SPECIES COLONIZATION AND EXTINCTION PROCESSES IN AN ISLAND BIRD COMMUNITY

by

Kate Marie Johnson

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Abstract

Species invasion and range shifts are widely reported and facilitate novel interactions among potential competitors in plant and animal communities worldwide. However, predicting which novel interactions will result in the extirpation of subordinate competitors is challenging. Coexistence versus extinction as alternative outcomes of competition between resident and colonizing species may arise due to (1) variation in interaction strength, (2) change in other demographic drivers more influential than those linked to competition, or (3) differences in the extent to which resources are equitably partitioned between competitors, which may in turn depend on the spatial scale examined. To date, however, empirical studies suggest these factors rarely align to cause the competitive exclusion of native species. I used a combination of field experiments and demographic analyses to test the hypothesis that colonizing fox sparrows (*Passerella iliaca*) have caused the 0.6% per year decline of a song sparrow (*Melospiza melodia*) population resident on Mandarte Island, BC, Canada. Several lines of evidence indicate that interspecific competition for winter food has: a) reduced survival in juvenile song sparrows after colonization by fox sparrows in 1975, b) led to an inverse relationship between juvenile song sparrow survival and fox sparrow population size, c) excluded song sparrows from high-quality foraging sites in winter via consistent behavioural dominance by fox sparrows and complete overlap of fox and song sparrow preference for local seeds, despite d) no evidence of competition for breeding territories or nesting habitat. My results suggest that in the absence of rapid ecological or evolutionary shifts in niche dimension, song sparrows will likely be extirpated from Mandarte Is., thus demonstrating that competitive exclusion of native species can occur when interactions are strong and resources are not easily partitioned.

Preface

This thesis utilized 44 years of data collected by dozens of field teams between 1960 and 2015. I participated in data collection in 2014.

Chapter 2 of this thesis was completed with assistance from Corey Tarwater, Ryan Germain, Richard Schuster, Merle Crombie, Jessica Krippel, Nina Morrell, Nancy Chen and Peter Arcese. I collected data, designed the feeding experiments, conducted statistical analyses and wrote the chapter. Corey Tarwater designed the playback and arena experiments, participated in data collection, and provided statistical advice. Ryan Germain participated in data collection, and provided statistical advice as well as helpful comments on the chapter. Richard Schuster provided input on several statistical analyses. Merle Crombie, Jessica Krippel, Nina Morrell and Nancy Chen assisted with data collection. Peter Arcese provided input and feedback on the design of all of the experiments and statistical analyses, as well as helpful comments and advice on the paper. Chapter 2 will be submitted as a paper with Peter Arcese as a co-author.

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Acknowledgements

To my father, David Johnson,

who is always on my mind and in my heart.

"For in the end, it is all about memory, its sources and its magnitude, and, of course, its

consequences."

Elie Wiesel

Chapter 1: General Introduction

1.1   Interspecific competition and community structure

A wide range of opinions on the influence of competition on animal communities exists in the

ecological literature, but recently, outstanding questions on its role in determining species

abundance and distribution have received renewed interest due to the proliferation of invasive

species in native ecosystems and the need to predict their impacts on biodiversity (Mack et al.

2000). David Lack, an early proponent of the effects of interspecific competition (IC) on species

abundance and communities, suggested that competition occurred transiently, with only its

residual effects being readily observed (Lack 1944). His and other early studies of competition

focused on documenting niche separation between closely related species as evidence that IC

historically impacted the community and caused evolutionary divergence (Lack 1945, 1947,

1971, MacArthur 1958, Hutchinson 1959). Proponents of this view relied on the Gaussian

concept of competitive exclusion, which states that two species with identical ecologies cannot

coexist without the subordinate species being excluded or developing separation in its use of a

limiting resource (Gause 1934). Early studies attempted to test this hypothesis by comparing

species where they occurred in allopatry to those occurring in sympatry in an attempt to isolate

the effects of competition on niche dimension and the density of the focal species (Moreau 1966,

Lack 1971, MacArthur 1972, Diamond 1975). However, these early studies failed to account for

the potential for variation in sites or species history as alternative explanations of species'

differences, leading many authors to question the influence of IC in nature (e.g., Wiens 1977,

Connell 1980).

In the 1970s field experiments became increasingly common as tests for IC and demonstrated that its intensity can be highly variable in space and time, partly explaining the equivocal results of earlier authors (Löhrl 1977, Dhondt and Eyckerman 1980, Minot 1981). However, these early field experiments were often met with skepticism due to their poor perceived quality (Underwood 1986, Hairston 1989, Wiens 1989). More recent experimental tests for IC often span multiple years, are well-replicated and include proper controls (Dhondt 2012). This increase in the quality of experiments can be partly attributed to the establishment in the literature of a number of criteria that are necessary and sufficient to conclude that IC is occurring (Wiens 1989, Newton 1998, Dhondt 2012). In order to consider the existence of IC, intraspecific competition must already be occurring and potential competitors must share a limited resource. In order to prove the existence of IC, resource use by one species must affect its availability for the other species, and that species' abundance/distribution and fitness must be reduced as a result (Dhondt 2012). Of 102 experimental tests for IC in birds, Dhondt (2012) concluded that 71 provided evidence of IC via its effects on the demography and abundance of species with overlapping niches and shared, limited resources. A particularly good example by Cimprich and Grubb (1994) met all of the criteria for documenting IC between the Carolina chickadee (*Poecile carolinensis)* and the tufted titmouse (*Baeolophus bicolor*) in Ohio, USA. The authors noted that after experimentally removing the tufted titmouse, the Carolina chickadee expanded its foraging niche to include resources previously only exploited by the socially dominant congener. Crucially, they demonstrated that induced feather regrowth was greater in chickadees in the removal plots, indicating that tufted titmice reduced the nutritional condition of chickadees by 5–10%, and their fitness decreased as a result. However, Cimprich and Grubb (1994) were unable to document the demographic process that was affected by reduced fitness.

Dhondt (2012) concluded that IC is an important factor in structuring bird communities globally but that more investigation into the influence of IC on demographic processes is needed to clarify mechanisms of change in a species' abundance or distribution. Long-term studies with baseline data that pre-dates the arrival of a competitor can be particularly useful in providing key insights into the influence of IC on population processes.

1.2   Effects of invasive species on native communities

Understanding the role of competition in determining the abundance and distribution of species is becoming especially critical as invasive species proliferate in native ecosystems. Invasive species are a key driver of environmental change globally (Sala et al. 2000, McNeely et al. 2001) and recognized as a primary threat to nearly half of all species listed as endangered or threatened in the United States (Wilcove et al. 1998, Pimentel et al. 2005), including 70% of 98 imperiled bird species (Gurevitch and Padilla 2004). Invasive species can impact native populations through competition, predation, herbivory, parasitism, disease or hybridization (Simberloff 2005). Competition from invasive species is often coupled with rapid change in other factors, which has led some to question the prevalence of competitive exclusion of native species following invasion (Davis 2003, Gurevitch and Padilla 2004). For example, the Tahiti monarch (*Pomarea nigra*) is threatened by competition with the red-vented bulbul (*Pycnonotus cafer*) and common myna (*Acridotheres tristis*), but is also imperiled by habitat loss and predation by rats (BirdLife International 2000). Careful tests of species' response to invasion that de-couple the various drivers of change are needed to clarify the importance of competition with invasives as a threat to native species. Developing our understanding of the causes and consequences of change

in communities will help facilitate more focused and effective approaches to invasive species

management and their mitigation of potential threats (Gurevitch and Padilla 2004).

1.3   Range shifts in native species and the potential for novel interactions

Shifts in the distribution and abundance of native species due to climate and habitat change are

widely documented in numerous taxa (Davis and Shaw 2001, Parmesan 2006, Loarie et al. 2008)

and are creating novel ecosystems world-wide (Hobbs et al. 2006). To date, most work has

focused on the impacts of introduced exotic species on native ecosystems rather than the

potential for range shifts in native species to also alter communities (Sorte et al. 2010). However,

traditional definitions of native species as organisms that originated in an area without human

involvement, and invaders as exotic species whose presence is related to human activity, are

becoming increasingly blurred as both native and invasive species respond to changing climate

and habitat regimes though range shifts (Walther et al. 2009). In some instances, native species

may have similar impacts as exotic invaders in reorganized communities. For example,

migratory Lepidoptera (moths and butterflies) are increasing in southern Britain due to rising

temperatures and are potentially strong competitors with less-mobile resident species (Sparks et

al. 2007). Walther et al (2009) advocate for a more functional approach to invasive species

management whereby invading species are evaluated based on their impact on biodiversity and

ecosystem function rather than their origin.

     Although exotic invaders and range shifting species may function similarly in colonized

communities, there are also fundamental differences between species that enter a community

from an adjacent range and species that are introduced from a dissimilar habitat, and these

differences have ecological and evolutionary implications for species in the colonized

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community (Sorte et al. 2010). For example, range shifting species are predicted to impact a colonized community less because of their shared ecological or evolutionary history with the native population, meaning they are less likely to be disproportionately successful in their new range due to predator or competitor release (Strauss et al. 2006). Species in invaded communities might also have more time to adapt to range shifting species as their rate of spread tends to be slower than that of exotic species, which can proliferate rapidly in novel environments (Sorte et al. 2010). If there is gene flow between adjacent populations, the invaded population is more likely to have adaptive genes that could buffer it from strong interactions with the native colonizer (Strauss et al. 2006). Indeed, several studies have found that invading species impact a community more if they are phylogentically distant from the resident species (Lockwood et al. 2001, Ricciardi and Atkinson 2004, Strauss et al. 2006). However, despite these predictions, Sorte et al. (2010) found that the impacts of range shifts on native communities were often as great as exotic introductions in marine systems world-wide. Similarly, MacLeod et al. (2005) and Pauli et al. (2007) noted that poleward shifts in cetaceans and alpine vascular plants that were tracking suitable habitat sometimes occurred at the expense of cold-adapted species in their new habitat. This discrepancy between predictions and case studies suggests that the effects of range shifting species are likely to vary widely and depend on the traits of the interacting species and their community (Walther et al. 2009). However, additional case studies with detailed supporting data can provide valuable insight into the mechanisms through which adjacent populations might impact native communities through range shifts, and lead to more accurate predictions of the influence of biotic interactions in novel ecosystems.

1.4 Study system: the song sparrows of Mandarte Island

I studied the invasion of fox sparrows (*Passerella iliaca)* on Mandarte Island, BC, to test if IC is a sufficient explanation for an observed long-term decline in the resident song sparrow population that was first studied from 1960–1963 and then continuously since 1975. The song sparrows of Mandarte Is. have been studied in more detail than any other free-living bird population in North America, and the reproductive rate, annual survival and immigration status of *c.* 7000 individuals are precisely known over 39 years of study. My work will contribute to our understanding of competition in dynamic communities by rigorously testing for competition using field experiments and detailed supporting data, and offers a unique opportunity to document the long-term effects of competition on the demographic rates of a focal species. My study is also an excellent example of a native colonizer altering the population dynamics of a focal species in a novel ecosystem resulting from range shifts, and may help predict patterns of species and population persistence in modified landscapes.

1.5 Thesis overview

I use criteria established by Dhondt (2012) to test for IC between fox and song sparrows on Mandarte Is. and rule out alternative sources of competition. I begin by identifying the vital rate that is contributing most to the observed decline in this song sparrow population using a stage-structured life table response experiment. I then examine potential drivers of change in that vital rate in order to determine the relative influence of fox sparrows in explaining the population decline. I test for competition for food, space and nest-sites (Dhondt 2012) using a combination of field experiments and spatial analyses. I assess competition for breeding territory space using playback experiments to determine if song sparrows respond to simulated territorial intrusion by

fox sparrows, and by documenting overlap in territory boundaries. I predict that I will find no evidence of interspecific competition in the breeding season because field observations indicate that there is complete overlap in fox and song sparrow breeding territories and therefore song sparrows should not exhibit aggression during territorial intrusions by fox sparrows. I test for competition for nesting habitat using existing literature on trends in habitat quality and per capita reproductive output over time (Germain and Arcese 2014). I predict that the quality of nesting habitat and reproductive output of song sparrows has not declined as fox sparrows have increased because the frequency of nest parasitism by cowbirds has also decreased over this time, and cowbird parasitism rate is a strongly negative predictor of song sparrow reproductive rate on Mandarte (Smith et al. 2006c). I next assess competition for winter food resources by determining the extent of overlap in song and fox sparrow preference for local seeds, and by documenting behavioural dominance in interspecific contests for food in winter. I predict that fox and song sparrow preference for local seeds overlaps completely based on a similar study by Willson (1971), who documented nearly identical selection of commercial seeds by song and fox sparrows in Illinois, USA. I also expect to confirm an earlier result by Smith et al. (1980), who noted that fox sparrows were dominant to song sparrows in interactions at artificially provisioned feeders. Because juvenile song sparrows are socially subordinate to adult song sparrows (Smith et al. 1980), I expect juvenile song sparrow survival to have declined concomitant with increasing fox sparrows as resources become more scarce for the lowest ranking individuals (Lomnicki 1978). I conclude by making predictions on the future trajectory of this song sparrow population and by identifying characteristics that are generalizable to other invaded systems.

Chapter 2: Species Colonization and Extinction Processes in an Island Bird Community

2.1 Introduction

Invasive species are a key threat to global biodiversity and a major cause of species decline and extinction in island ecosystems (Reaser et al. 2007). High profile invaders such as the brown tree snake (*Boiga irregularis*; Fritts and Rodda 1998) and alien pathogens such as avian malaria (Van Riper et al. 1986) have led to the extirpation of many vertebrates, and other invaders now threaten 43% of 1186 severely imperiled bird species globally (BirdLife International 2000). In addition to alien invaders, native species are shifting in range and abundance, which is resulting in novel interactions between colonizers and historically resident species (Parmesan 2006). However, the outcomes of these novel interactions remain difficult to predict.

Colonizing species have the potential to change community structure and alter native species abundance through competitive, predatory, or mutualistic interactions (Dhondt 2012). However, despite several well-documented cases of niche displacement and competitive exclusion by invaders (Petren and Case 1996, Holway 1999, Byers 2000), empirical and comparative studies suggest that extinctions due to competition are rare in comparison to those via intertrophic interactions such as predation and parasitism (Davis 2003, Sax et al. 2007, Gonzales and Arcese 2008). Differences in the response of native to invading species could arise because the long time-periods over which competitive exclusion occurs are eclipsed by rapid, parallel changes in factors such as habitat quality, or because some native species are able to

adapt to increased competition via ecological or evolutionary shifts in niche or character (Davis 2003, Gurevitch and Padilla 2004, Reaser et al. 2007, Stuart et al. 2014).

Variation in the response of native species to invading controphics (species in the same trophic level) may also be attributed to processes acting at different spatial scales (Davis 2003, Gurevitch and Padilla 2004, Sax et al. 2007). For example, native and invasive species richness is often inversely related at local scales via competition, but positively related at larger scales due to extrinsic factors (e.g. resource availability, disturbance regime) that promote species richness overall (Shea and Chesson 2002, Davies et al. 2005, Bennett et al. 2012). Competition may also be less influential in large, spatially heterogeneous environments if resources are more easily partitioned as a result (Chesson 2000, Davies et al. 2005, Melbourne et al. 2007, MacDougall et al. 2009). In contrast, competition is predicted to intensify on islands and in isolated water bodies to the degree that environments are more homogeneous and trophic complexity is reduced (Davies et al. 2005). However, despite the contention that competitive exclusion by invaders is a key threat to the persistence of native species on islands (Simberloff 2005, Reaser et al. 2007) a dearth of rigorous examples has led some authors to question the magnitude of the invasive threat (e.g., Davis 2003, Gurevitch and Padilla 2004).

I studied the response of a song sparrow (*Melospiza melodia*) population resident on Mandarte Is., BC, to the colonization of fox sparrows (*Passerella iliaca)* to test if interspecific competition is sufficient to explain a long-term decline in song sparrow abundance. Specifically, I used a combination of field experiments and demographic analyses to test for interspecific competition following criteria established by Dhondt (2012). I first identified the demographic vital rate contributing most to the song sparrow decline using 37 years of data. Second, I tested whether competition with fox sparrows for food, territory or nesting habitat could explain

observed changes in the dynamics of this song sparrow population. My results suggest that controphic colonizers have the potential to cause rapid decline in established species by limiting their access to winter food and highlight the potential for colonizing species to drive community composition in relatively simple, insular ecosystems.

2.2 Methods

2.2.1 Study system

Mandarte Island is a *c.* 6-ha islet in the southern Gulf Islands of British Columbia, Canada, on which a resident population of song sparrows was monitored from 1960–1963 and 1975–2014. Song sparrows are a small (*c.* 24 g) passerine that breeds throughout North America in densities typically ranging from 1–9 breeding pairs/ha (Arcese et al. 2002). Song sparrows on Mandarte Island typically lay 2–4 eggs in open-cup nests, raise 1–4 broods annually and defend territories (200–5000 m^2) year round. Territories are mapped annually in March and April and monitored every 2–5 days to document ownership, breeding phenology and success. All nestlings were colour-banded and followed until the end of parental care (24–30 days post-hatch) and their recruitment to, or disappearance from the island. As a consequence, all song sparrows on the island are uniquely marked, and their population size, age structure, reproductive rate, juvenile and adult survival, and immigration status are precisely known (see Smith 2006 for a complete description of methods).

Fox sparrows are approximately 19% larger than song sparrows in mass and linear morphological traits. Like song sparrows, they are territorial, multi-brooded, open-cup nesters (Weckstein et al. 2002). Although fox sparrows are native to the region, they were not recorded on Mandarte Island prior to 1975 (Drent et al. 1964, National Audubon Society 2010). The

number of breeding fox sparrows on Mandarte Island was recorded in 12 years since 1960 and their territories were mapped in 2010 and 2013–2015.

I determined long-term rates of change in the number of song and fox sparrow breeding females using a generalized linear model with a Poisson distribution and log link for fox sparrows, and a linear model with a Gaussian distribution for song sparrows. Year was included as a fixed effect in both models. I also used breakpoint regression and the segmented package (Muggeo 2003) to test for a difference in the rate of change in song sparrow population size before and after colonization by fox sparrows, with the expectation that the decline in song sparrow abundance began after 1975. All statistical analyses (see below) were performed in R 3.1.3 (R Core Team 2015) and time series analyses were checked for temporal autocorrelation with none found.

2.2.2 Demographic rates

I estimated temporal trends in demographic vital rates across the study period to identify the rate that contributed the most to the population decline in song sparrows. I used a stage-structured life table response experiment (LTRE) to determine the contribution of each vital rate to population growth in each year from 1975–2014. To do so, I divided the population into juveniles and adults because other analyses have revealed only small differences in survival and reproductive rate in adults of different ages. Juvenile survival was defined as the fraction of yearling males and females that survived from the end of parental care (day 24 after hatching) to April 30th of the following year. Adult survival was estimated as the fraction of males and females in April 30th of year t that survived to year $t + 1$. Resighting rate on Mandarte Island exceeds 99% (Wilson et al. 2007). Reproductive rate was defined as the mean number of independent young produced per

female annually, excluding birds subject to feeding experiments in 1979 (n = 70), 1985 (n = 87) and 1988 (n = 114) due to the demonstrated effects of supplemental food on reproduction (Arcese and Smith 1988). Juvenile survival was unknown in 1979 and 1980 and reproductive rate unknown in 1980 due to limited sampling effort in 1980. Adult survival was unknown in 1975.

To pursue a life table response experiment, a treatment matrix including juvenile and adult survival and average adult reproductive rate was constructed for each of the 37 years of study. The vital rates in each year were arranged in separate 2 (row) x 2 (column) treatment matrices. The first column of every matrix contained the vital rates of juveniles, and the second column contained the vital rates of adults. The first row of every matrix contained the reproductive rate of juveniles and adults, and the second row contained juvenile and adult survival. Juveniles do not reproduce; therefore the entity in the first row of the first column was always zero. The treatment matrix was compared to a single 2 x 2 reference matrix of average vital rates across all years to determine the contribution (c_{ij}) of each vital rate to population growth in every year following Caswell (pg. 74; 1996),

$$c_{ij} = \left(a_{ij\,ref} - a_{ij\,trt}\right) * s_{ij\,ref} \qquad \text{eqn. 1}$$

where a_{ij} is the (i,j) element of a, the reference (*ref*) or treatment (*trt*) matrix (i.e. juvenile survival, adult survival or adult reproductive rate), and s_{ij} is the sensitivity of the reference matrix, which is the impact of an absolute change in a vital rate on population growth (de Kroon et al. 1986), and was calculated following Caswell (pg. 74; 1996). Therefore, the contribution of a vital rate to population growth was dependent on the magnitude of change in that vital rate

relative to the reference matrix, and the sensitivity of the reference matrix to variation in that vital rate. Analyses were carried out using the popbio package (Stubben and Milligan 2007). I identified trends in vital rate contribution across the study period using a separate linear model with a Gaussian distribution for each vital rate. Year was a numeric variable and was included as a predictor in all models.

Because the LTRE indicated that juvenile survival was the most influential factor affecting population growth over the study period, I next tested for a significant effect ($\alpha \leq 0.05$) of fox sparrow abundance on variation in juvenile song sparrow survival. I used a linear model with a Gaussian distribution and fox sparrow and song sparrow population size as predictors. Song sparrow population size was included as a covariate because it historically explained the majority of variation in juvenile survival (Smith et al. 2006b). Estimates of fox and song sparrow population size and song sparrow juvenile survival were available for 10 years between 1960 and 2014.

2.2.3 Competition for winter food

Dhondt (2012) conducted an extensive review to identify space, nesting habitat and food as common limiting factors in avian communities. I explored the potential for interspecific competition for winter food between fox and song sparrows using a seed preference experiment to determine diet overlap and an arena experiment to assess behavioural dominance in contests over winter food. I also assessed the breadth of winter resources available to song and fox sparrows by determining the type and abundance of seeds in soil samples, because prior evidence indicates that song sparrows feed almost entirely on seeds in winter (Tompa 1963). I collected ~250ml of soil from 15 locations dispersed throughout Mandarte Is. in December 2013. I then

extracted the seeds using a sieve, and determined the volume and identity of all seed types to species.

I next tested for seed preference of fox and song sparrows in March 2015 using seeds of the species that I determined were most common in the soil samples. I collected, cleaned and froze the seeds the prior summer to prevent desiccation. Seeds were separated by type into identical 98cm^3 circular depressions in a 60 (length) x 12 (width) x 3 (height) cm plywood feeder to ensure equal coverage, and their position was rotated among depressions across trials. Feeders were placed on the ground at 6 locations across the island known to host relatively high fox and/or song sparrow abundance but distant from each other to insure independence. At each trial I measured the proportion of time a visiting fox or song sparrow spent feeding on each seed type during 14 visits by song sparrows and 50 by fox sparrows, with 6 different song and 9 different fox sparrows visiting in total. A visit was the duration of time between picking up the first seed at the feeder to when the lower mandible stopped moving after eating the last seed before leaving the feeder. An incident of seed selection began when an individual picked up the first seed in cup x and ended when its lower mandible stopped moving after feeding at cup x. Seed types that were not visited were assigned a feeding duration of 0. I assessed overlap in the proportion of visit time spent at each seed type using a generalized linear mixed model with a quasibinomial distribution and logit link. Each visit to the feeder was numbered and included as a random effect along with the identity of the bird at the feeder. I used the glht function in the "multcomp" package (Hothorn et al. 2008) to assess significance of all pairwise comparisons of species and seed type using Tukey contrasts adjusted for unequal group size (Tukey 1949, Kramer 1956).

I conducted arena experiments in October 2013 to assess species dominance in behavioural interactions over winter food by placing ~250ml of commercial bird seed in piles on

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trails at 5 locations dispersed across the island. Video cameras recorded the patterns of displacement of 19 different fox and song sparrows in 68 interactions. I assessed dominance using a GLMM with a binomial distribution (logit link) and fox and song sparrow identity as random effects. I determined whether the observed displacement rate differed from the null expectation of equal displacement of fox and song sparrows using a log likelihood ratio test. I conducted a separate feeding experiment in March 2015 to determine whether species dominance was consistent across studies. I spaced 20 feeders (15 by 20cm plastic tray attached to a wooden stake) filled with 250ml of commercial birdseed across the island and monitored interactions using video cameras. I assess dominance at the feeders by recording the winner and loser in 31 interactions between 20 different song sparrows and 16 different fox sparrows.

2.2.4   Competition for space

I determined whether fox and song sparrows compete for breeding territories (space) using playback experiments conducted just prior to breeding on April 9-11th, 2014, and by mapping territory overlap during breeding using outlines of fox and song sparrow territories in 2010, 2013 and 2014. Overlap was calculated using ArcMap (ESRI 2011). I used playbacks and a taxidermic mount placed at the center of 27 song sparrow territories to record the closest approach of territorial males and females to mounts during 12-minute trials that began with 2 minutes of pre-trial observation, followed by 5 minutes of playback, and finishing with 5 minutes of observation with the mount covered and playback stopped. To test for species-specific responses by song sparrows, I used fox sparrow, song sparrow and Swainson's thrush (*Catharus ustulatus*) mounts presented in random order, with the latter as a control given its similar size to fox sparrows but status as a migrant. All mounts were displayed in a neutral, perched position. Trials were

conducted throughout the day, but were separated by at least 1 hour on a focal territory and its neighbouring territories. Closest approach to the taxidermic mount was assumed to indicate aggression (Jankowski et al. 2010). Statistical analyses were conducted to assess differences in approach distance between mount types. Closest approach was rounded to the nearest foot and modeled using a GLMM with a negative binomial distribution and log link with the identity of the male territory owner included as a random effect. I included the time of day, whether the focal pair was singing before the playback began, and whether its neighbours also responded to the playback as covariates. "Time of day" was a categorical variable with the finishing time of the trial grouped as morning (before 10am, n = 22), midday (10–1pm, n = 27), afternoon (1–4pm, n = 6) or evening (after 4pm, n = 22). The covariates "focal pair singing before playback" and "neighbours responding to playback" were binomial variables. The focal pair was singing before the playback began in 15 out of 76 trials, and its neighbours responded to the playback in 58 out of 76 trials.

2.2.5   Competition for nesting habitat

I followed Germain and Arcese (2014) to estimate and test for trends in the number of independent song sparrow young produced (nesting habitat quality) in a uniform network of 20 x 20 m grid cells overlaying the island, under the assumption that competition with fox sparrows could lead to declines in nesting habitat quality for song sparrows as fox sparrow density increased. Specifically, I used a linear mixed model with year as a fixed effect and grid cell identity as a random effect, to test whether habitat quality declined over the study period. I also tested for trends in the reproductive rate in song sparrows using a GLMM with a negative binomial distribution and log link. Reproductive rate was measured as the total number of

independent young produced per female annually. Year was included as a fixed effect and individual identity was assessed as a random effect due to repeated measures of individuals between years.

2.3   Results

2.3.1   Population size and demography

The number of breeding female song sparrows declined at 0.6% per annum (β = -0.57 ± 0.15 SE, $t(42)$ = -1.45, p < 0.001, R^2 = 0.26), despite varying widely over 44 years (range = 4–71, mean = 35.5 ± 17.4 SD; figure 1). Conversely, fox sparrow population size increased linearly (range = 1– 30 females, β = 0.06 ± 0.01 SE, $z(10)$ = 9.00, p < 0.001 [log link]; figure 1). Contrary to my expectation, I did not find a difference in the rate of change in song sparrow population size before and after colonization by fox sparrows in 1975 ($t(41)$ = -0.45, p = 0.75), however the strength of this analysis is limited by only 4 years pre-colonization data. Juvenile survival varied widely throughout the study (range = 0.04–0.88, mean = 0.38 ± 0.18 SD, n_{yrs} = 37), as did adult survival (range = 0.07–0.88, mean = 0.59 ± 0.17 SD, n_{yrs} = 38) and reproductive rate, which was measured as the total number of independent young produced per female annually (range = 1.10– 6.90, mean = 3.25 ± 1.32 SD, n_{yrs} = 38).

In contrast, the contribution of adult survival to population growth was approximately zero for the duration of the study (range = -0.39–0.25, mean = 0.01 ± 0.20, $t(35)$ = 1.29, p = 0.20, R^2 = 0.05; figure 2c), meaning that variation in adult survival had little influence on population growth. The contribution of reproductive rate also did not differ significantly from zero throughout the study (range = -0.32–0.19, mean = 0.01 ± 0.10 SD, $t(35)$ = -1.29, p = 0.21, R^2 = 0.05; figure 2b), although it tended to contribute positively to population growth near the

end of the study. Conversely, juvenile survival contributed most to population growth in 21 of 37 years, and its contribution also declined dramatically (range = -0.63–0.61, mean = -0.03 ± 0.28, β = -0.01 ± 0.004 SE, $t(35)$ = -3.37, p = 0.002, R^2 = 0.25; figure 2a), meaning that it increasingly drove population growth downward. Juvenile survival was the only factor that differed significantly from zero throughout the study ($t(35)$ = 3.37, p = 0.002), and it was also a strong negative contributer in the latter half of the study, indicating that it was the only demographic rate able to drive the observed decline in song sparrow abundance.

The fraction of juvenile song sparrows surviving overwinter declined dramatically as the population size of fox sparrows increased over the study period. The model predicted a 39% decline in juvenile song sparrow survival from 0.38 ± 0.05 SE in 1960 to 0.23 ± 0.06 SE in 2014 as the fox sparrow population increased from 0 to 30 females (figure 3). Juvenile song sparrow survival was inversely related to the population size of fox sparrows (β = -0.009, ± 0.003 SE, $t(7)$ = -2.51, p = 0.04, R^2 = 0.48), but not related to song sparrow population size ($t(7)$ = -1.31, p = 0.23), indicating that song sparrow abundance is no longer a good predictor of juvenile survival.

2.3.2   Competition for winter food

The combined soil samples were comprised of 64% blackberry (*Rubus armeniacus*) seeds, 17% Oregon grape (*Mahonia aquifolium*) and cherry (*Prunus emarginata*) seeds combined, and 8% of both Nootka rose (*Rosa nootkensis*) and elderberry (*Sambucus racemosa)* seeds. Three other seed types were identified but combined they comprised less than 3% of the total volume of seeds, suggesting that the resource base in winter is very narrow for granivorous species like song and fox sparrows. My results parallel vegetation cover on the island with the exception of grape and cherry plants, which are not present on Mandarte Is., and snowberry (*Symphoricarpos*

albus), which was not found in the soil samples but is very locally abundant. Because Oregon

grape and cherry seeds are likely inedible for song and fox sparrows due to their size (~1.5x

larger than all other seed types), I used blackberry, Nootka rose, elderberry and snowberry seeds

to test for seed preference. I found complete overlap in the seed preference of fox and song

sparrows (figure 4). The proportion of time spent feeding on each seed type did not differ

between species (blackberry: $z(59) = -0.81$, p = 1.0, elderberry: $z(59) = -0.19$, p = 1.0, rose:

$z(59) = -0.37$, p = 1.0, snowberry: $z(59) = -0.18$, p = 1.0).

Song sparrows were displaced from winter food by fox sparrows in 91% of 68 contests

($X^2 = 25.6$, df = 1, p < 0.001) during the arena experiment, with the losing song sparrows

remaining in arenas after only 18% of interactions. In a separate feeding experiment, song

sparrows were displaced in 100% of 31 contests with fox sparrows at the feeders, indicating

strong and consistent behavioural dominance by fox sparrows.

2.3.3   Competition for space

There was complete overlap in fox and song sparrow breeding territories in 2010, 2013 and 2014

(figure 5), indicating that neither species defended exclusive access to space. Song sparrows

came closer to the conspecific mount than they did to the fox sparrow or control (Swainson's

thrush) ($t(41) = -7.83$, p < 0.001 and $t(41) = -8.28$, p < 0.001), and there was no difference in

approach distance to the fox sparrow and Swainson's thrush ($t(41) = -0.82$, p = 0.42) during

playback experiments (figure 6). Closest approach to taxidermic mounts ranged from 13–82 ft

for male and female song sparrows (mean = 35.6 ft ±16.3 SD, n_{obs} = 76). Song sparrows do not

discern between territorial intrusions by fox sparrows and a non-competitor control species

during the breeding season, indicating that song and fox sparrows are not competing for territory space.

2.3.4 Competition for nesting habitat

I found no change in the quality of nesting habitat over time ($t(2671) = -1.29$, p = 0.20), and the number of independent young per female has increased since 1975 ($\beta = 0.014$, SE = 0.002, $t(643) = 6.63$, p < 0.001, $N_{yrs} = 38$ [log link]). Reproductive rate and the quality of nesting habitat did not decline over time as expected if fox and song sparrows were competing for nesting habitat. Personal observations confirm that fox sparrows tend to nest in dense, high-foliage vegetation, while song sparrows prefer the shrub edge.

2.4 Discussion

Since 1960, song sparrows have declined 0.6% per year as fox sparrows have increased linearly to now outnumber song sparrows. Juvenile song sparrow survival contributed more to song sparrow population growth than adult survival and reproductive rate for the majority of the study, and juvenile survival was also the only vital rate that contributed negatively to population growth, indicating that the observed decline in song sparrow abundance was driven by decreased juvenile survival. I found a significant negative correlation between juvenile song sparrow survival and fox sparrow population size as expected if competition with fox sparrows were causing the decline in this song sparrow population. I assessed the potential for competition over food, space and nest-sites following Dhondt (2012). Territory maps indicated nearly complete overlap of fox and song sparrow breeding territories, and mount presentations revealed no response of song sparrows to simulated fox sparrow intrusions. The quality of song sparrow

nesting habitat did not change over time, and the reproductive rate in song sparrows increased. In contrast, prior results show that adult and juvenile survival is limited by winter food in most years, and I found complete overlap in song and fox sparrow preference for local seeds. In addition, winter arena experiments showed that song sparrows were consistently displaced by fox sparrows in contests over shared resources, suggesting competition for winter food.

Dhondt (2012) outlined several criteria as preconditions for demonstrating a role of interspecific competition in structuring avian communities. In order to consider the existence of interspecific competition, intraspecific competition must already be occurring and potential competitors must share a limited resource. In order to prove the existence of interspecific competition, resource use by one species must affect its availability for the other species, and that species' abundance/distribution and fitness must be reduced as a result (Dhondt 2012). I used these criteria to test if interspecific competition explained the long-term decline of song sparrows following the colonization of Mandarte Island by fox sparrows in 1975. I assessed competition for territory space and nesting habitat using playback experiments to test for the presence of interspecific territoriality during the breeding period, and I identified trends in site-specific reproduction to test if the quality of song sparrow nesting habitat quality declined as fox sparrow numbers increased. Territory maps indicate that both song and fox sparrows exhibit intraspecific territoriality in the breeding season (Figure 5). Thus, if interspecific competition for breeding space occurs, I predict each species to defend territories against breeding pairs of the other species as well as conspecifics. In contrast, I found that song sparrows did not respond to simulated territorial intrusions by fox sparrows and that song and fox sparrow breeding territories overlapped completely, failing to support the hypothesis for interspecific competition for breeding territory space. I further expected that fox and song sparrows might compete for

nesting habitat at finer scales than I was able to measure, but that as the competitively dominant species increased, the subordinate species would more frequently nest in lower quality habitat and display declines in per capita and site-specific reproductive output as a consequence. However, I found no evidence of declines in nesting habitat quality in song sparrows over time and, in contrast to my prediction, I observed a significant increase in per capita reproductive rate, indicating an absence of interspecific competition for nesting habitat.

In contrast to finding no evidence for interspecific competition during the breeding period, I conducted experiments for seed preference and interspecific dominance at artificially provisioned feeders in winter that provided strong support for the presence of interspecific competition for winter food, and the competitive dominance of fox over song sparrows. Specifically, I documented complete overlap of fox and song sparrow preference for local seeds, confirming Willson's (1971) earlier finding of strong niche overlap of fox and song sparrows in Illinois, U.S.A. In addition, I demonstrated consistent dominance of fox sparrows in interactions over winter food, indicating that fox sparrows can limit song sparrow access to food resources at the time of year when song sparrow mortality is highest due to strong intraspecific competition for food (Arcese 1989, Arcese et al. 1992). I thus confirmed Dhondt's (2012) requirement that potential competitors share a limiting resource over which intraspecific competition already occurs, and determined that resource use by fox sparrows affects its availability for song sparrows through interference competition.

Lomnicki (1978) predicted that increased resource scarcity should result in more pronounced dominance hierarchies, leading to unequal partitioning of resources and decreased survival of the lowest-ranked individuals. Prior observations at winter feeding sites indicate that juvenile song sparrows are subordinate to adults in behavioural interactions (Smith et al. 1980),

and as expected, subordinate song sparrows experience lower winter survival in years of severe resource limitation (Arcese and Smith 1985, Smith et al. 2006a). Decreased juvenile song sparrow survival coincident with increasing fox sparrows is consistent with the prediction that fox sparrows limit juvenile song sparrows' access to resources and intensify competition for winter food. Indeed, I found a significant inverse relationship between the survival of juvenile song sparrows and the population size of fox sparrows. My observations are therefore consistent with Dhondt's (2012) final requirement that song sparrow abundance and fitness declined as resource use by fox sparrows increased. Because overwinter juvenile survival contributed most to population growth and Dhondt's (2012) criteria for proving the existence of interspecific competition are satisfied, I conclude that interspecific competition for winter food is very likely causing the song sparrow population decline.

My results are also similar to several other studies that document an increased role of food limitation following the introduction of a closely related competitor. Interspecific competition between resident and colonizing ground finch species on Daphne Major, Galapagos, is a particularly well-known example. In this case, a drought-mediated drop in seed abundance caused these species to compete intensely for food and diverge in bill size (Grant and Grant 2006). Similarly, Stuart et al. (2014) documented rapid evolution in perch height and morphology in a native species of lizard following the invasion of a congener with overlapping diet and habitat requirements. Jankowski et al. (2010) provide strong evidence that spatial segregation in habitat use by closely related bird species also occurs along elevational gradients in which distributional boundaries are reinforced by interference competition. Given strong interspecific competition for winter food, the above results predict that song and fox sparrows

may also diverge in morphological traits linked to feeding and/or in foraging habitat, with diet overlap reduced as a result.

However, competitive exclusion of song sparrows by fox sparrows may be the more likely outcome of interspecific competition on Mandarte Island, because persistence requires that there is sufficient heterogeneity in habitat for niche separation to occur, and sufficient time for character displacement to evolve. Soils samples indicated that niche breadth on Mandarte Island is probably very narrow for song and fox sparrows, which may preclude sufficient ecological differentiation in niche breadth between these species to allow coexistence. Therefore, even in the event of rapid character displacement, adaptation could be flooded by immigration from populations that are not adapted to fox sparrow presence. Christmas Bird Count surveys indicate that fox sparrows are increasing regionally (National Audubon Society 2010), meaning that spatial segregation of habitat use in winter might be expected on other islands with a broader range of available feeding niches. It is unlikely that song sparrows are forced to compete as intensely on neighbouring islands as they do on Mandarte Is, because the surrounding islands are larger and have more spatially heterogeneous environments, meaning that immigrants are likely to dilute local adaptation and prevent niche displacement that reduces the potential for interspecific competition. Therefore, I predict that the song sparrow population will continue to decrease and the probability of extinction will increase exponentially (Arcese and Marr 2006).

There are several alternate explanations for the decline in song sparrow abundance, and although many are less plausible than interspecific competition with fox sparrows, others require further investigation. One such explanation is increased brood parasitism by cowbirds (*Molothrus ater*), which Jewell and Arcese (2008) predicted would result in long-term declines of song sparrows regionally. However, although cowbirds were historically common on

Mandarte Is., they parasitized nests only once in the last 15 years. In addition, Smith et al. (2006a) found no effect of cowbird parasitism on the survival of juveniles, indicating that cowbirds are not a sufficient explanation for the decline in this song sparrow population. Another possible explanation is that tonic changes in climate have reduced the carrying capacity of song sparrows on Mandarte Is. Indeed, previous fluctuations in song sparrow population size were mainly due to population crashes precipitated by cold winter weather (Arcese et al. 1992, Keller et al. 1994, Smith et al. 2006b). However, future population crashes are now unlikely due to climate amelioration (Arcese and Norris unpubl. results), meaning the observed trends in song sparrow population size are in contrast to expectations if severe winter weather were still the primary driver of population growth. In addition, the occurrence of dramatic reductions in population size at the beginning of the study might have contributed to my inability to detect a change in the rate of song sparrow decline after colonization by fox sparrows. Smith et al. (2006c) noted that shrub cover on Mandarte Is. decreased by 7% between 1986 and 2006, and suggested that reduced cover from trees and shrubs could result in increased predation, disease or food shortage for song sparrows. However, sustained increases in predation or disease that match the trends in song sparrow population size were not documented, making these unlikely explanations. In addition, I would not expect fox sparrow population size to increase if vegetation change were resulting in decreased food resources. However, although I documented complete overlap in the seed preference of fox and song sparrows, it is possible that their realized niche differs, and that changes in food resources have benefited fox sparrows but not song sparrows. Perhaps a more likely explanation is that competition with fox sparrows is exacerbating an increase in food limitation due to vegetation change, and that both of these factors are driving the decline in song sparrow abundance. These possibilities would be best

investigated by removing all fox sparrows from Mandarte Is. to determine whether juvenile survival increases to the levels before fox sparrow invasion.

Competitive exclusion by colonizing species is often considered less threatening to native species than change in factors such as habitat and climate (Davis 2003, Gurevitch and Padilla 2004). However, I expect that novel interactions between closely related or morphologically similar species will arise increasingly often due to climate-related shifts in species ranges (Parmesan 2006). Interspecific competition tends to cause relatively slower rates of change than these other factors, making it difficult to test rigorously. My study demonstrates that interspecific competition as a consequence of species colonization events can drive change in community structure, and that biotic interactions may increase in importance as causes of community change as abiotic factors continue to reshuffle communities.

2.5   Conclusion

My results offer a plausible example of competitive exclusion by a colonizing species linked to food limitation, and are in contrast to examples indicating that exotic invasions rarely result in the extirpation of native species. However, the colonization of Mandarte Island by fox sparrows suggests that when competitive interactions are strong and niches are narrow, competitive exclusion becomes more likely. Such conditions are particularly likely to occur in island ecosystems, which also support a high fraction of the world's endemic species and thus contribute fundamentally to global biodiversity. The potential for competition between colonizing and native species to threaten to global biodiversity should therefore not be understated.
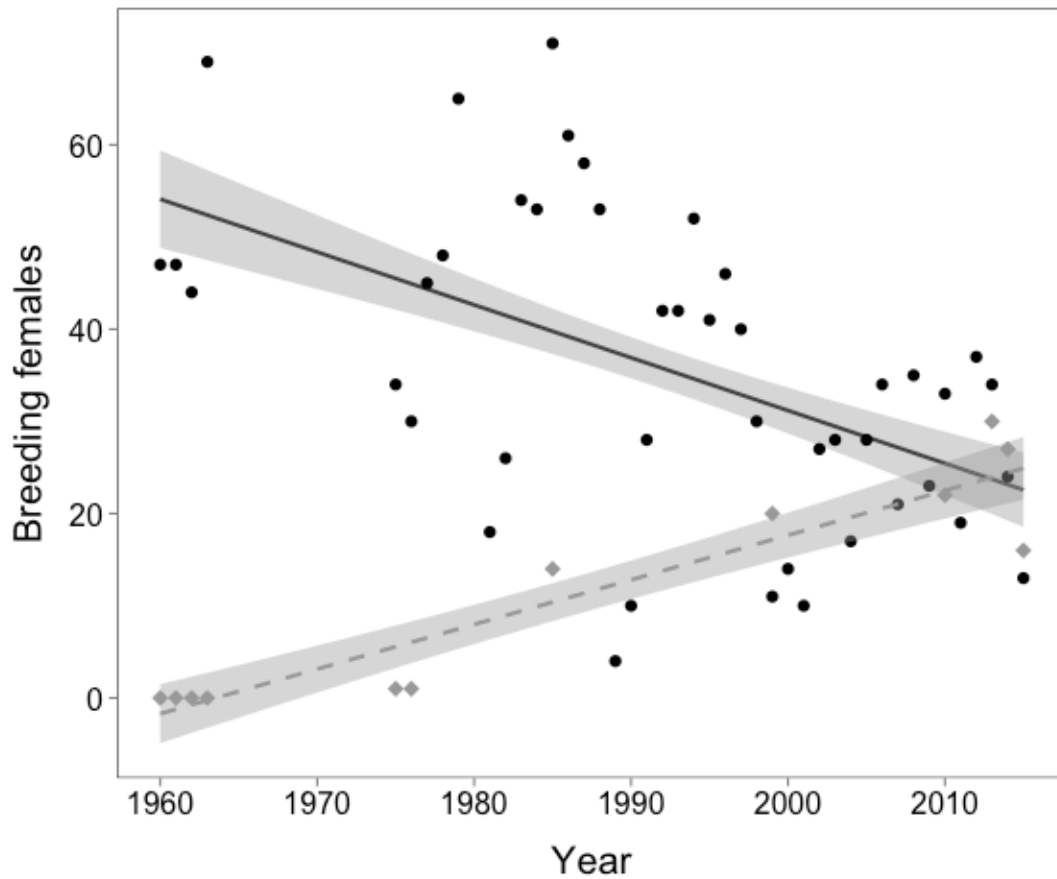
Figure 1 Number of breeding female song sparrows in 44 years from 1960–63 and 1975–2015 (black circles) and fox sparrow breeding females in 12 years from 1960–2015 (grey diamonds). Song sparrow population size has declined significantly over the study period while fox sparrow population size has increased linearly. Shaded areas represent predicted values ± 1 SE.
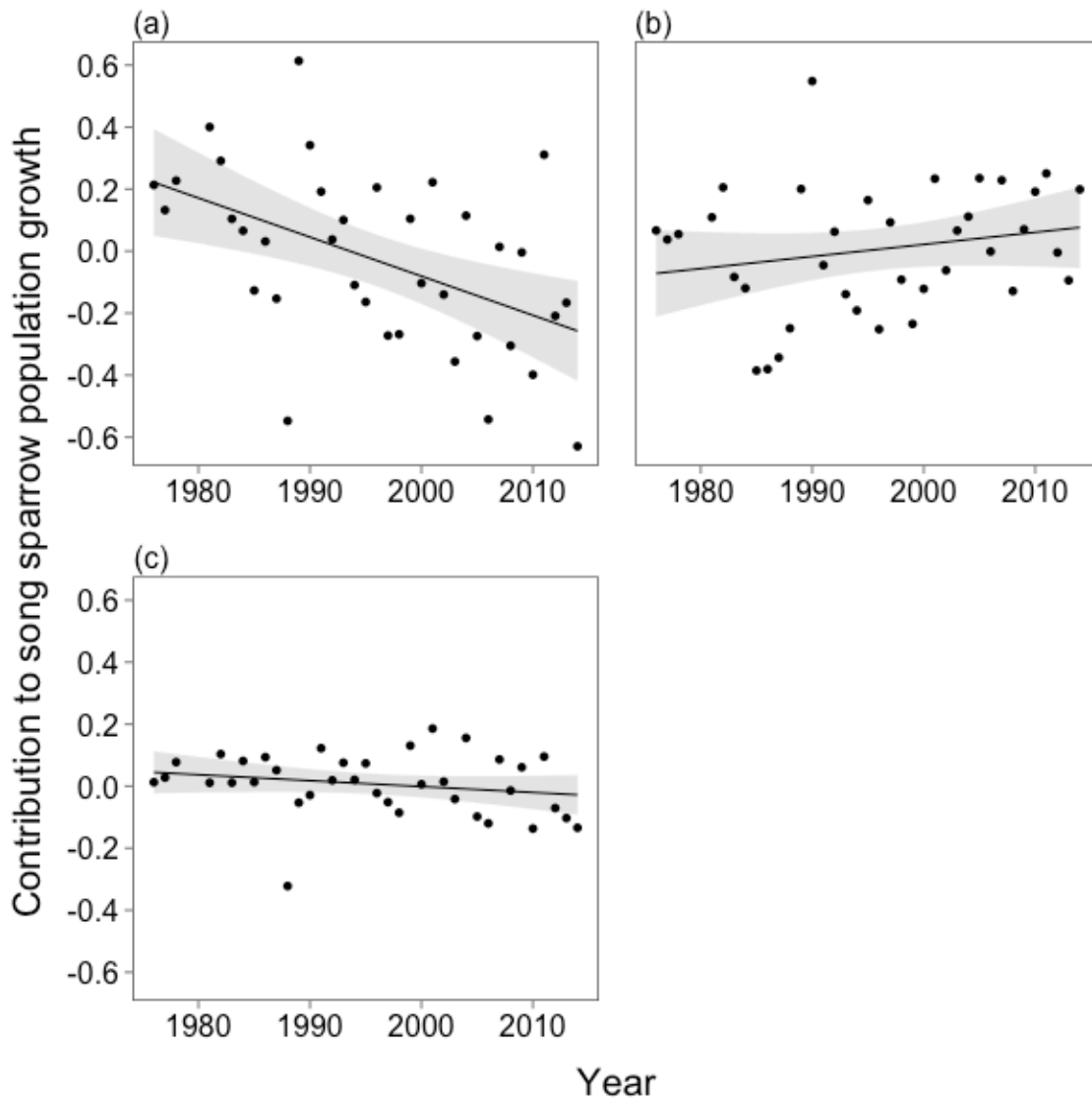
Figure 2 Contributions of (a) juvenile survival, (b) adult reproductive rate and (c) adult survival to song sparrow population growth from 1975–2014, derived from a stage-structured life table response experiment (see Methods). The contribution of juvenile survival changed significantly over time, but reproductive rate and adult survival remained approximately zero, indicating that the observed decline in song sparrows is best explained by the decrease in juvenile survival. The shaded areas around the line indicate predicted values ± 1 SE.

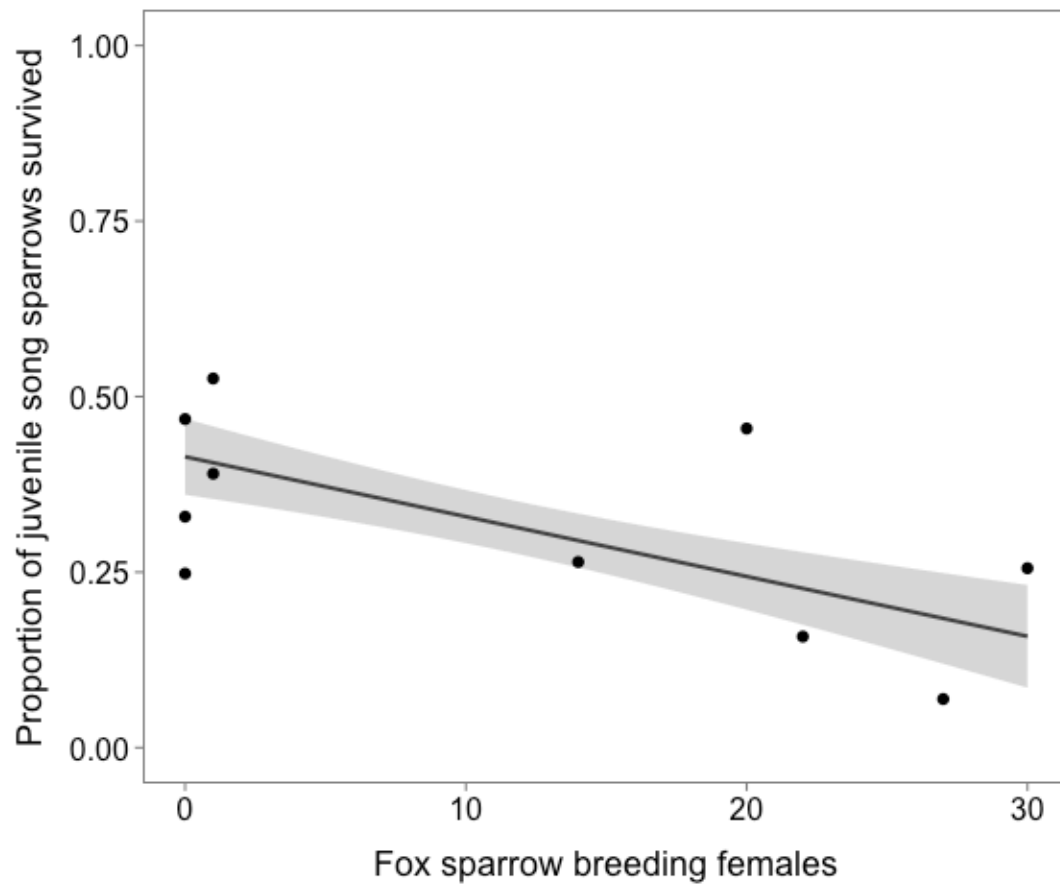**Figure 3** Expected juvenile song sparrow survival declined as the number of fox sparrow breeding females increased. The shaded areas around the line indicate predicted values ± 1 SE. The black circles are observed juvenile song sparrow survival in each study year for which fox sparrow population size was known (N_{yrs} = 10).
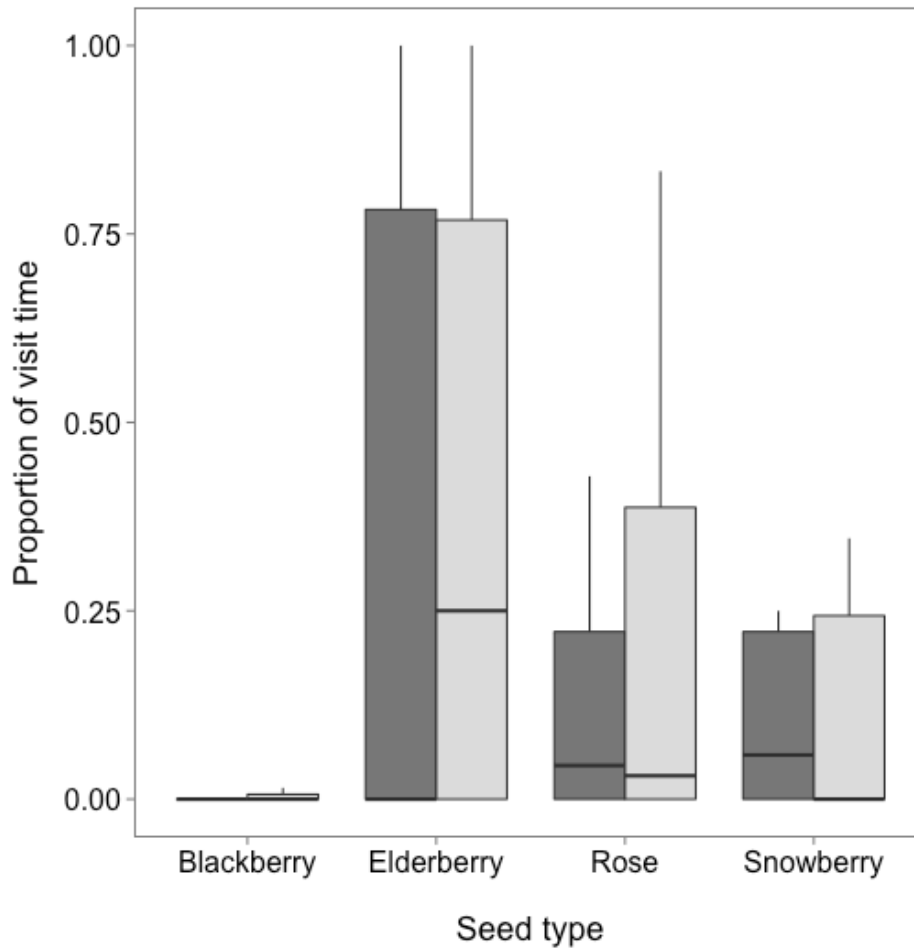
Figure 4 Proportion of time song (dark) and fox (light) sparrows fed on each seed type during feeder visits (see Methods). Seeds were presented by type in identical circular depressions in plywood feeders dispersed across Mandarte Island. Fox and song sparrow seed preference overlapped completely. Whiskers represent approximate 95% confidence intervals around the median (solid line), and the box spans the lower and upper quartiles (25%–75%).
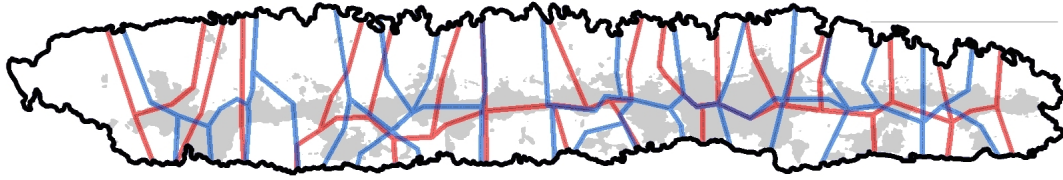
Figure 5 Song (red) and fox (blue) sparrow territory outlines in late April 2014, indicating that song and fox sparrow territories overlapped almost completely.
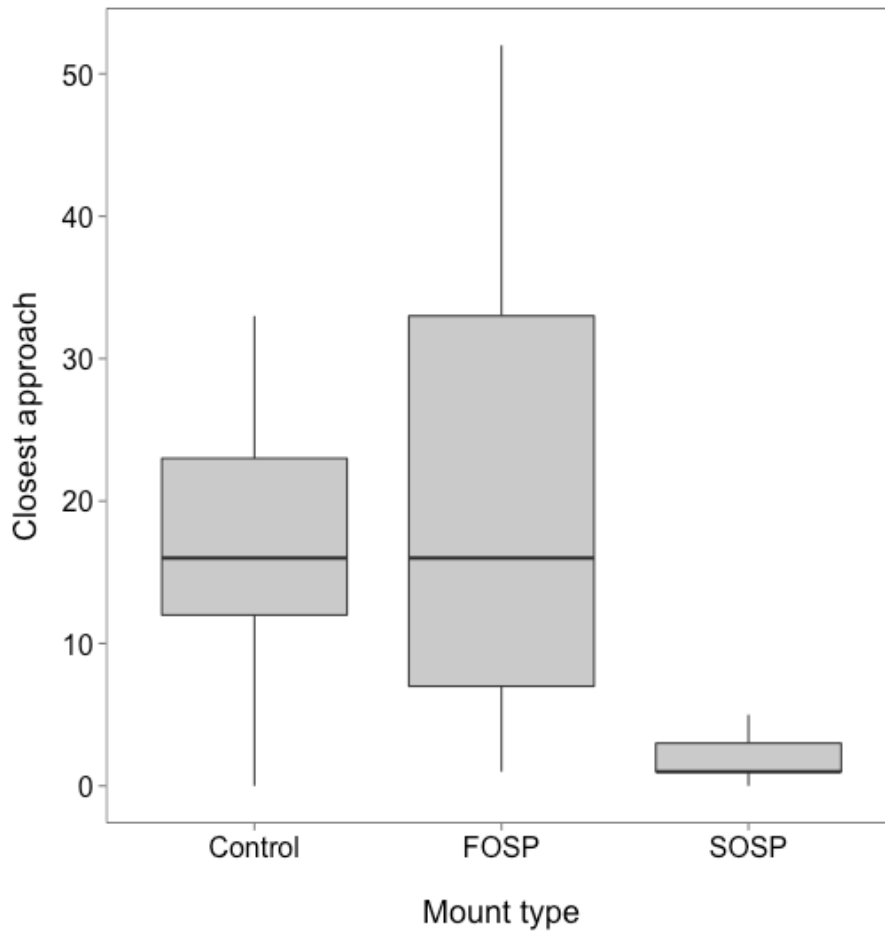
Figure 6 Closest approach by territorial male and female song sparrows to taxidermic mounts presented at the center of song sparrow territories during playback trials. Song sparrows (SOSP) came closer to the conspecific mount than to the fox sparrow (FOSP) or control (Swainson's thrush) mounts, and there was no difference in song sparrow response to the fox sparrow and control mounts, indicating that song sparrows do not respond to simulated territorial intrusions by fox sparrows. Whiskers represent approximate 95% confidence intervals around the median (solid line), and the box spans the lower and upper quartiles (25%–75%).

Chapter 3: General Conclusion

Global change in habitat and climate are re-organizing communities and generating novel biotic interactions that have the potential to profoundly alter ecosystems world-wide (Hobbs et al. 2006). The role of competition with colonizing species as a primary driver of the abundance and distribution of native species is debated in the literature. Some ecologists suggest that native extinctions are rarely caused by competition with invasives (Davis 2003, Gurevitch and Padilla 2004, Sax et al. 2007), others consider competition with invasive species to be a primary threat to native biodiversity, particularly in isolated systems (Sala et al. 2000, McNeely et al. 2001, Reaser et al. 2007). Moreover, questions related to differences in native species' response to exotic invaders versus native colonizers that are undergoing range shifts as they track changes in climate or habitat are just beginning to be investigated (Sorte et al. 2010). These questions require urgent attention given the rate and magnitude of global change that is already underway, as well as the potential for compounding effects from multiple stressors to impact communities in ways that will be difficult to predict without detailed supporting information from scientific, evidence-based evaluations of invasive species impacts on native communities (Gurevitch and Padilla 2004, Parmesan 2006). Careful tests of native species' response to colonizers with overlapping niche requirements are needed to resolve existing issues on the role of competition as a driver of community change. Long-term studies can provide especially valuable insight into the cumulative consequences of changes in the biotic community for focal species.

3.1 Interspecific competition between fox and song sparrows on Mandarte Island

I addressed all of Dhondt's (2012) criteria for documenting interspecific competition between song sparrows and fox sparrows on Mandarte Island. Existing literature indicated that on Mandarte Is., adult and juvenile song sparrow mortality is highest overwinter when intraspecific competition for food is strongest (Arcese 1989, Arcese et al. 1992). I confirmed my prediction that fox and song sparrow preference for local seeds overlaps completely, and that fox sparrows reduced song sparrow access to resources during feeding experiments due to social dominance. Because juvenile song sparrows are socially subordinate to adult song and all fox sparrows (Smith et al. 1980), the observed decline in juvenile song sparrow survival is consistent with the hypothesis that fox sparrows have intensified competition for winter food and driven the decline in song sparrow abundance. I also confirmed my prediction that song and fox sparrows do not appear to be competing in the breeding season for nesting habitat or territory space. Although I did not directly document the effects of reduced access to resources on the fitness of individual juvenile song sparrows, their fitness must have decreased in order for survival to decrease.

3.2 Broader implications

My test for competition between song sparrows and fox sparrows on Mandarte Island is a well-documented example of a colonizing species correlated with the decline in a native population by decreasing its access to shared resources. Dhondt (2012) noted that very few studies track the effects of interspecific competition on the demographic rates of a focal population, and they therefore lack a mechanistic understanding of how competition causes changes in species abundance. My research attempts to address this gap by documenting some potential effects of competition by a colonizing species on the demographic rates of a focal native species over 39

34

years. My study suggests that interspecific competition can intensify existing modes of population regulation and drive changes in population abundance in systems that are relatively simple because of narrow niche breadth. It implies that native species with expanding ranges can threaten adjacent focal species through interspecific competition.

3.3   Limitations and future directions

Although all of my observations are consistent with the prediction that fox sparrows increase resource limitation for song sparrows via interference competition, I was only able to infer that winter food resources were limited based on patterns of mortality. I am unable to draw a casual link between the observed increase in fox sparrows and the declining song sparrow population without a removal experiment. I attempted to conduct a winter removal experiment to determine whether song sparrows respond to the presence of fox sparrows at artificially provisioned feeders by altering their abundance or distribution. However, I was unable to alter local fox sparrow density with targeted removals at feeders. Removing all fox sparrows from Mandarte Is. and determining whether juvenile survival increases to the levels before fox sparrow invasion is the definitive test for interspecific competition. Based on the current trends in survival (see Chapter 2, figure 3), I expect that if conditions at the beginning of the study were restored by removing all fox sparrows, the proportion of juvenile song sparrows surviving overwinter would nearly double from 0.23 (± 0.06 SE) in the last year of study, to 0.38 (± 0.05 SE) in the first year of study, and the population size of song sparrows would quickly increase as a result. In addition to monitoring changes in juvenile song sparrow survival after removing fox sparrows, measures of body fitness should also be collected from juveniles. Despite high annual variation in survival, future researchers could detect an immediate increase in fitness by assessing differences in the

rate of induced feather regrowth pre and post fox sparrow removal following Cimprich and Grubb (1994). Confirming this prediction would represent strong evidence that competition with fox sparrows for winter food is causing the observed decline in this song sparrow population.

Dhondt (2012) noted that very few studies of interspecific competition tested for reciprocal effects in both potentially competing species, and suggested that competition might be more symmetric than is often assumed. My study was limited by a lack of data on fox sparrow demography, which reduced the level of detail in which I was able to assess the correlation between song and fox sparrow population size, and also precluded a comparison of the relationship between fox sparrow vital rates and song sparrow population size. Contrary to my expectation, I did not find a difference in the rate of change in song sparrow population size before and after colonization by fox sparrows. This result may support alternate hypotheses discussed in Chapter 2, or it could also be due to limited observations of song sparrow population size in the absence of fox sparrows. A removal experiment offers the best chance of excluding alternate explanations for the decline in song sparrow abundance, but questions related to the reciprocal impacts of interspecific competition on fox sparrows will remain to be investigated in other systems.

My current results strongly suggest that fox sparrows limit access by song sparrows to shared food resources via interference competition. However, I did not address the possibility that exploitative competition is also occurring. Fox sparrows might also decrease the abundance of shared resources by preferring and/or being more efficient at handling the most abundant seeds. Soil samples indicate that blackberry (*Rubus armeniacus*) is the most abundant seed type on Mandarte, and fox sparrows spent an average of 5% (± 2 SE) more time feeding on blackberry seeds during seed preference experiments than song sparrows did, suggesting that

song sparrows prefer blackberry seeds less than fox sparrows. Although there was no statistical difference in the proportion of time that song and fox sparrows spent feeding on blackberry, this could be due to the small sample size of the experiment (14 visits by song sparrows and 50 visits by fox sparrows). Future researchers should replicate my seed preference experiment as well as estimate fox and song sparrow handling time of local seed types in order to test whether fox sparrows are more efficient at feeding on blackberry seeds and are thereby indirectly reducing their abundance for song sparrows.

Two other studies documenting increased food limitation following the introduction of a closely-related competitor have also observed the evolution of character displacement as a consequence, resulting in reduced competition for resources (Grant and Grant 2006, Stuart and Losos 2013). Standard morphometric measurements of adult song sparrows were collected in 30 years between 1975 and 2013, and preliminary analysis suggests that song sparrow morphology has changed over this time (Johnson and Arcese, unpubl. results). However, trends in song sparrow morphology also appear to have fluctuated throughout the study period and thus do not clearly support the expectation that song and fox sparrows will diverge in traits linked to feeding in order to reduce competition. One way to determine whether fox sparrows are driving morphological change in song sparrows on Mandarte Island might be to compare the patterns observed on Mandarte to those of immigrants and residents of neighbouring islands in order to determine whether song and fox sparrows are more different in sympatry than in allopatry, as predicted if character displacement were occurring. If further investigation indicates that changes in song sparrow morphology are not related to competition with fox sparrows, my prediction that niche breadth on Mandarte Island is too narrow to support sufficient ecological differentiation to allow coexistence will be supported.

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