter-to-low summer and (b) in a peak summer in a winter-to-peak summer transition obtained by varying the local (*l*) and non-local (*nl*) closest approach to winter equilibrium indicated by $\kappa_{winter,l}$ and $\kappa_{winter,nl}$, respectively. The smaller κ_{winter} is the closer the dynamics at the end of winter are to the winter equilibrium. Blue indicates that the surplus stock is closer to the summer equilibrium and yellow indicates that the stock is the furthest from the summer equilibrium. RCP scenarios are shown (blue-historical, green-RCP 2.6, yellow-RCP 4.5, and red-RCP 8.5).

The transition sets for LSA for winter-to-peak summer transition is given by

$$\sigma^T_{l,l} = \{\text{brown lemming}, \text{collared lemming}, \text{arctic fox}\} \tag{3.42}$$

$$\sigma^T_{nl,l} = \{\ \} \tag{3.43}$$

$$\sigma^T_{l,nl} = \{\text{snow goose}, \text{snowy owl}\} \tag{3.44}$$

$$\sigma^T_{nl,nl} = \{\ \}. \tag{3.45}$$

Fig. 3.6b for C^T_l in this transition shows that there is a strong dependence on $\kappa_{winter,l}$ (provided by the residents) as opposed to $\kappa_{winter,nl}$ (provided by the migrants). This pattern may be due to winter-to-peak summer transitions having a larger difference between brown lemming equilibria leading to the local species dominating the largest surplus stock in a peak summer.

A general pattern from both Fig. 3.6a and Fig. 3.6b is that the further the system is from the winter equilibrium at the transition, the larger surplus stock is available to local species for the low summer. This is illustrated by the location of progressively extreme RCP scenarios tending towards the yellow region and agrees with Fig. 3.2b.

3.4.4 Resilience under RCP climate change scenarios

Fig. 3.7 shows that the resilience decreases (time to get close to the new equilibrium increases) in winter-to-low summer and winter-to-peak summer transitions as the length of summer increases for more extreme RCP scenarios. As the length of winter decreases so the dynamics end further from the winter equilibrium, it takes longer for the system to get close to the summer equilibrium (Fig. 3.2d). The opposite is true for the summer-to-winter transitions. The greater lower bound defining the resilience for the entire system is thus provided by the winter-to-peak summer transition in part because the distance between the winter and peak summer equilibria is large (~ 90 compared to ~ 47 for winter-to-low summer, in units of biomass given by dry kg km^{-2}).

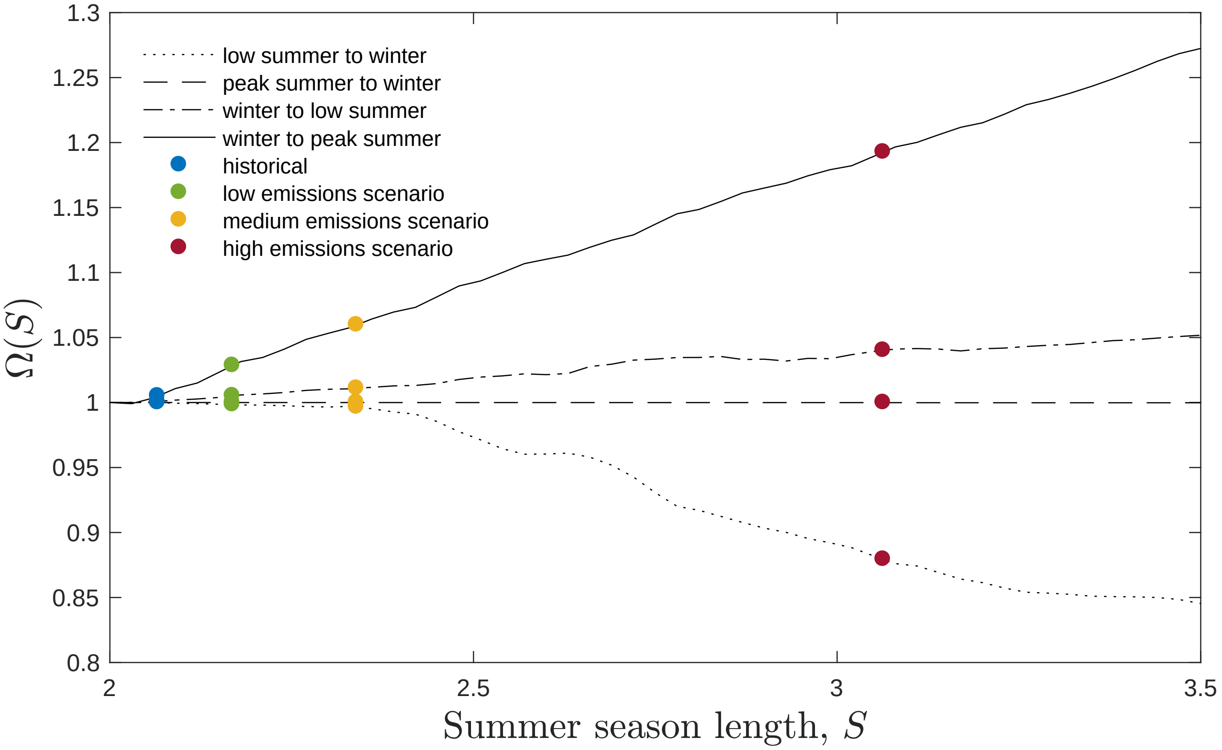

Figure 3.7 Greatest upper bound on the amount of time, for systems with multiple-equilibria, to get close to an equilibrium after a seasonal perturbation. The allowable transitions are indicated in the legend. For winter-to-low summer, this normalized metric measures the extra time is takes to get to the low summer equilibrium from the WC (worst-case) point compared to the time it takes to get close to the low summer equilibrium from the winter equilibrium. The normalization is with respect to the historical estimate of resilience; values greater than one represents that this extra time is a certain times more than the historical estimate and less than one that the extra time is less. Similar interpretations hold for the other transitions.

3.5 Discussion

A fundamental feature of modelling the dynamics of seasonal food webs is the existence of multiple distinct equilibria. This feature is a basic requirement of any multi-season model as migrants alter the food web topology of resident communities and modify species interactions ([5], [8]). The multi-equilibrium nature of seasonal systems has not been given a firm footing in theoretical studies; however, the idea that changes in parameters, which determine the behaviour of state variables and their interactions, due to environmental drivers could lead to so-called alternative stable states is a recurring theme in ecology [26]. The recognition of shared features in seasonal communities may allow the identification of coherent patterns of change across ecosystems structured by temporal variation. Furthermore, by framing our multi-season model as a hybrid dynamical system (HDS), we are able to use the theory underlying these systems (namely, hybrid Lyapunov stability theory) to gain tractability on seasonal systems, which can not be found in existing studies on seasonal community dynamics (although see [27]). An important contribution of this study is meaningful ecological interpretations of highly abstract mathematical objects in HDS and deciphering the implications that these objects have for the stability of seasonal ecological systems in response to climate change.

The expression and interpretation of the Lyapunov function for our model has been used in different contexts in theoretical ecology. MacArthur's [28] consumer-resource model found a quadratic Lyapunov expression, which he called Q, and with which he used to study species packing (i.e. coexistence of multiple competitors). His analysis was based on the minimization of Q which he showed was equivalent to a weighted square deviation of the available production from consumer harvesting abilities. His model assumes resources are at equilibrium and, furthermore, that the interaction matrix exhibits linear independence; in other words, the resource has a positive stable equilibrium. Chesson [29] extended MacArthur's model by showing how to determine whether consumers have linear independent resource utilization. Although we do not explicitly study species coexistence, our model can be likened to a consumer-resource model. We do not assume that resources are at their equilibrium due to the seasonality, but do retain the constraint of linear independence. In this study, we open a new frontier for Lyapunov functions in ecology in the context of multi-seasonality. Our interpretation of a Lyapunov function as the surplus stock, or the prey biomass available for consumption by predators beyond what is needed to maintain species at their equilibrium, lends itself to study 1) how stock is transferred between seasonal food webs and 2) how this stock contributes to the stabilization/destabilization of trophic interactions.

We examine the surplus stock transferred from winter-to-summer transitions and find that the species with comparatively large distances between winter and summer equilibria likely contribute to surplus stock in the summer (Fig. 3.1c). Moreover, summer surplus stock may be larger if migrant species fail to get close to their winter equilibria. Our findings suggest that the importance of contributions to local surplus stock between seasons in part depends the distances between their equilibria. These results highlight the need for characterizing the dynamics for 1) all seasons and 2) between all ecosystem localities connected by migrants. [30] argues that winter is a critically important season, setting the stage for spring dynamics. Our study demonstrates that without accurate data on winter dynamics, it is impossible to predict contributions to surplus stock coming from migrants vs. residents. [31] highlight the need for quantifications of animal inputs from migrations of which few empirical studies achieve due to the difficulties with animal tracking. However, it is widely acknowledged that inputs across ecosystem boundaries from animal movements are essential to local dynamics ([8], [32]). Our study addresses both of these points. We develop a measurement based on raw biomass values which can inform us about biomass available for consumption between seasons. We also find that migrant dynamics in seasons when they are decoupled from resident communities in their breeding grounds may have massive effects on this stock, and, therefore, on the prevailing resident communities.

We find that impact migrants can have on local stock tend to destabilize trophic dynamics in the resident communities of which they are seasonally part of under climate change in two novel ways. Firstly, migrants can led to less predictable dynamics with increasing summer season length. From our analysis of the surplus stock in winter-to-summer transitions, we find that for progressively longer summer season lengths predicted from more extreme climate change scenarios that these stocks increase. The degree of the change depends on both migrants and residents, with migrants showing the potential to increase surplus stock if their equilibria are pushed far from each other. The larger surplus stocks imply less predictability in the overall dynamics. The second result has both a conceptual leap as well as theoretical value. We develop a new concept for defining resilience in systems where there are multiple stable equilibria switched between season. This measure depends on how close to the equilibrium the system gets in the previous season in order to determine how close it will get to the equilibrium of the current season. We find evidence that larger distances between equilibria and longer summer season length leads to a destabilization of local resident dynamics through increasing the time it takes to get close to the current equilibrium.

Our framework gives a strong theoretical foundation upon which to build multi-season models in ecology by clarifying important concepts to seasonal food web dynamics, in particular, as it pertains to communities with seasonal migrations. Our approach lends itself to identifying coherent patterns of ecological change as seasonal food webs are all characterized by distinct equilibria. In the next stage of the development of the theory of seasonal food webs, bounds on stability need to move beyond just season-to-season transitions to include past information on species interactions. This is especially important with climate change as it is altering trophic interactions in time through changes in the timing and magnitude of temporal variation of abiotic and biotic processes. Climate change is occurring simultaneously with seasonal dynamics, not independent of it. Including seasonal movements and couplings across ecosystem boundaries is not just an exercise in accounting, it is a necessity if we are going to fully understand the impact of climate change on ecological processes.

Data accessibility

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Author contributions

CH developed the study with input from FG and DG. CH developed the novel theory and performed the analyses. CH wrote the manuscript with input from FG and DG.

Competing interests

We have no competing interests.

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3.7 Supplementary Information

3.7.1 Definitions

Dynamics, parameters, and equilibria

The continuous dynamics are assumed to be of a Lotka-Volterra type with linear functional responses and intraspecific competition terms. In general, the set of differential equations for a given seasonal food web q can be written:

$$\frac{dB_i}{dt} = \dot{B}_i = b_i^{(q)} B_i + \sum_j \alpha_{ij}^{(q)} B_j B_i \tag{3.46}$$

where the b_i are intrinsic growth rates and α_{ij} are the interaction coefficients. We find from a previous study that suitable parameter estimates for unknown parameters which reproduce the qualitative biomass dynamics from data are

$$b_{winter} = (3.7588, 8.7888, 0.1394, -0.8003, 6.8620) \tag{3.47}$$

$$b_{low} = (0.9068, 9.9698.2.1270, -9.9993, 3.1959) \tag{3.48}$$

$$b_{peak} = (0.4576, 9.9690, 16.1250, -9.9982, -3.5495) \tag{3.49}$$

and

$$\alpha^{(winter)} = \begin{bmatrix} -0.1481 & 0 & 0 & -13.5012 & 0 \\ 0 & -6.8874 & 0 & -19.9908 & 0 \\ 0 & 0 & -0.0437 & 0 & 0 \\ 1.7848 & 0.2341 & 0 & -1.0430 & 0 \\ 0 & 0 & 0 & 0 & -56.6439 \end{bmatrix}. \tag{3.50}$$

The winter equilibrium given the above parameter choices we have that the equilibria for each seasonal food web is

$$\mathbf{B}^*_{winter} = (0.5440, 0.4853, 3.1902, 0.2724, 0.1211) \tag{3.51}$$

$$\mathbf{B}^*_{low} = (1.0033 \times 10^{-05}, 6.7017, 49.5234, 0.0304, 0.0171) \tag{3.52}$$

$$\mathbf{B}^*_{peak} = (88.2520, 0.0126, 22.8457, 0.0439, 0.1019) \tag{3.53}$$

3.7.2 Lyapunov functions

Denote the local and non-local species sets in seasonal food web q by:

$$\sigma_l^{(q)} = \{\text{local species in seasonal food web } q\} \tag{3.54}$$

$$\sigma_{nl}^{(q)} = \{\text{non-local species in seasonal food web } q\}. \tag{3.55}$$

We identify in the main text that Lyapunov functions for local dynamics are given by

$$V_{\sigma_l} = \sum_{i \in \sigma_l} A_i \left(B_i - B_i^* - B_i^* \ln \left(\frac{B_i}{B_i^*} \right) \right) \tag{3.56}$$

where $i = \{bl, cl, sg, af, so\}$ where $i = bl$ labels the brown lemming, $i = cl$ labels the collared lemming, $i = sg$ labels he snow goose, $i = af$ labels the arctic fox, and $i = so$ labels the snowy owl. Each term in the sum above is positive, and vanishes at $B_i = B_i^*$, i.e. the equilibrium. The A_i for winter are given by

$$A_i = \alpha_{4,i}^{(winter)} / \alpha_{i,4}^{(winter)} \text{ for } i = bl, cl \tag{3.57}$$

$$A_{af} = 1 \tag{3.58}$$

for the low summer by

$$A_i = \alpha_{4,i}^{(low)}/\alpha_{i,4}^{(low)} \text{ for } i = bl, cl, sg \tag{3.59}$$

$$A_{af} = 1 \tag{3.60}$$

and for the peak summer by

$$A_i = \max(\alpha_{4,i}^{(peak)}/\alpha_{i,4}^{(peak)}, \alpha_{5,i}^{(peak)}/\alpha_{i,5}^{(peak)}) \text{ for} i = bl, cl, sg \tag{3.61}$$

$$A_j = 1 \text{ for } j = af, so. \tag{3.62}$$

Lyapunov functions for non-local dynamics are taken to be of the form

$$V_{\sigma_{nl}} = \sum_{i \in \sigma_{nl}} \frac{1}{B_i^*}(B_i - B_i^*)^2. \tag{3.63}$$

Seasonal systems

Each seasonal food web is associated with a Lyapunov function $V^{(q)}(\mathbf{B})$ which is a scalar function of biomasses, $\mathbf{B}$, that can be used to prove stability properties for a specific equilibrium, $\mathbf{B}^{*(q)}$. For a many-species system, the total Lyapunov function is the sum of the individual species' Lyapunov functions:

$$V^{(q)}(\mathbf{B}) = V_{bl}^{(q)}(\mathbf{B}) + V_{cl}^{(q)}(\mathbf{B}) + V_{sg}^{(q)}(\mathbf{B}) + V_{af}^{(q)}(\mathbf{B}) + V_{so}^{(q)}(\mathbf{B}) \tag{3.64}$$

where

$$V_i^{(q)} = \text{ Lyapunov function for species } i \text{ in seasonal food web } q \tag{3.65}$$

and

$$V^{(q)} = \text{ total Lyapunov function.} \tag{3.66}$$

Define the set of allowed transitions T as ordered pairs of food webs, where $T = q_1 q_2$ says an allowed transition during the dynamics is from food web q_2 to food web q_1. Before the transition to q_1, the Lyapunov function for q_2 gets to within some κ_{q_2} of its equilibrium $\mathbf{B}^*_{q_2}$ (recall that a Lyapunov function decreases in time and is zero at its equilibrium). Let the set of biomasses generating Lyapunov functions within κ_{q_2} of the q_2 equilibrium be denoted by

$$\mathcal{B}_{q_2}(\kappa_{q_2}) = \{\mathbf{B} : V^{(q_2)}(\mathbf{B}) \leq \kappa_{q_2}\} \tag{3.67}$$

At the transition time, the worst-case (i.e. largest) value that the Lyapunov function can take (or what we will refer to as the available stock) that the q_2 dynamics can have is given by

$$V^T_{\kappa_{q_2}} = \max_{\mathbf{B}\in\mathcal{B}_{q_2}} V^{q_1}(\mathbf{B}). \tag{3.68}$$

Let $\boldsymbol{\kappa} = [\kappa_{q_1}, \kappa_{q_2}, \cdots, \kappa_{q_n}]$ and define the set

$$\mathcal{N}(\boldsymbol{\kappa}) = \bigcup_q \mathcal{B}_q(\kappa_q). \tag{3.69}$$

If the state is in the set $\mathcal{N}(\boldsymbol{\kappa})$ then it is near one of the equilibria. This set is a useful indicator when a state gets close to any one of the equilibria in our hybrid system. Also let, for some transition $T = q_1 q_2$,

$$\mathcal{A}_T = \{\mathbf{B} : V^{q_1}(\mathbf{B}) \leq V^T_{\kappa_{q_2}}\} \tag{3.70}$$

which tells us the set of possible states the system can be in after a transition. Define the union of these post-transition sets as:

$$\mathcal{L}(\boldsymbol{\kappa}) = \bigcup_{T} \mathcal{A}_T \tag{3.71}$$

where T is over all possible transitions. This set tells us all possible states that the system can take, so long as we are always within κ_{q_2} of the equilibrium state of seasonal food web q_2 before each transition $T = q_1 q_2$.

Lastly, we introduce the notion of a reference state $\mathbf{B}_T^R$. We must have that:

$$\mathbf{B}_T^R \in \mathcal{A}_T \tag{3.72}$$

This is because the reference state is supposed to represent a typical value of the system. If the reference state is not within the corresponding transition set, then it cannot be a value that the system may typically take. Lastly define the value of the various Lyapunov functions at a reference point $\mathbf{B}^R$ as:

$$\begin{aligned} V_R^{(q)} &= V^{(q)}(\mathbf{B}^R) & (3.73)\\ &= V_{bl,R}^{(q)} + V_{cl,R}^{(q)} + V_{sg,R}^{(q)} + V_{af,R}^{(q)} + V_{so,R}^{(q)} & (3.74)\\ &= V_{bl}^{(q)}(\mathbf{B}^R) + V_{cl}^{(q)}(\mathbf{B}^R) + V_{sg}^{(q)}(\mathbf{B}^R) + V_{af}^{(q)}(\mathbf{B}^R) + V_{so}^{(q)}(\mathbf{B}^R). & (3.75) \end{aligned}$$

An example of a possible reference state which would be appropriate over all transitions is the mean equilibrium value. A second set of appropriate reference points could be the equilibrium point $\mathbf{B}_{q_1}^*$ for the seasonal food web q_1 with the transition $T = q_1 q_2$.

Scaling of Lyapunov functions

There is a redundancy in the definition of a Lyapunov function. That is, it can be multiplied by an arbitrary positive number and still remains a Lyapunov function for the system. This scale affects the specific value of κ, μ, and the upper and lower bounds (b and a, respectively). We can use this redundancy to be able to compare κ_q for the different seasonal food webs. We choose the scaling such that the Lyapunov functions for each seasonal food web are one at the mean equilibrium, $\bar{\mathbf{B}}^* = (1/|q|)\sum_q \mathbf{B}^*$, where $|q|$ is the number of different food webs in the hybrid model. Therefore, we can define a scaling

$$\bar{V}^{(q)} = V^{(q)}(\bar{\mathbf{B}}^*) \tag{3.76}$$

such that

$$\hat{V}^{(q)}(\mathbf{B}) = \frac{1}{\bar{V}^{(q)}} V^{(q)}(\mathbf{B}) \tag{3.77}$$

which is unity when $\mathbf{B} = \bar{\mathbf{B}}^*$ for each q.

Choosing a Reference Point

The reference point exists to allow more realistic values to be obtained from the estimates. It is a very conservative assumption that all other species will have zero Lyapunov function when the species under consideration reaches its largest value in the real dynamics, having a reference point is a less conservative assumption. The cost is that a bound can no longer be considered mathematically strict, and that one must justify a choice for the reference point. It is important to note a few things about choosing a reference point.

1. The choice of the reference point affects the size of the computed values, but not their relationships to one another. A fixed and reasonable choice of reference points will still allow inferences to be made about the system.

2. Bad choices of reference points will over-constrain the species under consideration. This is a good method to find when a bad reference point has been chosen. For example, a bad reference point would tell us that a maximum population estimate was zero.

3. Quantities using the same reference point can be reliably compared to one another.

3.7.3 Some extra remarks on the concept of dwell time stability

Defining a lower bound on the dwell time

The idea behind this is that first, the system gets within κ_{q_2} of the equilibrium of q_2 just before the transition $T_1 = q_1 q_2$. We wish to find the dwell time $\tau^{q_1 q_2}$, such that the system can get within κ_{q_1} of q_1 just before the transition T_2. If the switching time is less than this bound, the system will therefore stay within $\mathcal{L}(\boldsymbol{\kappa})$ during the whole of the time between the two transitions. To perform this calculation we define a ratio as follows:

$$\frac{V^{(q_1)}(\mathbf{B})}{V^{(q_2)}(\mathbf{B})} \leq \mu(\kappa_{q_2}) \, \forall \, \mathbf{B} \in \mathcal{L}(\boldsymbol{\kappa}). \tag{3.78}$$

We also assume that we have an ε_q such that:

$$\dot{V}^{(q)} \leq -\varepsilon_q V^{(q)} \Rightarrow V^{(q)}(\mathbf{B}(t)) \leq e^{-\varepsilon_q t} V^{(q)}(\mathbf{B}(0)). \tag{3.79}$$

Take the transition time for T_1 to be equal to t_1 and the transition time for T_2 to be equal to t_2. Also assume that initially, we are within κ_{q_2} of the equilibrium of the q_2 system. We then have:

$$V^{(q_1)}(\mathbf{B}(t_1)) \leq \mu(\kappa_{q_2}) V^{(q_2)}(\mathbf{B}(t_1)) \tag{3.80}$$

$$\Rightarrow \quad V^{(q_1)}(\mathbf{B}(t_1)) \leq \mu(\kappa_{q_2}) \kappa_{q_2} \tag{3.81}$$

$$\Rightarrow \quad e^{-\varepsilon_{q_1}(t_2 - t_1)} V^{(q_1)}(\mathbf{B}(t_1)) \leq e^{-\varepsilon_{q_1}(t_2 - t_1)} \mu(\kappa_{q_2}) \kappa_{q_2} \tag{3.82}$$

$$\Rightarrow \quad V^{(q_1)}(\mathbf{B}(t_2)) \leq e^{-\varepsilon_{q_1}(t_2 - t_1)} \mu(\kappa_{q_2}) \kappa_{q_2}. \tag{3.83}$$

So, if we require the inequality:

$$e^{-\varepsilon_q(t_2 - t_1)} \mu(\kappa_{q_2}) \kappa_{q_2} \leq \kappa_{q_1} \tag{3.84}$$

then we have that:

$$V^{(q_1)}(\mathbf{B}(t_2)) \leq e^{-\varepsilon_{q_1}(t_2-t_1)}\mu(\kappa_{q_2})\kappa_{q_2} \leq \kappa_{q_1} \tag{3.85}$$

as desired. Therefore, for this to be true we require:

$$\tau^{q_1 q_2} = (t_2 - t_1) \geq \frac{\ln\left(\frac{\kappa_{q_2}\mu(\kappa_{q_2})}{\kappa_{q_1}}\right)}{\varepsilon_{q_1}}. \tag{3.86}$$

This dwell time can be interpreted as the time required for the switched system to get "close" (in the sense of κ) to the equilibrium in each season before switching to the next one. The smaller the actual switching time is in comparison to this value, the further from the equilibria the system has the possibility of moving. This makes a good measure of stability for a hybrid system with multiple distinct equilibrium, as the further from the equilibria the system is, the less likely to be predictable the system is.

The Estimation of μ

Each of our Lyapunov functions are exponentially stable in the sense that we can bound them by "quadratic functions" (roughly speaking as we are in a five-dimensional state space):

$$a^{(q)}||\mathbf{B} - \mathbf{B}^*_\mathbf{q}||^2 \leq V^{(q)}(\mathbf{B}) \leq b^{(q)}||\mathbf{B} - \mathbf{B}^*_\mathbf{q}||^2 \tag{3.87}$$

$$\dot{V}^{(q)}(\mathbf{B}) \leq -\varepsilon||\mathbf{B} - \mathbf{B}^*_\mathbf{q}||^2 \tag{3.88}$$

where $\varepsilon = \min\{\varepsilon_q\}$. In our case, with the local and non-local Lyapunov functions, we have:

$$V^{(q_2)}(\mathbf{B}) = V_l^{(q_2)}(\mathbf{B}) + \gamma V_{nl}^{(q_2)}(\mathbf{B}) \tag{3.89}$$

where γ is an arbitrary constant. One can write:

$$a_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_l^2+\gamma a_{nl}^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_{nl}^2 \le V^{(q_2)}(\mathbf{x}) \le b_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_l^2+\gamma b_{nl}^{(q_2)}||\mathbf{x}-\mathbf{B}^*_{\mathbf{q_2}}||_{nl}^2 \quad (3.90)$$

$$\dot{V}^{(q_2)}(\mathbf{B}) \le -\varepsilon_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_l^2-\gamma\varepsilon_{nl}^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_{nl}^2. \quad (3.91)$$

If γ is chosen such that:

$$\gamma=\frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}} \quad (3.92)$$

Then the above becomes:

$$a_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||^2 \le V^{(q_2)}(\mathbf{B}) \le b_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_l^2+\frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}}b_{nl}^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_{nl}^2 \quad (3.93)$$

$$\dot{V}^{(q_2)}(\mathbf{x}) \le -\varepsilon_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_l^2-\frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}}\varepsilon_{nl}^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||_{nl}^2. \quad (3.94)$$

If the non-local Lyapunov function is already quadratic, then $a_{nl}^{(q_2)}=b_{nl}^{(q_2)}$. In that case:

$$a_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||^2 \le V^{(q_2}(\mathbf{B}) \le b_l^{(q_2)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||2 \quad (3.95)$$

$$\dot{V}^{(q_2)}(\mathbf{B}) \le -\min\left\{\varepsilon_l^{(q_2)},\frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}}\varepsilon_{nl}^{(q_2)}\right\}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||^2 \quad (3.96)$$

and the quadratic bound on the total Lyapunov function is given by the coefficients from the bound on the local Lyapunov function. We want $\mu(\kappa)\in(1,\infty)$ such that:

$$\frac{V^{(q_1)}(\mathbf{B})}{V^{(q_2)}(\mathbf{B})} \le \mu(\kappa) \text{ for } q_1,q_2\in Q,\ \forall\mathbf{B}\in\mathcal{L}(\kappa)-\mathcal{N}(\kappa). \quad (3.97)$$

Then, for *every* transition with dwell time $\tau^{q_1q_2}$ satisfying

$$\tau^{q_1q_2}>\tau_b=\frac{\log\mu(\kappa)}{\varepsilon}, \quad (3.98)$$

where τ_b is a lower bound on the dwell time, the trajectory of the hybrid system globally converges to $\mathcal{L}(\kappa)$.

Our goal in this section is to find a μ for our hybrid system. Given our condition of exponential stability above, we have that

$$\frac{V^{(q_1)}(\mathbf{B})}{V^{(q_2)}(\mathbf{B})} \leq \frac{b^{(q_1)}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_1}}||^2}{V^{(q_2)}(\mathbf{B})} \leq \frac{b^{(q_1)}}{a^{(q_2)}}\frac{||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_1}}||^2}{||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}||^2} := P(\mathbf{B}). \tag{3.99}$$

It follows that to find a μ we want to maximize $P(\mathbf{B})$. To do this, we fix the denominator as the set of points on the sphere

$$\mathcal{S}_R = \{\mathbf{x} \in \mathbb{R}^5 : ||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_2}}|| = R\}. \tag{3.100}$$

We want to find the $\mathbf{B}_\mu$ such that

$$\mathbf{B}_\mu = \max_{\mathbf{B}\in\mathcal{S}_R}||\mathbf{B}-\mathbf{B}^*_{\mathbf{q_1}}||. \tag{3.101}$$

By the triangle inequality, $\mathbf{B}_\mu$ lies on the line connecting the equilibria; that is,

$$\mathbf{B}_\mu = \mathbf{B}^*_{\mathbf{q_2}} + \lambda_\mu \frac{(\mathbf{B}^*_{\mathbf{q_2}} - \mathbf{B}^*_{\mathbf{q_1}})}{||\mathbf{B}^*_{\mathbf{q_2}} - \mathbf{B}^*_{\mathbf{q_1}}||}. \tag{3.102}$$

for some $\lambda_\mu \in \mathcal{R}$. In terms of λ_μ we have

$$P(\lambda_\mu) = \frac{b^{(q_1)}}{a^{(q_2)}}\frac{(1+\lambda_\mu)^2}{\lambda_\mu^2} \tag{3.103}$$

plugging in Eq.(3.102) into Eq.(3.99). This function is monotonically decreasing for $\lambda_\mu > 0$. By the triangle inequality, we want $\lambda_\mu > 0$; therefore, we identify $\lambda_\mu = R$ for positive λ_μ. (Note that when $\lambda_\mu = 0$ then $\mathbf{B}_\mu = \mathbf{B}^*_{\mathbf{q_1}}$). Based on these results, we make the following claim:

$$\frac{V^{(q_1)}(\mathbf{B})}{V^{(q_2)}(\mathbf{x})} \leq P(\mathbf{B}) \leq P(\mathbf{B}_\mu),\ \forall \mathbf{B} \notin \mathcal{B}_R \subset \mathcal{N}(\kappa) \text{ for some } \kappa \tag{3.104}$$

where

$$\mathcal{B}_R = \{\mathbf{B} \in \mathbb{R}^5 : ||\mathbf{B} - \mathbf{B}^*_{\mathbf{q_2}}|| \leq R\} \tag{3.105}$$

is the ball of radius R around $\mathbf{B}^*_{\mathbf{q_2}}$. See Supplementary Fig. 3.8. The main points are that the result follows from the triangle inequality and the monotonically decreasing nature of P. To identify R, we need to define the set $\mathcal{B}_R$ such that it is a subset of $\mathcal{N}(\kappa)$. The set $\mathcal{B}_R$ is a subset of $\mathcal{N}$ if:

$$b_l^{(q_2)}||\mathbf{B} - \mathbf{B}^*_{\mathbf{q_2}}||_l^2 + \frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}} b_{nl}^{(q_2)}||\mathbf{B} - \mathbf{B}^*_{\mathbf{q_2}}||_{nl}^2 < \kappa_l + \frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}}\kappa_{nl} \tag{3.106}$$

and consequently if:

$$b_l^{(q_2)}||\mathbf{B} - \mathbf{B}^*_{\mathbf{q_2}}||^2 < \kappa_l + \frac{a_l^{(q_2)}}{a_{nl}^{(q_2)}}\kappa_{nl} = \kappa \tag{3.107}$$

where we have taken the upper bound on the Lyapunov function for q_2. It follows immediately that

$$R = \sqrt{\frac{\kappa}{b_l^{(q_2)}}}. \tag{3.108}$$

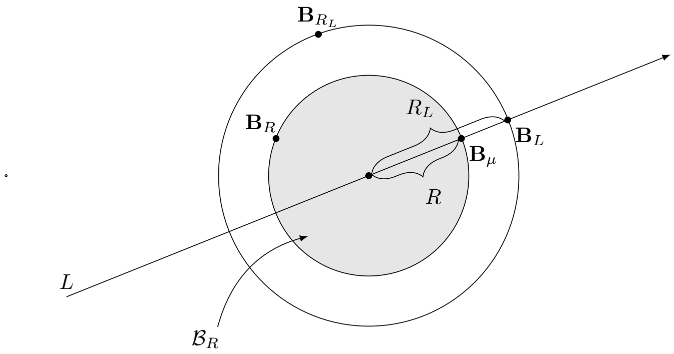
Therefore, we have

$$\mathbf{B}_\mu = \mathbf{B}^*_{\mathbf{q_1}} + \sqrt{\frac{\kappa}{b_l^{(q_2)}}}\frac{(\mathbf{B}^*_{\mathbf{q_1}} - \mathbf{B}^*_{\mathbf{q_2}})}{||\mathbf{B}^*_{\mathbf{q_1}} - \mathbf{B}^*_{\mathbf{q_2}}||}. \tag{3.109}$$

Finally we can compute $\mu(\kappa)$:

$$\begin{aligned} \mu(\kappa) := P(\mathbf{B}_\mu) &= \frac{b_l^{(q_1)}}{a_l^{(q_2)}}\frac{||\mathbf{B}_\mu - \mathbf{B}^*_{\mathbf{q_1}}||^2}{||\mathbf{B}_\mu - \mathbf{B}^*_{\mathbf{q_2}}||^2} && (3.110) \\ &= \frac{b_l^{(q_1}b_l^{(q_2)}}{a_l^{(q_2)}\kappa}\left(||\mathbf{B}^*_{\mathbf{q_2}} - \mathbf{B}^*_{\mathbf{q_1}}|| + \sqrt{\frac{\kappa}{b_l^{(q_2)}}}\right)^2. && (3.111) \end{aligned}$$

It can be seen that the lower bound on dwell time, τ_b, depends on two terms: (1) the distance between the equilibria of two seasons and (2) the radius of the smallest allowable ball centred on $\mathbf{B}^*_{\mathbf{q_2}}$ which is contained in $\mathcal{N}(\kappa)$. By smallest allowable we mean that there is a minimum $\mathbf{B}_{min}$ (which sets $b_l^{(q_2)}$) below which the upper bound on $V^{(q_2)}$ is no longer an upper bound because $V^{(q_2)}$ is becoming arbitrarily large. We find that as $\mathbf{B}^*_{\mathbf{q_1}} \to \mathbf{B}^*_{\mathbf{q_2}}$, τ_b becomes smaller and so solution trajectories in an active season can get close to its equilibrium for smaller dwell times.



$$P(\mathbf{B}_\mu) > P(\mathbf{B}_L) \;\; \forall \;\; R_L > R$$
$$P(\mathbf{B}_\mu) > P(\mathbf{B}_R) \;\; \forall \;\; \mathbf{B}_\mu \neq \mathbf{B}_R$$
$$P(\mathbf{B}_L) > P(\mathbf{B}_{R_L}) \;\; \forall \;\; \mathbf{B}_L \neq \mathbf{B}_{R_L}$$

Figure 3.8 The main points are that the result follows from the triangle inequality and the monotonically decreasing nature of P.

3.7.4 Bimodality of κ in low and peak summers from climate change scenarios

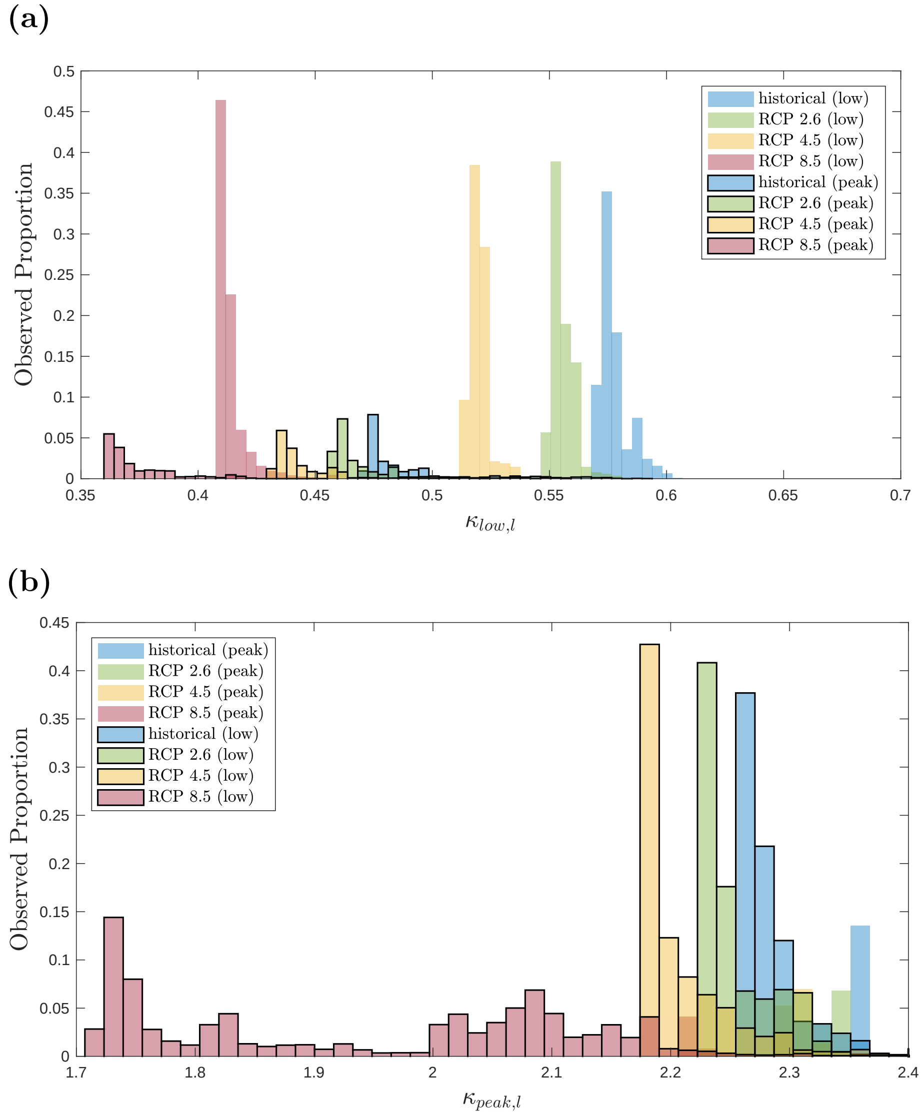
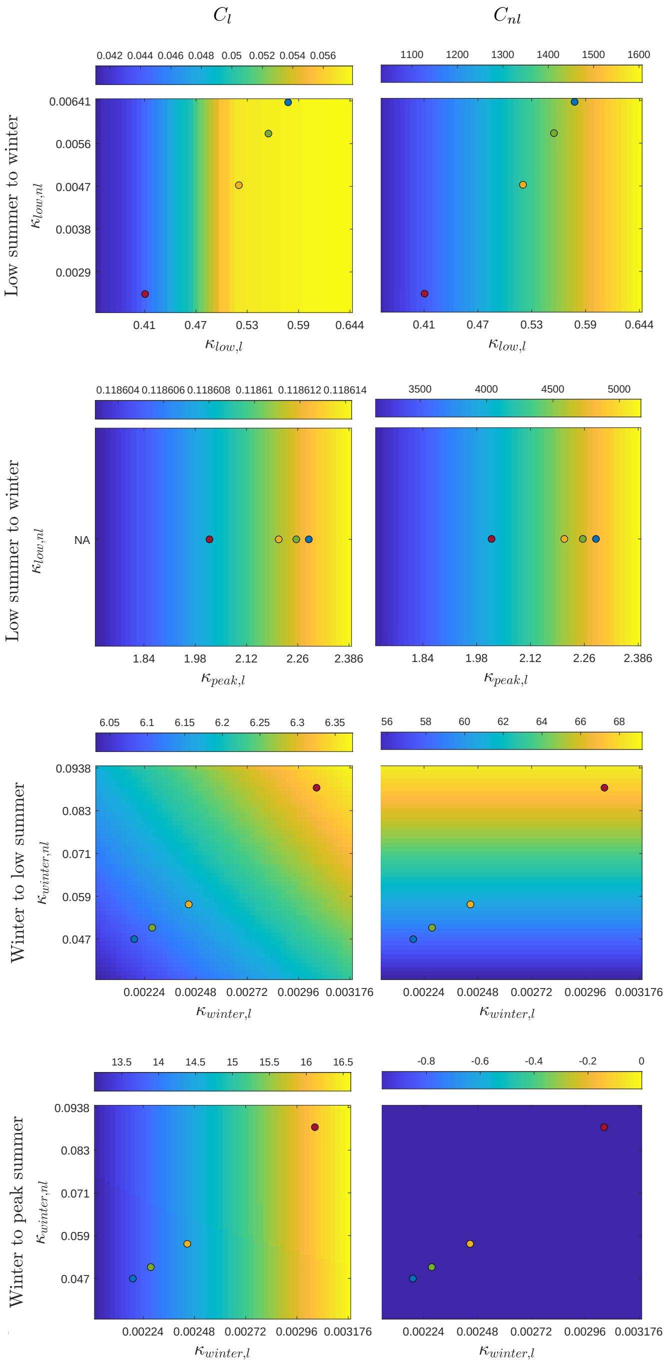


Figure 3.9 Plots of κ for the (a) the low summer and (b) the peak summer distinguishing between whether the previous summer was a crash or a peak. We find in (a) that a peak being the previous summer to a crash generates the minor modes and crashes preceding crashes generate the major modes for κ_{crash}. The opposite is true for κ_{peak} in (b).

3.7.5 Available stock for transitions between seasons

Consider the low summer-to-winter and winter-to-low summer transitions in Fig. 3.10. For low summer-to-winter, C_l^T only has a contribution from the resident species: brown lemmings, collard lemmings, and arctic foxes even though $\kappa_{low,nl}$ exists (from the snowy owl). C_{nl}^T comes from the snowy owls and stays with them across the transition. From winter-to-low sumer, we find that C_l^T has contributions from the resident species through $C_{l,l}^T$ but also from the snow goose through $C_{l,nl}^T$. The snow goose contributes through its latent winter stock to the local stock in a low summer. Again, C_{nl}^T is purely provided by the snowy owl. Peak summer-to-winter and winter-to-peak summer transitions show different relations to available stock. During a peak summer-to-winter transition, C_l^T has a contribution from $C_{l,l}^T$ from the resident species but now there is no contribution from $C_{l,nl}^T$ because $\kappa_{peak,nl}$ does not exist (i.e. there are no non-local species in the peak summer). This is in contrast to a low summer-to-winter partitioning. From winter-to-peak summer, we have that $C_{l,l}^T \gg C_{l,nl}^T$ (from inspection of the data). This means that the available stock in the peak for local species (which are all five of our species) come predominanly from the resident species. Here C_{nl}^T is zero since $C_{nl,l}^T$ and $C_{nl,nl}^T$ are both empty.



Locality set algebra:

$$\sigma_{l,l} = \{bl, cl, af\}$$
$$\sigma_{nl,l} = \{sg\}$$
$$\sigma_{l,nl} = \{\ \}$$
$$\sigma_{nl,nl} = \{so\}$$

Locality set algebra:

$$\sigma_{l,l} = \{bl, cl, af\}$$
$$\sigma_{nl,l} = \{sg, so\}$$
$$\sigma_{l,nl} = \{\ \}$$
$$\sigma_{nl,nl} = \{\ \}$$

Locality set algebra:

$$\sigma_{l,l} = \{bl, cl, af\}$$
$$\sigma_{nl,l} = \{\ \}$$
$$\sigma_{l,nl} = \{sg\}$$
$$\sigma_{nl,nl} = \{so\}$$

Locality set algebra:

$$\sigma_{l,l} = \{bl, cl, af\}$$
$$\sigma_{nl,l} = \{\ \}$$
$$\sigma_{l,nl} = \{sg, so\}$$
$$\sigma_{nl,nl} = \{\ \}$$

Figure 3.10 Heat map for the available stock from transitions between seasons, smaller values are blue and large values are yellow. The locality set algebras are shown on the far right.

Conclusion

C.1 Discussion of thesis objectives

My thesis is an examination of the stability of ecological responses in highly non-equilibrium communities to possible environmental pressures due to climate change. Two types of ecosystems are considered: a tropical planted forest and an Arctic tundra food web. Firstly, I investigate the effect of extreme climate events, in particular drought, on the growth response and mortality of tree communities across a gradient of species richness. I develop a statistical test for the detection of stress response in growth and mortality at the plot-level using effect sizes accounting for the large individual variability across a gradient of species richness. Furthermore, I examine how species richness may buffer communities from tree die-off or loss of resilience. Secondly, I develop a multi-season model for a simple Arctic tundra food web with migrating species (brown lemming-collared lemming-arctic fox-snow goose-snowy owl) in the form of a hybrid dynamical system with multiple equilibria. I construct an algebra which can account for seasonal shifts in biomass due to migrants and develop a measure of resilience for multi-equilibrium systems and study the effect of increasing the length of summer.

The specific objectives of my thesis is to test stabilizing mechanisms. The first is the insurance hypothesis which says that diversity can buffer communities to environmental fluctuations. In my first chapter I show that monocultures exhibit significant effect sizes during drought episodes compared to communities with two-, three-, and five-species whose effect sizes were nonsignificant. I then find evidence that there may be a diversity effect on loss of resilience or die-off, with monoculture and two-species communities showing signs of spectral reddening. These results suggest that for a tropical planted forest, diversity in the form of species richness may dampen tree communities to instability due to extreme events. The second is the hypothesis that migrants can promote stable trophic interactions by coupling and decoupling from pathways at different times depending on when they are plentiful or scarce. Predation by snowy owls in the summer is a source of instability driving multi-periodic cycling by crashing brown lemming populations. By decoupling owls in the winter and in summer when the brown lemming density is low, seasonality prevents the owl from completely exploiting available resources. I find that the longer migrants spend coupled to resident dynamics through increasing the summer season length, more time is needed for the the winter resident community to recover to their equilibrium. Furthermore, the further the distance between equilibria in each season the greater the time to recovery; in other words, resilience decreases. The distance between winter and summer equilibria can be pushed further apart by migrants which may be the case for snow geese. Consequently, each of my specific objectives provide evidence for a general mechanism through which biodiversity can give rise to stability; that is, species modify their interactions to compensate for changes in their environment. However, certain types of migrations may serve to amplify destabilizing effects of longer summers.

Generically all communities in ecology are non-equilibrium systems because they involve multiple layers of interactions; interactions between non-equilibrium systems and climate can possibly lead to novel dynamics. Collectively, the objective of my thesis is to explore the possibility that loss of stability is a coherent impact of climate change across, possibly disparate, complex ecological communities. For both tree communities in the tropics and seasonal predator-prey communities in the Arctic, I find evidence for a loss of stability due to patterns of climate change. Two possible mechanisms for stability which may be more generally applied to other communities in the context of climate change are: 1) the "distance" between stable behaviours corresponding to different environmental conditions, and 2) the time spent under a given set of conditions. Climate change can directly impact how much time is spent under a given set of conditions; this mechanism completely depends on the environment. In fact, it is commonly observed in climate models that extreme behaviours will become more normal as climate change progresses and, moreover, that growing periods will be extended. This should lead to a decrease in stability because an ecological system is spending longer time under conditions that are not usual and, thus, the second observed mechanism applies. It may also be the case that a changing climate can modify the "distance" between stable behaviours corresponding to different environmental conditions. In some systems, this overlap of behaviours may decrease, thus being in tension with the second mechanism described above for driving instability. This mechanism depends on biotic-abiotic interactions unlike the first mechanism. These considerations suggest that the interaction between a non-equilibrium system and a changing environment depends on the response of the system. For communities in which the effect of climate is expected to produce even more unusual behaviour, we expect a coherent response in that there should be a decrease in stability. My first and last chapters bear out these ideas in different ways. I find that more frequent extreme wet and dry years lead to a decrease in stability for the monocultures and also that longer summer seasons may mean it takes longer for resident communities to reach its normal winter behaviour. The mechanisms described above tie the two disparate systems together, and provides a link which could encompass a larger variety of ecological communities. The applicability of this argument would have to be confirmed experimentally in many different communities, which is outside the scope of this thesis, but could provide an excellent starting point for further research.

C.2 Contribution of research to scientific knowledge

C.2.1 Contribution to the problem: Does diversity beget stability?

Pimm provided a possible resolution to the diversity-stability debate with the recognition that there are many possible definitions of diversity as well as stability. One pair of definitions may indicate stability while another pair may indicate a negative relationship. I show in my three chapters that the possible pairs to examine diversity-stability relationships are actually much larger than those explored by Pimm. His study focused on definitions which can be applied to systems with an equilibrium. However, both of my studies are of highly complex systems which are non-equilibrium by nature. Entirely new ways to characterize stability are needed thus complicating the diversity-stability debate even further. I also explore what has been referred to as an underappreciated dimension of biodiversity: migration. Migration represents a seasonal shift in biodiversity, extending the idea of a static species richness. These types of temporal variation in biodiversity also adds another layer of complexity to problem of whether diversity begets stability.

C.2.2 Contributions to methodology

In my first chapter, I introduce a method for the detection of stress response using bootstrap hypothesis testing in systems with large individual tree variability which is the case for forest communities. To precisely determine stress response, one would need a parametric method which would require information about tree neighbours, light cover, temperature, soil condition, etc. However, it is difficult if not impossible to have all of this information so nonparametric methods such as bootstrapping must be used. In many forest ecosystems, studies have defined normal (for example, pre-drought conditions) community performance such as productivity through temporal means. However, this definition is the most coarse measure of "normal" functioning to assess stability in forests and likely leads to a mislabelling of what is "normal". It is difficult to localize in time when the return to normality has occurred and, furthermore, a time average should not be expected to capture such behaviour in a non-equilbrium system. Using resamples from bootstrapped data, a more suitable expectation of normal behaviour can be achieved to measure the effects of stress, such as extreme drought. Furthermore, there remains a temporal axis to the resampled data which means that return to normal can be localized to the timing of data sampling.

In my second and third chapters, I introduce a hybrid dynamical system (HDS) as a framework for multi-season models with migration. Although HDS ideas can be found on multiple occasions in the ecological literature, the fundamental concepts which give theory to these systems have not entirely come to fruition. In particular, a Lyapunov function captures essential information about the stability of these systems when they are structured by multiple equilibria. Not only do Lyapunov functions capture stability information, they also be given a precise ecological interpretation; namely, in predator-prey systems they represent how much biomass can be used for consumption. Although, in general, identifying the functional forms of Lyapunov functions is horrendously difficult, I prove that for many predator-prey systems with different dimensionality it is possible to identify coefficients for these functions through a negative definite constraint with (known) interaction coefficients. Furthermore, I develop an algebra, which I call the locality set algebra, which can be used to organize systems with different groups of species interacting at different times. This algebra gives a way to handle the accounting (i.e. of biomass transfer) for seasonal systems which have migrating species coupling and decoupling from communities which is, to the best of my knowledge, absent in community models. Lastly, I construct a measure of resilience which can handle systems with multiple equilibria based on "how close" a system gets to an equilibrium before switching.

C.3 Future research directions

Moving forward, my thesis may help to lay the foundation for future studies investigating stability in a more general sense. Firstly, the tree biodiversity-ecosystem functioning experiment from my first chapter is part of a global collection of tree biodiversity experiments known as TreeDivNet. There are sites encompassing boreal, temperate, Mediterranean, subtropical, and tropical ecosystems. A comparison of diversity-stability relationships across a strong climatic gradient, in the different forest types, and with different measures of diversity (i.e. taxonomical and functional) would be possible using the methodology of my first chapter. Thus far, performing stability analyses in forest biodiversity experiments have been hampered by the relatively short-term data available for some sites owing to the multidecadal timescale of stand development. However, conducting such a collective study in the future may provide new insights about possible ways to maintain forest resilience across ecosystem types.

In my last two chapters, the "plague of parameters" for more complex food web models was brought to light in the construction of models which incorporate seasonality. Although approaches exist (e.g. allometric relationships), there is still a need to explore mathematical methods which can give good estimates for parameters using data which, ideally, is collected from all seasons. In addition to inspiring further investigation into the problem of parameter estimation, another research direction is to add in extra layers to my temporal, food web network to be able to incorporate more realistic predator behaviours; for example, including a spatial layer would allow the inclusion of important spatial scales in predator-prey interactions. Arctic foxes are extremely territorial and, consequently, only have access to certain prey at any given time. Also, snowy owls may be able to couple different communities of lemmings thereby providing a means through which lemming population cycles can synchronize throughout the Arctic. More generally, putting seasonal dynamics on metaweb networks constructed from mechanistic models may help us to realize a General Ecosystem Model (GEM) for the Arctic as a whole. Such GEMs may help us understand macro-ecological processes from underlying mechanisms and, therefore, would allow us to make better predictions about the impact that climate change will have on the stability of communities.