The Role of Plant-Bird Interactions in the Invasion of *Juniperus bermudiana* in Hawaii: Integrating Experiments, Behavior, and Models

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Abstract of the Dissertation

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Studies of the factors promoting biological invasions often focus on the effects of invasive species within a single trophic level. However, successful control of an invasive species requires a clear understanding of its interactions with the community, particularly if the continual establishment and expansion of an invasive species is dependent on these interactions. Currently, there is limited knowledge on how the processes that mediate avian seed dispersal can impact the distribution and spread of a exotic plant species, despite the awareness of birds to be the main dispersal agent for many successful plant invasions. This dissertation focuses on the seed dispersal cycle from seed availability to avian seed deposition and attempts to link these processes to the germination and recruitment of an exotic plant, *Juniperus bermudiana* (Bermuda Juniper) in the West Maui Mountains of Maui, Hawaii. Specifically this research conducts: (1) greenhouse and field experiments to determine the effects of environmental heterogeneity on *J. bermudiana* establishment across the study site; (2) behavioral studies to quantify seed disperser effectiveness of *J. bermudiana's* avian foragers; and (3) a computer simulation model to determine which factors can best predict the distribution and spread rate of *J.*

bermudiana on a landscape level. The successful invasion of *J. bermudiana* in Hawaii is not likely to be limited by the abundance of seeds or by the abundance of effective seed dispersers. Instead, it is likely that low germination and seedling survival rates have limited the establishment of *J. bermudiana* in the study site. I have incorporated data from these field experiments and behavioral studies into a spatially explicit, computer simulation model that aims to predict the distribution and spread rate of *J. bermudiana* over time on a landscape level. This model aims to inform restoration and conservation management of the study site and potentially other threatened Hawaiian forests where bird-dispersed invasive plants are present. By integrating field experiments, behavioral studies, and models, this approach can serve as a blueprint for studies of other bird-dispersed invasive plants, and also target future control efforts in the management of this and other invasive plant species.

To Henry and Wai Ching Woo

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PROLOGUE

The number of studies on biological invasions has dramatically increased over time since its emergence as a new discipline marked by Elton's seminal publication in 1958, *Plant and Animal Invasions*. From agricultural-based qualitative studies to more conservation-based research, the focus of research on biological invasions has changed over the years. Since its inception, however, biological invasions have been argued to provide a unique opportunity of studying fundamental ecological processes. Biological invasions are, in a sense, natural experiments that can be used to test theories in population dynamics, community assembly, and ecosystem-level processes across a variety of study systems. I see biological invasion research serving a dual purpose: to answer theoretically-motivated fundamental questions in ecology and to inform practical restoration and conservation applications.

The number of exotic species being introduced to novel habitats has continued to increase at an alarming rate. Furthermore, many exotic species have been documented to impact native fauna and flora negatively (e.g., Heywood 1989, Humphries et al. 1991, Fritts and Rodda 1998). In the U.S., Hawaiian endemics constitute a large percentage of the imperiled flora and fauna threatened by invasive species (Gurevitch and Padilla 2004), yet relatively little is known about the basic biology and ecology of these invaders, particularly in their incipient stages. To date, biological invasion research is biased towards exotic species that have already successfully invaded. Research on exotic species before they become invasive pests, however, is critical in understanding how an introduced species can change population, community and ecosystem-level processes and, in turn, determine whether they will become successful invaders. Implications of this approach can also be potentially more efficient in targeting invasive species control and management.

When first introduced to a novel environment, exotic plant species depend on their interactions with that new environment to be able to invade successfully. In particular, many exotic plants rely on the effective seed dispersal by its foragers to successfully spread in distribution in their new environment. Relatively little is known about how animal-mediated seed dispersal can affect plant invasions despite its clear importance in the spread of many invasive plants around the world. The reason for this lack of knowledge is likely due to the difficulty of linking seed dispersal processes to plant demography studies (Wang and Smith 2002). Understanding the seed dispersal cycle as a continual loop (i.e., from seed availability to seed movements to germination of seedlings to adult recruitment, which then influences the next generation of seed availability and so on; Wang and Smith 2002) will elucidate our knowledge of how animal-mediated seed dispersal can influence vegetation structure.

With birds known to be the main dispersal agent for many exotic species, research on avian seed dispersal in the context of the seed dispersal cycle can serve the dual purpose of understanding how these interactions shape exotic plant distributions while informing invasive species management. The goal of this thesis is to essentially break down the seed dispersal cycle into separate processes to better realize its effects on the role plant-bird interactions have on the invasion success, distribution, and spread of an exotic plant, *Juniperus bermudiana* (Bermuda Juniper) in Maui, Hawaii (Figure 1). To accomplish this goal, I integrated behavioral observations with field experiments to quantify the effect of avian seed dispersal on the establishment and growth of *J. bermudiana* in the West Maui Mountains. Additionally, I developed a conceptual framework for a spatially explicit computer simulation model incorporating my findings in the field to predict which factors are most sensitive to the future distribution and spread of *J. bermudiana*. As a result, this research has implications for both fundamental issues in seed dispersal ecology and its effects on plant community structure as well as in applied ecology by informing invasive species management and control.

There are several characteristics of *J. bermudiana* in the West Maui Mountains of Maui, Hawaii that make it an excellent study system. Introduced to forest reserves in all Hawaiian Islands by 1921 (Little and Skolmen 1989), *J. bermudiana* is known to depend on avian seed dispersal in its home range in Bermuda (D.B. Wingate, *personal communication*) as well as in Hawaii (Woo, *personal observation*). *J. bermudiana* is also known to be invasive on the mid-Atlantic island of St. Helena where it was introduced in the 1930s (Ashmole and Ashmole 2000). Although *J. bermudiana* is not at this point a major invasive pest in the West Maui Mountains, a similar fate could occur in Hawaii. The distribution of *J. bermudiana* in the study site exhibits at least 3 distinct levels of invasion: monotypic stands are present where *J. bermudiana* was first introduced, clumped individuals are present where *J. bermudiana* has now successfully established, and sparse individuals are starting to colonize at the invasion front of the *J. bermudiana* distribution. The distribution of *J. bermudiana* across the landscape and its dependence on avian seed dispersal provides both a rare and ideal opportunity for studying how the different stages of seed dispersal can shape plant distributions. With at least 41% of Hawaii's exotic plants dependent on avian seed dispersal (Staples et al. 2000), this research can also proximately inform other invasive bird-plant systems across the islands.

Research for this thesis was conducted from 2003 to 2006 and incorporates greenhouse, laboratory and field studies. Findings from this research is presented in the next three chapters, each highlighting different stages of the seed dispersal cycle and its implications on the role bird-plant interactions have on the distribution and spread of *J. bermudiana*. To conclude, an epilogue provides a brief overview of the results of this research and how it contributes to the basic biology, ecology and conservation of biological invasions.

More specifically, the first chapter of this dissertation explores how functional behaviors of avian seed dispersers can offer predictions on the invasion success of *J. bermudiana*. That is, how do the functional services of different foragers change seed dispersal effectiveness in terms of forager identity and abundance, foraging behavior, and disperser movements? Results of this study will provide insight as to whether the presence of *J. bermudiana* foragers will likely facilitate its invasion success or whether this system is dispersal limited.

Chapter two continues on to the next stage of the seed dispersal cycle by examining the role avian seed dispersers play on the introduction, colonization and establishment of *J. bermudiana* seedlings in the study site. *J. bermudiana* seed germination and seedling growth after avian seed handling and deposition was deduced by comparing ideal versus realized environments (greenhouse versus field experiments, respectively). The goal of this part of the study was to determine whether *J. bermudiana* was recruitment limited and, if so, discern whether this limitation was due to either the quality of avian seed deposition or from the heterogeneous environment in the study site.

Chapter three incorporates data on avian seed dispersal from chapters two and three with data from the literature on *Juniperus* demography in an attempt to close the seed dispersal cycle. The conceptual framework and beginning stages of a spatially explicit computer simulation model in the context of the seed dispersal loop were developed in hopes of predicting the future distribution and spread of *J. bermudiana* in the study site. By linking seed dispersal studies with estimates of demographic parameters in model simulations, more information can be gained as to what factors of the exotic plant-bird interaction will be most sensitive to the spatial distribution of *J. bermudiana* in the West Maui Mountains.

Lastly, an epilogue provides a brief summary of my research and its contributions to both seed dispersal ecology and invasion biology. With the increasing number of exotic species being introduced globally, studies on nascent invasions can serve the dual purpose of understanding basic population and community dynamics while targeting invasive species control efforts. My approach of integrating behavioral studies, greenhouse and field experiments, and simulation modeling provides a more thorough understanding of how plant-animal interactions can shape vegetation structure. I hope to continue to connect the fields of ecology, invasion biology, and conservation by using this approach as a template for future studies on other plant-bird systems so as to contribute to basic ecological principles while informing invasive species management.

FIGURES

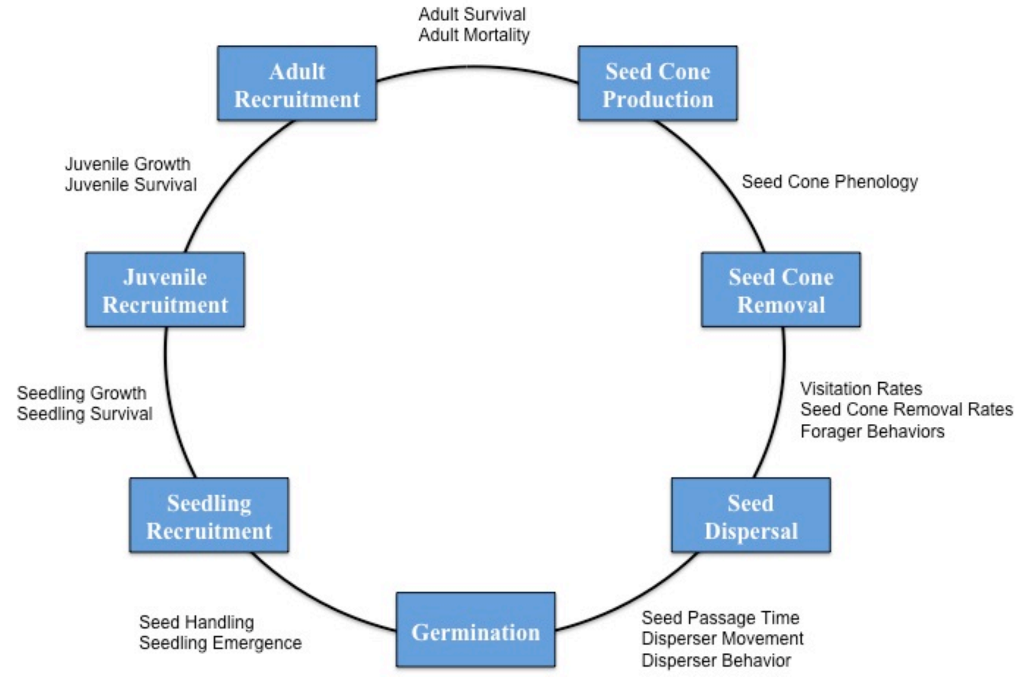

Figure 1. The seed dispersal cycle (adapted by Wang and Smith 2002) in the context of *Juniperus bermudiana*. The different processes of the seed dispersal cycle addressed in this thesis are shown in boxes; data collected for each these processes follow each box along the cycle.

I. Implications of forager behaviors on the seed dispersal cycle: A case study with *Juniperus bermudiana* in Maui, Hawaii

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ABSTRACT

Recent studies have highlighted the importance of grouping foragers by the functional services they provide to exotic plants in order to better understand community structure and overall invasion success. This study focuses on the effects of bird-plant interactions on the effective seed dispersal of an exotic plant, *Juniperus bermudiana*, in Maui, Hawaii in the context of functional forager behaviors. Forager identity and abundance, foraging behaviors, and disperser movements were measured to quantify seed dispersal effectiveness and potential invasion success of *J. bermudiana*. Field studies revealed seed gulpers and seed predators to be the only two functional foragers for *J. bermudiana* seed cones, with seed gulpers being far more abundant than seed predators. Additionally, seed cone removal rates between seed gulpers and seed predators were not significantly different. Further, the low abundance of fairly sedentary foragers compared to the abundant flock-feeding foragers suggests that seeds are likely to be dispersed across the West Maui Mountains of Hawaii. Different movement patterns within the flock-feeding foragers (i.e., *Zosterops japonicus*) reveal different dispersal patterns that may affect seed shadows. Results of this study suggest effective seed dispersal by *J. bermudiana* foragers is not likely limiting its invasion success in the study site.

INTRODUCTION

Animal-mediated seed dispersal is an important fundamental ecological process that contributes to the structure and function of many plant communities (Levin et al. 2003). However, little data exist on the functional role of frugivore dispersers on plant community structure (e.g., Dennis and Westcott 2006), and even fewer have attempted to understand these interactions in the context of biological invasions. Biological invasions provide an unprecedented opportunity for ecological studies (Vitousek et al. 1987), allowing us to measure how the functional services of frugivores can change plant community structure in the presence of an introduced plant species. Further, with birds known to be the main dispersal agent for many exotic plant species, we still have limited knowledge about how they contribute to successful invasions (Gosper et al. 2005). Recent reviews highlight the importance of understanding what functional services frugivores provide for exotic plants and how this knowledge can, in turn, help manage invasions (Gosper et al. 2005, Buckley et al. 2006).

The seed dispersal cycle includes a number of processes that incorporate different animal-plant interactions, including fruit removal, seed handling and disperser movement (Schupp 1993, Wang and Smith 2002). Further examination of these interactions reveals several functional frugivore behaviors (e.g., seed gulpers versus seed predators; relatively sedentary foragers versus flock-feeders) that can ultimately affect the invasion success of an exotic plant. For example, the invasive fate of an exotic plant whose seeds are only handled by seed gulpers (i.e., foragers that swallow whole or parts of a fruit, expose whole seeds to their gut for a certain period, and then either defecate or regurgitate viable seeds) will be very different than the invasive fate of an exotic plant whose seeds are only handled by seed predators (i.e., foragers that lethally damage seeds either during mandibulation or gut passage; Levey 1987, Gosper et al. 2005).

This study attempts to measure how these different functional frugivore behaviors in the seed dispersal cycle can affect seed dispersal effectiveness of an exotic plant. Seed dispersal effectiveness can be determined in both the quantity and quality of seed dispersal. The quantity of seed dispersal describes the number of seeds removed from the parent tree; the quality of seed dispersal describes the successful dissemination of seeds into a site that favors germination and growth of that seed (Herrera and Jordano 1981, Jordano 1992, Schupp 1993). Whether functional frugivore behaviors contribute positively or negatively to seed dispersal effectiveness can ultimately shape plant community structure; thus, understanding these functional behaviors can also lend insight on the potential distribution and spread of an exotic plant.

In particular, this study investigates how forager identity and abundance, foraging behavior and disperser movements affect the quality and quantity of seed dispersal for an exotic plant visited by numerous forager species. Specifically, I ask (1) how can the relative abundances of different forager species contribute to overall seed dispersal effectiveness; (2) how can the functional foraging behaviors of dispersers affect seed dispersal effectiveness; and (3) how can the functional movements of dispersers provide insight into seed dispersal effectiveness? I answer these questions using the invasion of *Juniperus bermudiana* (Bermuda Juniper) in Maui, Hawaii. Endemic to Bermuda and introduced to Hawaii as an ornamental, *J. bermudiana* is known to depend on several different avian seed dispersers in its native range. Preliminary observations showed this dependence to also be true in Hawaii, where several invasive birds were seen to visit *J. bermudiana* adults (Woo, *personal observation*). In Maui, *J. bermudiana* produces copious ripe seed cones (with 2-3 seeds per seed cone) annually from the end of September to December, a period when several different species of avian foragers visit *J. bermudiana* adults.

In this study, I predict that (1) the abundance, species identity and prevalence of *J. bermudiana* foragers will collectively determine which species will have the most impact on the quantity of seed dispersal; (2) the presence of avian seed predators of *J. bermudiana* will lower seed dispersal effectiveness; and (3) the foraging behaviors and movement patterns of *J. bermudiana's* flock-feeders will be an important influence on its distribution and spread rate. By first identifying the potential foragers and then measuring seed dispersal effectiveness in the context of their functional services, I hope to better determine how forager behaviors can predict changes in plant distributions. In addition, describing these functional services in the context of biological invasions further allows us to better predict invasion success of an exotic plant dependent on avian seed dispersal as well as understand the basic ecological processes of plant community structure.

METHODS

Study system and location

J. bermudiana (Cupressaceae) was the dominant endemic tree in Bermuda until a catastrophic introduced scale epidemic killed 95% of the population in the late 1940s and early 1950s (D.B. Wingate, *personal communication*). Records show that as many as 6,500 *J. bermudiana* trees were introduced to forest reserves on all of the Hawaiian Islands by 1921 (Little and Skolmen 1989). *J. bermudiana* is fully naturalized and remains invasive on the mid-Atlantic island of St. Helena where it was introduced in the 1930s (Ashmole and Ashmole 2000). It has been suggested that *J. bermudiana* is dispersed by a number of different bird species. In its home range, *J. bermudiana* is dispersed by *Sturnus vulgaris* (European Starling), *Dumetella carolinensis* (Gray Catbird), and *Sialia sialis* (Eastern Bluebird) (D.B. Wingate, *personal communication*). My initial field observations on Maui, Hawaii revealed two dominant foragers of *J. bermudiana* seed cones: *Zosterops japonicus* (Japanese White-Eye) and *Cardinalis cardinalis* (Northern Cardinal), both which are exotic to the Hawaiian Islands.

Field research was conducted on privately owned land in the West Maui Mountains of Maui, Hawaii. Permission was granted to conduct research in both the Kapunakea Preserve (20° 55’ 30” N, 156° 38’ 13” W), owned by The Nature Conservancy of Hawaii, and in the Pu’u Kukui Watershed (20° 56’ 26” N, 156° 37’ 58” W), owned by Maui Land and Pineapple Company, Honolua Division. This area of West Maui Mountains has several different vegetation zones, ranging from arid scrub at the lowest elevations to very wet rainforests at its highest elevational peak of 1764 meters (Scott et al. 1986). The West Maui Mountains, a volcanic system dating 1.3-1.6 million years old, is also slit by deep amphitheater-headed valleys (Stearns 1966), which result in distinct upward-sloping ridges across the entire mountain range. *J. bermudiana* has formed dense monotypic stands on one of the ridges in the Pu'u Kukui Watershed area since its time of introduction in the early 1930s.

My study focused on three specific ridges, on one of which *J. bermudiana* was first planted (in the Pu'u Kukui Watershed area, hereafter Ridge 1). The ridge leeward (i.e., south) of Ridge 1 (on the Kapunakea Preserve, hereafter Ridge 2) has many well-established *J. bermudiana* adults, while the ridge most leeward of the three ridges (also on the Kapunakea Preserve, hereafter Ridge 3) has fewer than 20 *J. bermudiana* adults. Ridge 3 is on the edge of the *J. bermudiana* distribution, and is therefore considered to be the potential invasion front for this species. The study site for all three ridges extends from 350m at the lowest elevation (bordering pineapple/sugar cane fields) to 700m at the highest elevation (bordering wet high elevational forests). The vegetation zone of most of the study site can be characterized as a mesic low elevational forest, dominated by the native *Metrosideros polymorpha* (Ohi'a lehua) and a variety of exotic plant species, including *Psidium cattleianum* (Strawberry Guava), *Schinus terebinthifolius* (Christmas Berry), *Grevillea robusta* (Silky Oak), and several different *Eucalyptus* species. The study site is also dominated by a variety of invasive bird species; some of which were introduced and established on Maui as early as 1880 (e.g., *Carpodacus mexicanus,* House Finch) and others as late as 1929 (e.g., *Z. japonicus; Cardinalis cardinalis*, Northern Cardinal) (Caum 1933). Due to the prevalence of avian disease transferred by various mosquito populations in the lower elevations (Englund and Preston 2000), most native birds (e.g., *Vestiaria coccinea*, 'I'iwi) are most commonly found only in the higher elevations of the West Maui Mountains and are therefore absent in the study site.

Calculating bird assemblages and abundance with bird point counts

The variable circular-plot method was used to record all bird occurrences in the study site (Reynolds et al. 1980). A total of 27 bird point count locations (10 on Ridge 1, 10 on Ridge 2, 7 on Ridge 3) were placed along three transects (one transect per ridge). Transects ran from lower (approximately 350m) to higher elevations (approximately 700m), with point counts located every 200m. All point counts took place within the first 3 hours of sunrise, but after the dawn choir, and each point count lasted 10 minutes. The

10-minute period was chosen to be long enough to get an accurate record of birds in each point count location, but short enough so that the assumption of an instantaneous count was not seriously violated. Auditory, visual, or combined counts for all bird species were recorded within a radius of 20m from the center of each point count location. Birds that flew over the point count location without stopping were recorded but were not used in any analyses because they were not considered to be utilizing the survey area. All 27 point counts were conducted at the beginning, middle, and end of *J. bermudiana* seed cone maturation (late September, late October and late November, respectively), in both 2004 and 2005 field seasons.

Quantifying forager visitation and seed cone removal rates with focal tree watches

Focal tree watches were conducted to determine the number of visits, visitation lengths and seed cone removal rates of all avian foragers in mature *J. bermudiana* individuals with ripe seed cones. Tree watches occurred throughout the morning until noon, and each watch lasted 60 minutes. Trees with ripe seed cones were randomly chosen on all three ridges, at different elevations. Before the start of each watch, I hid at least 5m away from focal tree and waited at least 5 minutes for equilibration of bird activity in focal tree area. During each tree watch, the following data was recorded on each individual entering and leaving a focal tree: bird species, duration in tree, and seed cone removal rate of *J. bermudiana* seeds (only when clearly visible through binoculars). I completed a total of thirty-eight tree watches (13 on Ridge 1, 24 on Ridge 2 and 1 on Ridge 3) from September to December, in 2004, 2005 and 2006 field seasons.

Understanding seed disperser movements with bird follows

Bird follows were carried out to determine individual bird distances traveled and time spent on each ridge. The goal was to elucidate any patterns in bird movement in the study site, particularly short versus long distance dispersal events. Bird follows occurred throughout the morning until noon. I took data on the following flight and movement patterns of *Z. japonicus*: the total time spent (seconds) in a tree; distance traveled (in meters) to next tree; total time spent (in seconds) in the second tree; distance traveled (in meters) to next tree; and so forth until the individual was lost or had left the ridge. If an individual flew off a ridge, an approximate distance (in meters) was estimated; if an individual flew more than 25m at any one time either up or down in elevation along a ridge, an approximate distance (in meters) was also estimated (individuals that flew more than 25m on a ridge were usually lost during the follow). For any distances less than 25m, a tape measure was used to quantify distances between trees. I also noted any foraging behavior (e.g., seed cone ingestion), possible observer influence on the bird's behavior, and which neighboring ridges an individual flew towards, if applicable. Bird follows in which I influenced bird movements or flight patterns were not used in analyses. All bird follow data was taken during September-November 2006.

Statistical analyses

Calculating bird assemblages and abundance with bird point counts. A nonparametric multivariate analysis approach was used to determine whether bird assemblages differed between year and ridges in the study site. Original bird count data were recalculated with a square root transformation, adding 0.5 to each count to replace the large number of zeros in the data set (Sokal and Rohlf 1995). A resemblance matrix of similarities was calculated with the transformed data set; Bray-Curtis coefficients (i.e., Sorenson distance for quantitative data) were used as the distance measure as recommended for count data (Quinn and Keough 2002, McCune & Grace 2002). A 2-way analysis of similarities (ANOSIM) (Clarke and Green 1988, Clarke 1993, Clarke and Warwick 1994) was used to test whether there were differences in bird assemblages between years and ridges. No interaction effect can be tested with an ANOSIM; only the main effects of years and ridges could be analyzed. Global R values for these analyses can range from -1 to +1, where R=0 indicates that there is random sampling between replicates (no concordance) and R=1 indicates that replicates of a site type are more similar to each other than to any replicates of another site type (concordance). PRIMER 6 (Clarke and Warwick 2001) was used for this analysis.

Quantifying forager visitation and seed cone removal rates with focal tree watches. The number of visits to *J. bermudiana* adults was analyzed using a 2-way analysis of variance (ANOVA) to test whether the number of visits differed between species, between ridges, and if there was an interaction effect between species and ridges. Prior to analyses, data were subjected to a square root transformation, adding 0.5 to each visitation count to replace any zeroes in the data set (Sokal and Rohlf 1995). Since there was only 1 tree watch for Ridge 3, data from that tree watch was omitted in the analysis; only differences in *J. bermudiana* visits between Ridge 1 and Ridge 2 were compared. Transformation of the data fulfilled the assumptions of an ANOVA (i.e., normality of residuals and homogeneity of variances) and analyses were conducted using JMP 5.1.2 (SAS Institute, Inc.).

Seed handling between the main foragers of *J. bermudiana* seed cones differed and could be categorized into two different functional seed handling techniques: seed gulpers and seed predators. For example, *Z. japonicus* was categorized as seed gulpers, where they were consistently seen to ingest whole seed cones during tree watches. *C. cardinalis*, on the other hand, can be considered a seed predator, where their seed crushing behaviors have been documented to leave *Lonicera maackii* seeds inviable after defecation (Bartuszevige and Gorchov 2006). In this study, both *C. cardinalis* and *C. mexicanus* were catergorized as seed predators, as they were consistently seen crushing seed cones and likely destroying *J. bermudiana* seeds and preventing successful germination.

Failure time analysis using a log-rank test was used to compare the visitation duration of *J. bermudiana* foragers. Failure time analysis can be used to detect any differences between treatments or groups in which the time or rate until some event occurs in individual experimental units is measured (Fox 2001). In this analysis, the failure time was defined as the time it took for an individual to leave a *J. bermudiana* focal tree; there were no censored data in this data set as all birds were observed until departure. Data grouped by functional behaviors were used to test whether the distribution of *J. bermudiana* visitation lengths between seed gulpers and seed predators were different. *J. bermudiana* foragers were grouped in this analysis because of the implications of these functional groups for seed handling and dispersal. That is, the longer seed gulpers spend in focal trees, the more likely seed uptake increases; on the other hand, the longer seed predators spend in focal trees, the more seeds are rendered non-viable and not available for effective seed dispersal. Seed gulpers and seed predators were the only two types of seed handling behaviors observed during the tree watches. STATISTICA 6.1 (StatSoft) was used for these analyses.

Seed cone removal rates were also tested between seed gulpers and seed predators. Like visitation lengths, seed handling rates by the two forager types can give insight as to how many seeds are available for effective seed dispersal. Seed cone removal rates were not transformed because data met the assumptions of a one-way ANOVA; data were analyzed using a one-way ANOVA in JMP 5.1.2 (SAS Institute, Inc.).

Understanding seed disperser movements with bird follows. Failure time analysis was used to determine the distribution in time it took for individuals to fly at least 25m either along a ridge or off a ridge, thereby providing some estimate as to how often *Z. japonicus* performed potential long distance dispersal events. Failure time analysis using a Gehan's Wilcoxon test checked for any differences between the distribution of *Z. japonicus* movement on or off a ridge using STATISTICA 6.1 (StatSoft). Specifically, failure time was defined as the time it took for *Z. japonicus* individuals to move at least 25m either along a ridge (i.e., flying up or down in elevation along a ridge) or off a ridge entirely (i.e., flying across deep gulches to neighboring ridges). Results from this analysis compared whether *Z. japonicus* is more likely to move along a ridge, thereby potentially dispersing *J. bermudiana* seeds along an elevational gradient, or more likely to move across ridges, thereby potentially dispersing seeds along similar elevations but across ridges in the study site.

RESULTS

Calculating bird assemblages and abundance with bird point counts

During the 27-point counts in the study site (repeated 3 times in 2004 and 3 times in 2005), I recorded fifteen bird species in the study site, fourteen of which are considered exotic bird species in Hawaii. The only native species, *Himatione sanguinea*

(Apapane), was found in small numbers (0.10 ± 0.04 average number of visits per point count, N=17). By far, the most abundant species was *Z. japonicus*, accounting for 64% of the total bird counts (5.90 ± 0.30 average number of visits per point count, N=956). Substantially less prevalent than *Z. japonicus*, the second and third most abundant birds in the study site were *C. cardinalis* (1.02 ± 0.07 average number of visits per point count, N=165) and *Streptopelia chinensis* (Spotted Dove, 0.64 ± 0.09 average number of visits per point count, N=103), respectively (Table 1).

Although relative numbers may differ among bird species, bird assemblages as a whole did not differ between the three ridges (Global R=0.034, p=1.5) or between years (Global R=0.043, p=0.6) in the study site. That is, the ratio of abundances for each bird species did not differ significantly between ridges or between years for each point count. The inability to detect significant differences in bird assemblages with the ANOSIM may be due to low power but ratios between the 3 most abundant species were highly consistent between point count locations, ridges, and years (Woo, *personal observation*). In particular, *Z. japonicus* was consistently recorded at every point count location and was, by far, the most abundant and widespread bird species in the study site.

Quantifying forager visitation and seed cone removal rates with focal tree watches

Tree watches revealed 8 avian species visiting *J. bermudiana* individuals: *Z. japonicus, C. cardinalis, H. sanguina, Carpodacus mexicanus* (House Finch), *Mimus polyglottos* (Northern Mockingbird), *Padda oryzivora* (Java Sparrow), *Cettia diphone* (Japanese Bush-Warbler), and *Lonchura punctulata* (Nutmeg Mannikin). Of these species, *H. sanguina* was the only native species seen in *J. bermudiana*. However, *H. sanguina* and 4 exotic birds (i.e., *M. polyglottos, P. oryzivora, C. diphone, L. punctulata*) were never observed to forage for *J. bermudiana* seed cones. Only 3 of these 8 species were observed to actively forage for *J. bermudiana* seed cones: *Z. japonicus, C. cardinalis*, and *C. mexicanus.*

The number of bird visits from the 3 active *J. bermudiana* foragers did not differ significantly between Ridges 1 and 2 (F=2.63, DF=1, p=0.11). The average number of visits for Ridge 1 was 1.72 ± 0.55 individuals/tree watch hour and the average number of visits for Ridge 2 was 2.74 ± 0.41 individuals/tree watch hour. However, the number of visits did differ significantly between the three main foragers of *J. bermudiana* seed cones (F=46.14, DF=2, $p<0.0001$). *Z. japonicus* was, by far, the most frequent visitor to *J. bermudiana* (6.49 ± 0.59 average number of visits per tree watch hour) compared to *C. cardinalis* (0.38 ± 0.59 average number of visits per tree watch hour) and *C. mexicanus* (0.27 ± 0.59 average number of visits per tree watch hour) (Figure 1). That is, *Z. japonicus* was recorded to visit 86.8% of the total focal tree watches (i.e., 33 out of the total 38), while *C. cardinalis* and *C. mexicanus* were observed to visit at a much lower frequency (i.e., 18.4% and 15.8%, respectively). In the cases where multiple species were observed to visit focal trees at the same time, no aggressive behavior was exhibited between bird species except for one instance where *M. polyglottos* was observed to chase away a male *C. cardinalis* on Ridge 2. Lastly, there were no significant interactions between the two ridges and three bird foragers (F=1.20, DF=2, $p=0.30$).

Visitation durations of seed gulpers were significantly different from seed predators (failure time test statistic= 2.11, $p<0.05$). For *J. bermudiana* visitation duration data, *Z. japonicus* was the only seed gulper (N=31) and *C. cardinalis* and *C. mexicanus* were pooled as seed predators (N=4 and N=5, respectively). Approximately 50% of both seed gulpers and seed predators leave mature *J. bermudiana* individuals within a minute (Figure 2). After the first minute, visitation durations differed between seed gulpers and seed predators. Provided that a forager were to stay for at least a minute period, seed predators tend to stay almost twice as long as to seed gulpers. This result is not too surprising, however, as *C. cardinalis* are known to be fairly sedentary (Mountainspring and Scott 1985). *Z. japonicus*, alternatively, were consistently found to flock feed in the study site, moving frequently between trees before flying out of the focal tree area (i.e., >20m distance).

Seed cone removal by *J. bermudiana* foragers was difficult to observe and therefore difficult to quantify in the study site, resulting in a small sample size of observations (*C. cardinalis*, N=8; *Z. japonicus*, N=13; *C. mexicanus*, N=1). Of the observations that were made, however, seed gulpers (i.e., *Z. japonicus*, N=13) and seed predators (*C. cardinalis* and *C. mexicanus*, N=9) did not differ significantly in seed cone removal rates (F=0.65, DF=1, p=0.43), although the inability to detect differences may be due to low power. Looking at the seed cone removal rates for each forager separately, differences may be more apparent with a larger sample size (Figure 3).

Understanding seed disperser movements with bird follows

Z. japonicus movement patterns were that of flock-feeders, where individuals were likely to move in groups of 2 or more individuals at any given time. *Z. japonicus* have been documented to fly in flocks of up to 200 individuals in the non-breeding season (Mountainspring and Scott 1985). It was common to observe flocks of *Z. japonicus* individuals move short distances (<10m) from one tree species to another tree species before flying longer distances on or off a ridge (>25m) (Woo, *personal observation*). *C. cardinalis* and *C. mexicanus* were not likely to be effective seed dispersers of *J. bermudiana* due to their low abundance and fairly sedentary movements. As a result, bird follows focused only on *Z. japonicus* individuals.

A total of 115 *Z. japonicus* individuals were followed during the months of September to November 2006. Of the 115 follows, 23 were discarded due to observer influence on the birds' movements. Of the 92 bird follows remaining, 45 of them were censored data (i.e., these individuals were not followed to departure because they were lost in flight). The other 47 individuals were observed to fly at least 25 meters along the elevational gradient of a ridge (N=28 uncensored points) or off a ridge entirely (i.e., flying toward a neighboring ridge by flying across a gulch, N=19 uncensored points).

Analyses on the 92 follows revealed that if a *Z. japonicus* individual were to fly off a ridge, that individual would most probably do so within the first minute. However, the longer a *Z. japonicus* individual remains on a ridge, the more likely that individual will fly along the ridge as opposed to off the ridge (Figure 4). Failure time data revealed that there is a significant difference in the proportion of *Z. japonicus* flying at least 25 meters along a ridge versus off a ridge over time (failure time test statistic=-5.30, p<0.0001).

DISCUSSION

Although previous studies have linked exotic species invasions with the importance of avian seed dispersal (e.g., White and Stiles 1992), not many studies have focused on how avian seed dispersers contribute to the invasion success of an exotic plant (but see Deckers et al. 2008, Vitousek and Walker 1989). Like many traditional seed dispersal studies, this study focuses on understanding how quantifying seed dispersal effectiveness can contribute to plant community structure (e.g., Jordano and Schupp 2000), but in the light of an exotic plant in Hawaii.

Quantifying bird species counts and assemblages in the West Maui Mountains study site provides a coarse overview as to which species in the avian community are likely to be effective seed dispersers, and, in turn, make the greatest impact on *J. bermudiana* invasibility. The high abundance and widespread distribution of *Z. japonicus* throughout the study site makes this species the most likely agent for effective seed dispersal of *J. bermudiana*. Although the second most abundant bird in the study site is *C. cardinalis*, this species is far less prevalent compared to *Z. japonicus*, and is therefore less likely to make a significant impact on *J. bermudiana* invasion success irrespective of its functional behavior as a seed predator. Since bird assemblages do not differ among ridges in the study site implies that *Z. japonicus* is able to disseminate *J. bermudiana* seeds across all three ridges. As long as *Z. japonicus* consistently forages for *J. bermudiana* seed cones and disperses seeds across the study site, *Z. japonicus* will be a highly effective disperser in terms of quantity and quality of seed dispersal.

Understanding the functional behaviors of different *J. bermudiana* dispersers provides a more detailed look at effective seed dispersal compared to simple measures of bird counts in the study site. With *Z. japonicus* as the most abundant bird in the study site, it was not surprising to find *Z. japonicus* to also be the most frequent visitor of *J. bermudiana* adults. What may be more important, however, is how *Z. japonicus* handles *J. bermudiana* seed cones; *Z. japonicus* are seed gulpers and are likely to facilitate the *J. bermudiana* invasion by not only carrying seeds away from *J. bermudiana* source trees, but also providing positive seed handling after passing through their digestive system (see Chapter 2).

Alternatively, as seed predators, *C. cardinalis* and *C. mexicanus* could inhibit *J. bermudiana* invasion success in two ways: (1) by discouraging *Z. japonicus* from foraging for *J. bermudiana* seed cones (i.e., showing aggression towards *Z. japonicus* during foraging bouts in *J. bermudiana*) and/or (2) destroying *J. bermudiana* seeds at a much higher rate than *Z. japonicus* can ingest. *Z. japonicus* has been documented to have significant negative associations with other avian foragers in Hawaii (Mountainspring and Scott 1985), but have also been documented to have insignificant competitive interactions with other avian foragers on the Bonin Islands (Kawakami and Higuchi 2003). In this study, aggression was never observed between *Z. japonicus*, *C. cardinalis* and *C. mexicanus*; the observed associations were similar to the interactions of *Z. japonicus* and *Apalopteron familiare* on the Bonin Islands (Kawakami and Higuchi 2003). That is, in the rare occasions when *Z. japonicus* were observed to forage with either *C. cardinalis* or *C. mexicanus*, the different species foraged in different levels of the canopy. In this study, seed predator abundance and visitation rates were also significantly lower than that of seed gulpers. As a result, the effects of these seed predators are likely to be minimal. Collectively, the seed predators are also not likely to destroy more seeds than seed *Z. japonicus* can ingest because there are more seed cones available than could be eaten by both seed predators and seed gulpers (Woo, *unpublished data*). Additionally, seed cone removal rates were not significantly different between seed predators and seed gulpers. As a result, seed gulpers (i.e., *Z. japonicus*) are, by far, a more significant contributor to the number of *J. bermudiana* seeds removed than are seed predators.

Although the presence of seed predators could potentially delay the invasion success of *J. bermudiana*, the widespread abundance and foraging behaviors of seed gulpers would predict an overall facilitation of *J. bermudiana* in the study site. Further, the flock-feeding behavior of *Z. japonicus* provides further insight into *J. bermudiana* invasion success in terms of the quality of seed dispersal. Understanding *Z. japonicus* movements in terms of both short visitation movements between *J. bermudiana* adults and frequent long distance movements within and between ridges can provide invaluable insight to what seed shadow patterns emerge in the study site. Based on *Z. japonicus* follows and *Z. japonicus* distribution, *J. bermudiana* seeds should be disseminated in a variety of microhabitats, from dry scrub forests to wet high elevation forests. Short distance movements of *Z. japonicus* during *J. bermudiana* foraging bouts likely distribute seeds to areas that are already favorable to *J. bermudiana* germination, while long distance movements either along an elevational gradient along a ridge or onto neighboring ridges exposes *J. bermudiana* seeds to new microhabitats that can result in further plant spread. The implications of these movements will be important for predicting *J. bermudiana* invasion success, in terms of both distribution and spread rate.

The widespread prevalence and seed dispersal effectiveness of *Z. japonicus* in the West Maui Mountains is not surprising; other studies quantifying the effects of avian seed dispersal of Hawaiian plant communities almost always have *Z. japonicus* as the most effective seed disperser in the system, whether *Z. japonicus* is dispersing invasive plants (e.g., Vitousek and Walker 1989) or native plants (Foster et al. 2007). Similar to the *Prunus serotina* system in Flanders (Deckers et al. 2008), manipulating the seed disperser community is not feasible in this study and focusing on other processes in the seed dispersal cycle may be more robust in targeting invasive plant control efforts of *J. bermudiana* in the West Maui Mountains. For thorough understanding on the next stages of the seed dispersal cycle, however, further research needs to link *Z. japonicus* movements to *J. bermudiana* germination, seedling, and sapling success.

Determining the type of forager, seed handling, and forager movement can have important implications for the invasion success of an exotic plant; this information, in turn, can help describe the rate of spread of an exotic species. For example, if a plant depends on avian seed dispersal and has a high number of seed predators who are also territorial in the area (i.e., not likely to move outside of a given territory), invasive spread could be slow or almost non-existent. On the other hand, if the same plant had seed dispersers that feed in flocks and move around the landscape at high rates, invasive spread would likely be fast and effective. Conducting empirical studies of seed dispersal effectiveness in the context of functional behaviors of multi-species dispersers can reveal broad trends of invasive plant success in terms of facilitation and/or inhibition based on the behaviors of its dispersers. This invasive multi-species system approach may prove valuable in elucidating disperser traits that affect plant invasion success (Gosper et al. 2005). Directed studies pinpointing the specific stages of seed dispersal effectiveness from both a disperser perspective and a plant perspective will best inform conservation management strategies and invasive plant control.

TABLES

Table 1. Nomenclature, vernacular, family, and invasion status of the 15 species recorded during point count surveys in 2004 and 2005, listed by the total number of birds surveyed (N) and average number of visits per point counts survey. *Z. japonicus* was the most abundant bird species (N=956) compared the other the bird species (N=548).

Species	Common Name	Family	Status	N	Average # Visits / Point Count
Zosterops japonicus	Japanese White-Eye	Zosteropidae	Exotic	956	5.9012+0.3010
Cardinalis cardinalis	Northern Cardinal	Emberizidae	Exotic	165	1.0185+0.0658
Streptopelia chinensis	Spotted Dove	Columbidae	Exotic	103	0.6358+0.0926
Cettia diphone	Japanese Bush-Warbler	Muscicapidae, Subfamily Sylviinae	Exotic	60	0.3704+0.0532
Lonchura punctulata	Nutmeg Mannikin	Estrildidae	Exotic	40	0.2469+0.0738
Mimus polyglottos	Northern Mockingbird	Mimidae	Exotic	35	0.2160+0.0389
Carpodacus mexicanus	House Finch	Fringillidae, Subfamily Carduelinae	Exotic	33	0.2037+0.0412
Francolinus pondicerianus	Gray Francolin	Phasianidae	Exotic	32	0.1975+0.0418
Geopelia striata	Zebra Dove	Columbidae	Exotic	27	0.1667+0.0431
Garrulax canorus	Hwamei/Melodius Laughing Thrush	Muscicapidae, Subfamily Timaliinae	Exotic	19	0.1173+0.0282
Himatione sanguinea	Apapane	Fringillidae, Subfamily Drepanidinae	Endemic	17	0.1049+0.0367
Leiothrix lutea	Red-Billed Leiothrix	Muscicapidae, Subfamily Timaliinae	Exotic	8	0.0494+0.0192
Acridotheres tristis	Common Mynah	Sturnidae	Exotic	5	0.0309+0.0204
Francolinus francolinus	Black Francolin	Phasianidae	Exotic	3	0.0185+0.0106
Lonchura Malacca	Chestnut Mannikin	Estrildidae	Exotic	1	0.006173+0.006173

FIGURES

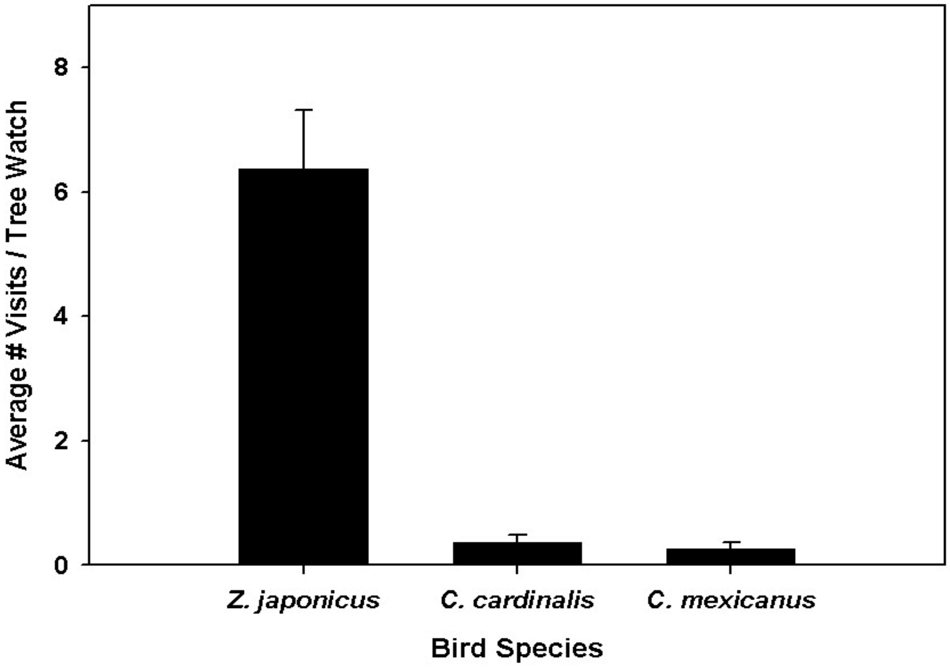

Figure 1. Average number of visits per tree watch for the 3 main foragers of *J. bermudiana* seed cones: *Z. japonicus*, *C. cardinalis* and *C. mexicanus*. *Z. japonicus* had significantly more visits per tree watch compared to *C. cardinalis* and *C. mexicanus* ($p<0.0001$).

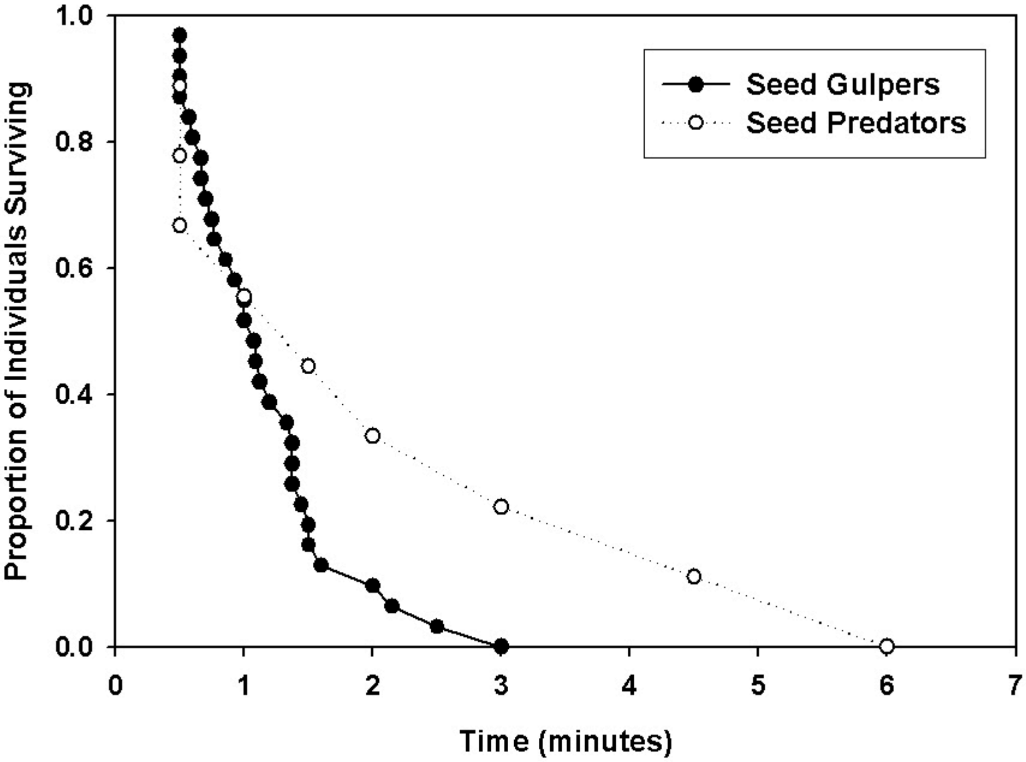

Figure 2. Proportion of individuals remaining in a *J. bermudiana* focal tree over time. Approximately 50% of both seed gulpers (N=31) and seed predators (N=9) are likely to leave a focal tree within a minute period upon arrival; differences are more apparent after that one-minute period.

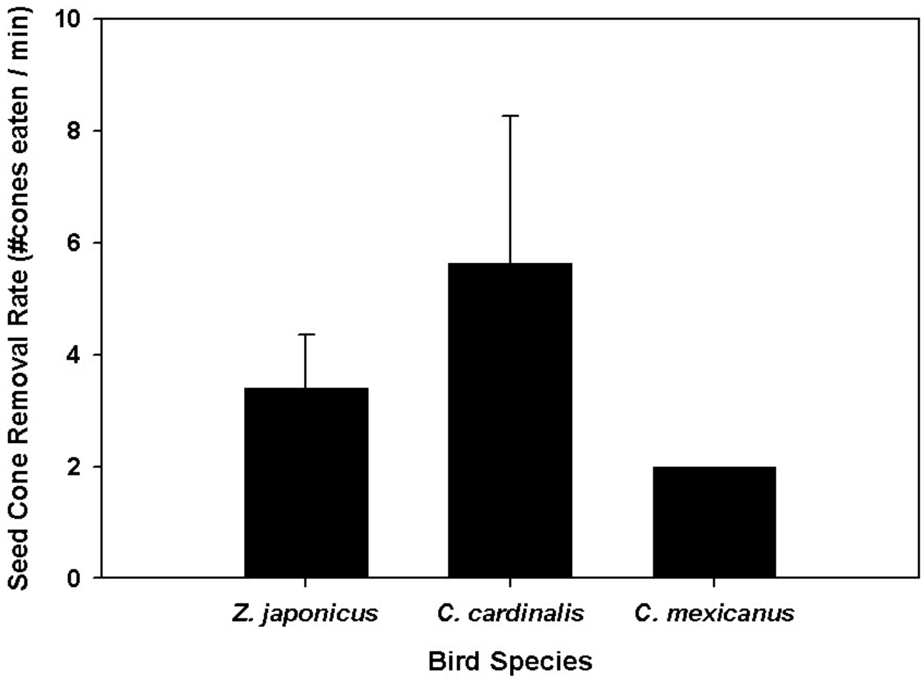

Figure 3. Seed cone removal rates for the 3 main foragers of *J. bermudiana* seed cones: *Z. japonicus, C. cardinalis* and *C. mexicanus*. No significant differences were found between removal rates (p=0.4307).

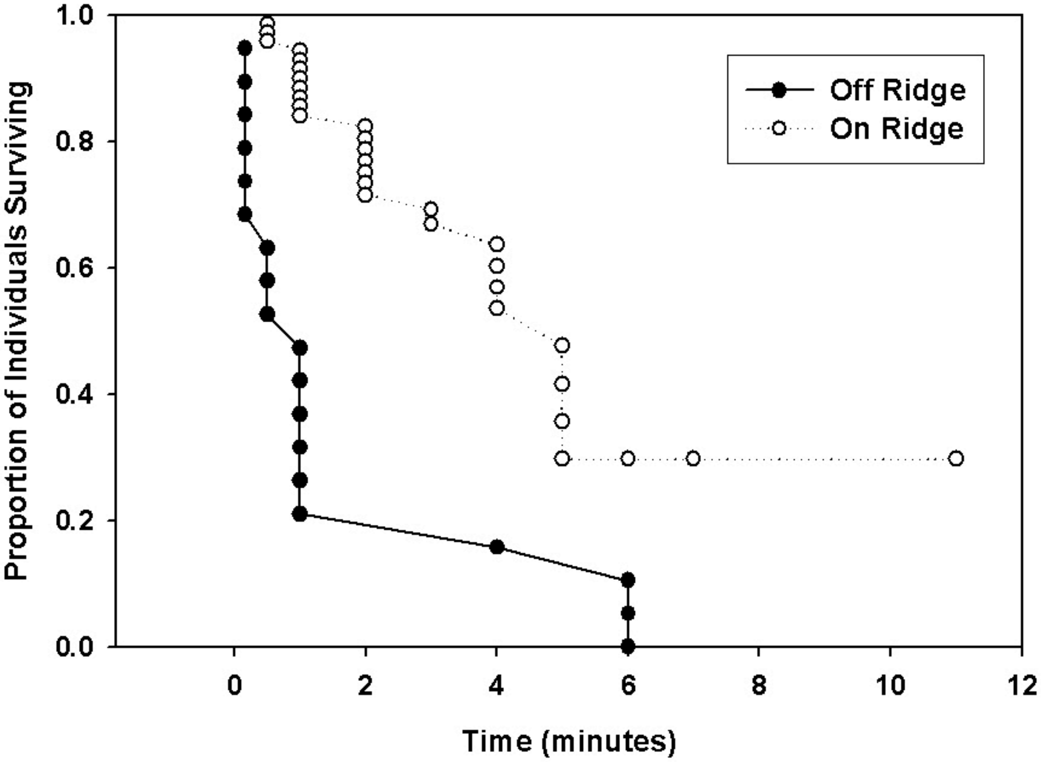

Figure 4. Proportion of *Z. japonicus* individuals remaining in an area before making a potential long distance dispersal event (>25m), either along a ridge (N=73) or off a ridge (N=19). *Z. japonicus* individuals flying off the ridge are likely to do so within a minute.

II. Is *Juniperus bermudiana* a lazy invader? Continuing the seed dispersal cycle with a closer look at the establishment phase of *J. bermudiana* in Maui, Hawaii

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ABSTRACT

Few studies focus on exotic species that are in the process of invading a novel habitat. Even rarer are studies that focus on the effects of animal-mediated seed dispersal on the potential invasion success of an exotic plant. This study centers on an exotic plant, *Juniperus bermudiana*, which exhibits distinct levels of invasion and depends on avian seed dispersal for its continual distribution and spread in Maui, Hawaii. By comparing greenhouse experiments with field studies, a better understanding is reached as to why *J. bermudiana* has been slow to invade since its introduction to the area almost 80 years ago. As expected, seed deposition is linked to the density of *J. bermudiana* source trees, but it still occurs in novel habitats across the landscape. Although avian seed handling is likely to positively affect *J. bermudiana* germination rates, *J. bermudiana* is limited by the establishment phase of invasion. In particular, seedling emergence and survival is limited by the harsh environmental conditions of the West Maui Mountains. Results of this study suggest that focusing on exotic species in the early stages of invasion may better target invasive species control efforts.

INTRODUCTION

Most studies in biological invasions focus on exotic species that have already successfully established and spread throughout their introduced habitat. However, the majority of exotic plant species fail to become invasive pests and, instead, typically follow the Tens Rule: 1 out of 10 imported exotic species gets introduced into the wild, 1 out of 10 of those introduced species actually establishes in the wild, and, finally, 1 out of 10 of those established species becomes an invasive pest (Williamson and Fritter 1986). Because studies of exotic plant species have generally focused on plants after they have become invasive, little is known about the early processes of invasion. Consequently, to fully understand the processes of how an exotic plant species invades, it is important to determine what factors contribute to the successful transition from the introduction to the establishment to the invasion of that species or, alternatively, what factors contribute to the failure of these transitions of that species.

In particular, the role of zoochory on the early stages of invasion is not well understood despite the large number of exotic plants that depend on animal-mediated seed dispersal. Studies that focus on the link between animal-mediated seed dispersal and exotic plant demography are rare, yet essential to fully understand and predict the success of an introduced plant in its novel habitat. This chapter attempts to address the role of animal-mediated seed dispersal on the introduction, establishment and potential invasion success of an exotic plant, *Juniperus bermudiana* (Bermuda Juniper) in Maui, Hawaii. Introduced to the West Maui Mountains by territorial foresters in the early 1930s, *J. bermudiana* has been considered to be a slow invader, spreading less than 2 kilometers from where it was first introduced. I had the unique opportunity to observe *J. bermudiana* species in distinct areas differing in levels of invasion (i.e., introduced, established, colonized areas). *J. bermudiana* also depends on avian seed dispersal for invasive spread, as birds gulp intact seed cones and likely defecate viable seeds.

With at least 41% of Hawaii's exotic plant species dependent on avian seed dispersal (Staples et al. 2000), considering the distinct stages of the seed dispersal cycle (Wang and Smith 2002) during the different stages of invasion may inform invasion success. I combined greenhouse experiments with field studies to better understand how the seed dispersal cycle can facilitate or inhibit the introduction, establishment, and, ultimately, invasion of *J. bermudiana* in the West Maui Mountains. More specifically, I asked (1) how does *J. bermudiana* density compare to seed shadows in the study site; (2) how does germination differ under greenhouse conditions versus field conditions; and (3) how might environmental gradients (i.e., water and light) affect *J. bermudiana* seedling growth?

Given that seed dispersal is not likely limiting in this system (see Chapter 1), understanding the next stages after seed dispersal may prove critical in determining why *J. bermudiana* has been slow to invade since its introduction almost 80 years ago. In the West Maui Mountains, the successful establishment of *J. bermudiana* in novel habitats is potentially influenced by two important rainfall gradients: (1) decreasing rainfall when moving from windward ridge to leeward ridge; and (2) decreasing rainfall when moving from high elevation to low elevation. These gradients create a diverse vegetation structure when moving across the mountainous, valley landscape and when moving across different elevations (Woo, *unpublished data*). I predict that the limiting step in this system is the establishment phase of *J. bermudiana* in the study site, due to the environmental gradients in the heterogeneous landscape.

J. bermudiana is one of many exotic plant species that depends on animal-mediated seed dispersal in the low to middle elevational forests in Hawaii. Currently, lowland ecosystems are already mostly dominated by exotic plant species, with more species starting to progress extensively into higher elevational forests in Hawaii (Vitousek et al. 1987). Results of this study aims to understand how avian seed dispersal dynamics can influence the introduction and establishment phases of the *J. bermudiana* invasion process and to relate this information to infer possible future invasion success. By studying exotic plant species before they become invasive pests, I hope to develop more effective exotic species control and management policies in Hawaii forests.

METHODS

Study species

J. bermudiana (Cupressaceae) was the dominant endemic tree in Bermuda until a catastrophic introduced scale epidemic killed 95% of the population in the late 1940s and early 1950s (D.B. Wingate, *personal communication*). Records show that as many as 6,500 *J. bermudiana* trees were introduced to forest reserves in all Hawaiian Islands by 1921 (Little and Skolmen 1989). *J. bermudiana* is fully naturalized and remains invasive on the mid-Atlantic island of St. Helena where it was introduced in the 1930s (Ashmole and Ashmole 2000). It has been suggested that *J. bermudiana* is dispersed by a number of different bird species. In its home range, *J. bermudiana* is dispersed by *Sturnus vulgaris* (European Starling), *Dumetella carolinensis* (Gray Catbird), and *Sialia sialis* (Eastern Bluebird) (D.B. Wingate, pers. comm.). My field observations on Maui, Hawaii, however, have revealed *J. bermudiana* seed cones to be effectively dispersed by the widely abundant, pervasive and exotic *Zosterops japonicus* (Japanese White-Eye) throughout the study site (see Chapter 1). Additionally, *J. bermudiana* typically produces ripe seed cones annually from mid-September to mid-December in the study site. The large variation in seed cone production can range from 0 seed cones to an estimated 24000 seed cones per individual adult tree.

Greenhouse experiments

*Study Location***.** Experiments were conducted at the State University of New York-Stony Brook Greenhouses, at Stony Brook, NY (40° 55’ 15” N, 73° 7’ 0” W).

Germination Experiment. J. bermudiana seed cones, randomly collected in Maui, Hawaii in November 2003 (see below for specific locations), were dissected for seeds. Seed cones typically encased 1-3 individual seeds. Individual seeds were subjected to one of 4 treatments before planting: (1) sandpaper (seeds rubbed in 60-grit coarse bare wood sandpaper for 15 seconds); (2) 0.1M acetic acid (seeds soaked in acid for 9 minutes); (3)

0.01M acetic acid (seeds soaked in acid for 9 minutes); and (4) stripped seed treatment (i.e., no treatment other than removing pulp from seed). Intact seed cones served as a second control, next to the stripped seeds. Treatments were generally based on what *J. bermudiana* seeds would experience through the digestive tract of *J. bermudiana's* main seed disperser, *Z. japonicus*. The 0.1M acetic acid treatments (pH=2.5) and the 0.01M acetic acid treatments (pH=3.5) simulated the range of acidic environments of a bird's digestive tract, particularly that of an avian gizzard and crop, respectively (Baumann et al. 1995). The sandpaper treatment simulated the grinding environment of the gizzard in the digestive tract, where food is generally processed with sand and grit (Ehrlich et al. 1988). The time seeds spent in these treatments were also based on seed treatment by *Z. japonicus*, where seed processing through the digestive tract are relatively short, lasting on an average of 9 minutes before seeds are excreted. There were 75 seeds per treatment (except in the case of the control, where there was 75 intact seed cones). For each treatment, 30 seeds were planted in each of 2 flatbeds (26cm x 53cm x 6cm), and 15 seeds were planted in round pots (21cm diameter x 21cm deep). Flatbeds and pots were randomly placed on one greenhouse bay, where a timed mister watered the seeds from December 13, 2003 to April 2, 2004. Weekly counts of seedlings present for each treatment were recorded starting from the first seedling emergence until the first week of April 2004.

Water Tolerance Experiment. A total of 64 *J. bermudiana* seedlings were randomly chosen from the germination experiment in April 2004. Each seedling was transplanted into a 0.5L pot (12cm diameter x 12cm height) with a 1:1 peat-soil mixture. Seedlings were immediately watered and 5 grams of Scotts Osmocote Plus Controlled Release Fertilizer (15N-9P-12K_2O, Longevity 3-4 months) was added to each pot. A randomized complete block design with replication was used in this experiment: 64 seedlings were randomly distributed among 8 blocks, each block with 4 seedlings undergoing high level water treatment and 4 seedlings undergoing low level water treatment. Seedlings were not moved once placed in their block position. High water treatment was characterized by saturating soil every day; low water treatment was characterized by saturating water every 4th day for the duration of the experiment. The water tolerance experiment started April 14, 2004 and ended June 30, 2004. Twelve dead *J. bermudiana* seedlings were replaced on or before April 29, 2004; no seedlings were replaced after that date. The height (cm) was measured May 23, 2004 and June 30, 2004. On June 20, 2004, all *J. bermudiana* seedlings were carefully sacrificed, rinsed and placed in an equatherm oven (Curtin Matheson Scientific, Inc., ~15.6ºC) before weighing; total biomass and biomass of roots and shoots were measured a week later, using a Sartorius Analytical Balance with 200g capacity and 0.001g readability.

Shade Tolerance Experiment. A total of 72 *J. bermudiana* seedlings were randomly chosen from the germination experiment in April 2004. Each seedling was transplanted into a 0.5L pot (12cm diameter x 12cm height) with a 1:1 peat-soil mixture. Seedlings were immediately watered and 5 grams of Scotts Osmocote Plus Controlled Release Fertilizer (15N-9P-12K_2O, Longevity 3-4 months) was added to each pot. Four shade boxes (40cm x 40cm x 40cm) were constructed from 60% black shade cloth stapled to the sides of wooden stakes. A nested block design was used: 4 blocks of 9 seedlings each were placed under shade boxes; 4 blocks of 9 seedlings each were placed under ambient light. Placement of seedlings and blocks were randomized; all 8 blocks fit onto a greenhouse bay and were not moved for the duration of the experiment. The shade tolerance experiment started April 13, 2004 and ended June 30, 2004. Two dead *J. bermudiana* seedlings were replaced on April 29, 2004; no seedlings were replaced after that date. The height of each seedling (cm) was measured May 21, 2004 and June 30, 2004. A LI-COR LI-250 Light Meter was used in the mornings and afternoons of May 27, June 21 and June 29, 2004 to test for any differences in light levels between ambient light blocks and shaded blocks. Fifteen-second light measurement averages ($\mu mol/sm^2$) were taken from each corner and center of a block, for a total of 40 light measurements. On June 30, 2004, all *J. bermudiana* seedlings were carefully sacrificed, rinsed and placed in an equatherm oven (Curtin Matheson Scientific, Inc., ~15.6ºC) before weighing; total biomass and biomass of roots and shoots were measured separately a week later, using a Sartorius Analytical Balance with 200g capacity and 0.001g readability.

Field experiments

Study Location. Field research was conducted on privately owned land in the West Maui Mountains of Maui, Hawaii. Permission was granted to conduct research in both the Kapunakea Preserve (20° 55' 30" N, 156° 38' 13" W), managed by The Nature Conservancy of Hawaii, and in the Pu'u Kukui Watershed (20° 56' 26" N, 156° 37' 58" W), managed by Maui Land and Pineapple Company, Honolua Division. This area of the West Maui Mountains has several different vegetation zones, ranging from arid scrub at the lowest elevations to very wet rainforests at its highest elevational peak of 1764m (Scott et al. 1986). The West Maui Mountains, a volcanic system dating 1.3-1.6 million years old, is also slit by deep amphitheater-headed valleys (Stearns 1966), which result in distinct upward-sloping ridges across the entire mountain range. *J. bermudiana* has formed dense monotypic stands on one of the ridges in the Pu'u Kukui Watershed area since its time of introduction in the early 1930s.

My study focused on three specific ridges (Figure 1), on one of which *J. bermudiana* was first planted (in the Pu'u Kukui Watershed area, hereafter Ridge 1). The ridge leeward (i.e., south) of Ridge 1 (on the Kapunakea Preserve, hereafter Ridge 2) has many well-established *J. bermudiana* adults, while the ridge most leeward of the three ridges (also on the Kapunakea Preserve, hereafter Ridge 3) has fewer than 20 *J. bermudiana* adults. Ridge 3 is on the edge of the *J. bermudiana* distribution, and is therefore considered to be the potential invasion front for this species. The study site for all three ridges extends from 350m at the lowest elevation (bordering pineapple/sugar cane fields) to 700m at the highest elevation (bordering wet high elevational forests). The vegetation zone of most of the study site can be characterized as a mesic low elevational forest, dominated by the native *Metrosideros polymorpha* (Ohi'a lehua) and a variety of exotic plant species, including *Psidium cattleianum* (Strawberry Guava), *Schinus terebinthifolius* (Christmas Berry), *Grevillea robusta* (Silky Oak), and several different

Eucalyptus species. The study site is also dominated by a variety of invasive bird species; some of which were introduced and established on Maui as early as 1880 (e.g., *Carpodacus mexicanus,* House Finch) and others as late as 1929 (e.g., *Z. japonicus; Cardinalis cardinalis*, Northern Cardinal) (Caum 1933). Due to the prevalence of avian disease transferred by various mosquito populations in the lower elevations (Englund and Preston 2000), most native birds (e.g., *Vestiaria coccinea*, 'I'iwi) are most commonly found only in the higher elevations of the West Maui Mountains and are therefore absent in the study site.

J. bermudiana Density Survey. An extension of the plot-less Point-Centered Quarter Method (PCQM) of vegetation sampling (Cottam and Curtis 1956) was used to measure *J. bermudiana* tree density across the study site. Parallel transects running the width of a ridge (generally running north to south) were established on an elevational gradient every 200m on Ridge 1, every 100m on Ridge 2 and every 200m on Ridge 3. Since Ridge 2 was only 60m wide at its widest point, transects were made every 100m instead of 200m. The total number of sampling points along transects depended on the width of each ridge; sampling points were 20m apart from one another along each transect. A total of 127 sampling points were conducted from September to November 2006: Ridge 1 had 68 points; Ridge 2 had 36 points; and Ridge 3 had 23 points. At each sampling point, the distance to the nearest tree (with a diameter at breast height (DBH, 1.3m), of at least 0.5cm) in each quadrant was measured in meters. An extension of the PCQM was also used: from the trees measured in each quadrant, the distance (m) to the next nearest tree was also measured, resulting in distance measures of 8 total trees per sampling point. In addition to distance measures, the following information was also recorded for each tree: species, DBH (cm), and, if the tree was a *J. bermudiana* individual, the number of seed cones present. No trees were measured more than once in any sampling point location and all trees were assumed to be randomly distributed around each sampling point location.

Field Germination Experiment. A total of 27 field plots were cleared in the study site during the last two weeks of November 2004 and the first week of December 2004: 9 plots on each ridge, with 3 plots located at low elevation (~444m), 3 plots located at medium elevation (~563m) and 3 plots located at high elevation (~671m). Each plot was randomly located at each elevation, no closer than 10 m to the next plot, under vertical vegetation structure and had an area of 1.5m x 1m. 1m x 1m area of each plot was cleared of any standing vegetation; the 0.5m x 1m area remaining was left with vegetation intact. Three separate germination experiments were conducted in each 0.5m x 1m subplot: (1) Intact seed cones in cleared vegetation; (2) Scarified seeds in cleared vegetation; and (3) Scarified seeds in standing vegetation. Ripe *J. bermudiana* seed cones were collected from random cone-bearing adults throughout the study site November 2004 and October 2005. In December 2004, 13 intact seed cones were planted on the top subplot of each cleared plot: in the first two rows, 5 seed cones were placed 0.1m apart along a row and between rows; a third row had 3 seed cones that were also 0.1m apart from the other seed cones. A 0.3m buffer zone of cleared vegetation surrounded the planted seed cones along two edges of the plot; a 0.15m buffer zone of cleared vegetation surrounded the planted seed cones on the remaining edges of the plot. For the other two subplots, seeds were dissected from pulp, scarified with coarse, 60-grit coarse bare wood sandpaper for 15 seconds and then soaked overnight in tap water before planting the next day. From November 7-11 2005, scarified seeds were planted in all plots on all three ridges. Forty scarified seeds were planted in each middle subplot: 5 rows of 8 seeds each were planted with rows located 0.05m apart and seeds planted 0.1m apart within each row. A 0.15m buffer zone of cleared vegetation surrounded planted seeds to each edge of the plot. Forty scarified seeds were also planted in each bottom subplot of standing vegetation; seeds were planted in the same manner as described for the middle subplot (Figure 2). Plots were only watered after initial planting (i.e., 1L tap water sprinkled over each subplot). The number of seedlings in all subplots was monitored and recorded September to November 2006.

Seed Rain Study. Seed traps were pots with cotton cloth seed collectors, similar to what has been used in other seed rain studies conducted in Hawaii (Drake 1998, Foster 2007). In this study, modified seed traps were made from black 7-gallon nursery pots (35cm diameter x 30cm deep; Classic 2800, Nursery Supplies, Inc.). Inside each pot, a 100% cotton fabric sheet was placed on top of charcoal fiberglass insect screening (Phifer Wire Products, Inc.), which was glued 15cm from the bottom of each pot with a glue gun (Adhesive Tech Ultimate Mini High Temp Glue Gun and Mini Round, Multi-Temp Glue Sticks). Each cotton sheet was secured with 4 nickel-plated straight pins. On the top of each pot, poultry netting (20 gauge, 1”mesh, Gilbert and Bennett Manufacturing Co.) was secured using 102mm multi-purpose ties (Catamount), which fastened the netting through 7-0.5” drilled holes near the top of each pot. Four tent stakes were used to secure each seed trap to the ground. A total of 108 seed traps were placed at different elevations on all three ridges: 40 on Ridge 1; 40 on Ridge 2; and 28 on Ridge 3. Specifically, 4 seed traps were placed randomly under some vertical tree branch structure, where birds have been observed to perch so as to most effectively capture seeds defecated by *Z. japonicus*. Each set of 4 seed traps were placed every 200m apart along each ridge, from low elevation to high elevation (approximately 350m to 700m, respectively). All seed traps were first placed in the field during the first two weeks of October 2005. Seeds were collected from October-November 2005 and from September-November 2006. After each collection period, new cotton sheets were placed on fiberglass mesh and poultry netting was re-fastened. All seed collections were inspected and shipped back to SUNY-Stony Brook, where they were put in an equatherm oven (Curtin Matheson Scientific, Inc., ~15.6ºC) before seed identification.

Statistical analyses

Greenhouse experiments

Germination Experiment. A Kolmogorov-Smirnov goodness of fit test for discrete ordinal scale data was used to test for differences in germination between the five different seed treatments. Treatments were ordered by intensity (i.e., sandpaper, 0.1M acid, 0.01M acid, stripped seed and, lastly, intact seed cones) before analysis. The goodness of fit of the observed to the expected cumulative frequency distribution was calculated for a critical d_{max} value as described in Zar 1996. The observed frequency of each treatment was based on the final number of seedlings emerging after 9-weeks; the expected frequency for each treatment was assumed to be equal across treatments (i.e., all seed treatments were likely to germinate equally).

Water Tolerance Experiment. A 2-way analysis of variance (ANOVA) was used to test for any differences in *J. bermudiana* biomass between water treatments, between blocks and whether there was an interaction effect between water treatments and blocks in the greenhouse bay. Similarly, a 2-way ANOVA was also used to test for any differences in *J. bermudiana* root-shoot ratios between water treatments, between blocks and whether there was an interaction effect between water treatments and blocks in the greenhouse bay. Data for both biomass and root-shoot ratios fit the assumptions of ANOVA (i.e., normality of residuals and homogeneity of variances). All analyses were conducted on JMP 5.1.2 (SAS Institute, Inc.).

Shade Tolerance Experiment. A nested analysis of variance (ANOVA) was used to test for any differences in *J. bermudiana* biomass among light treatments and among blocks, where 4 blocks were nested within each shade treatment. Similarly, a nested ANOVA was also used to test for any differences in *J. bermudiana* root-shoot ratios among light treatments and among blocks. A third nested ANOVA was conducted for the light measurement data, to ensure differences in available light between treatments. Before analysis, biomass was log transformed so that normality of residuals and homogeneity of variance assumptions were met for ANOVA. Data for root-shoot ratios were also transformed before analysis; an arcsine transformation for these data set resulted in meeting the assumptions of ANOVA (i.e., normality of residuals and homogeneity of variances). Light measurements were averaged before conducting analyses so as to get an average amount of light available from each measured position in each block throughout the day. Light measurements were also log transformed so that normality of residuals and homogeneity of variance assumptions were met for ANOVA. All analyses were conducted on JMP 5.1.2 (SAS Institute, Inc.).

Field experiments

J. bermudiana *Density Surveys. J. bermudiana* density of each sampling point was calculated from all 8 distances measured between trees and between sampling point to nearest tree in each quadrant. The second set of distance measures (i.e., distances between trees) were included in these analyses because locations of all trees and sampling point locations were assumed to be random, and therefore independent between all distance measures. That is, the distance between trees were independent of the distance between sampling point and tree in each quadrant. Density of each sampling point was calculated using the equation D=1/(average l^2), where l is the distance (m) between either trees or between sampling point to nearest tree in each quadrant. The proportion of *J. bermudiana* trees in each sampling point was calculated using $f_j=n_j/n$, where n_j is the total number of *J. bermudiana* trees and n is the total number of trees (i.e., 8 for all sampling point locations). *J. bermudiana* density, then, was calculated using $D_j=f_j*D$ (Causton 1988). Differences in *J. bermudiana* density between ridges were tested using a Kruskal-Wallis in JMP 5.1.2 (SAS Institute, Inc.) because the large number of zeroes in the data set made it difficult to adequately meet the assumptions of ANOVA.

Field Germination Experiment & Seed Rain Study. Descriptive summary statistics were used to illustrate findings from both the field germination experiment and the seed rain study. The small number of seedlings emerging from the germination experiment made it difficult to conduct any formal statistical analyses (e.g., analysis of variance). However, in addition to descriptive results of the seed rain study, a Kruskal-Wallis in JMP 5.1.2 (SAS Institute, Inc.) was used to test for any differences in the number of seeds trapped between ridges in the seed rain study; deviations from normality and violations of homogeneity of variances resulted in using a Kruskal-Wallis in lieu of a one-way analysis of variance. All analyses were conducted on JMP 5.1.2 (SAS Institute, Inc.).

RESULTS

Greenhouse experiments

Germination Experiment. The intensity of the 5 treatments (i.e., sandpaper, 0.1M acid, 0.01M acid, stripped seed, and intact seed cone) generally determined both rate and total number of seedling emergence. Although the first seedlings to emerge from the germination experiment did not occur until 2 months after initial planting, the first seeds to appear were from the most intense of the seed treatments, the sandpaper treatment (N=3). By the second week, a total of 58 seedlings had emerged, the majority of the seedlings still emerging from the sandpaper treatment (N=34). By the end of the 9-week period, a total of 185 seedlings had emerged: intact seed cones had 1.3% germination (N=1); stripped seeds had 56% germination (N=42); 0.01M acid treated seeds had 56% germination (N=42); 0.1M acid treated seeds had 44% germination (N=33); and sandpaper treated seeds had 89.3% germination (N=67) (Figure 3). The large difference between the sandpaper treatment and the intact seed cone treatment suggests seed treatment to be important for short-term germination success. Additionally, the similar germination results for the 0.1M acid, 0.01M acid and stripped seed treatments suggest that exposed seeds—whether treated with acid or not—increases germination, though not to the extent of the sandpaper treatment. If the acid and sandpaper treatments were to mimic the avian crop and gizzard, respectively, these results imply that treatment in the avian gizzard is a particularly important step for *J. bermudiana* seed germination. Significant differences between seed treatments (d_{max}=36, N=185, k=5, $p<0.001$) highlight the importance of seed treatment through the avian digestive tract, particularly with the sandpaper treatment.

Water Tolerance Experiment. As expected, *J. bermudiana* seedlings had significantly more biomass when given more water (F=6.9502, DF= 1, $p<0.05$, Figure 4a). However, when given more water, *J. bermudiana* allocated significantly more energy for roots than for shoots (F=9.0273, DF=1, $p<0.005$, Figure 4b). Although seedlings that received the high water treatment were generally bigger, the seedlings that received the low water treatment still appeared to be healthy. For the 11-week duration of the experiment, only 2 seedlings died from the low water treatment; all of the seedlings from the high water treatment survived. For both biomass and root-shoot ratios, there were no block effects (F=1.4830, DF=7, p=0.1971 and F=0.3177, DF=7, p=0.9422, respectively) or interaction effects between water treatment and blocks (F=0.5655, DF=7, p=0.7799 and F=0.3941, DF=7, p=0.9010, respectively).

Shade Tolerance Experiment. Results from the biomass measurements suggest that light to be a substantial resource to the growth of *J. bermudiana* seedlings. *J. bermudiana* seedlings had significantly more biomass in ambient light treatment blocks compared to shade treatment blocks (F=396.0454, DF=1, $p<0.0001$, Figure 5a). Although the difference in biomass between light treatments was large (Figure 5a), only 2 seedlings from the shade treatment died during the 11-week experiment. However, seedlings under the shade treatment were noticeably smaller, less green and appeared less healthy compared to those seedlings exposed to the ambient light treatment. When given more light, *J. bermudiana* seedlings also allocated significantly more energy to their roots compared to their shoots (F=9.8100, DF=1, $p<0.005$, Figure 5b). Biomass and root-shoot ratio data also showed no block effects in this analysis (F=1.6317, DF=6, p=0.1535 and F=0.2522, DF=6, p=0.9566, respectively). Lastly, as expected, ambient light treatment blocks received significantly more light than shade treatment blocks (523.94±12.60 μmol/sm^2 versus 81.27±12.60μmol/sm^2, respectively; F=552.2757, DF=1, $p<0.0001$).

Field experiments

<u>*J. bermudiana*</u> *Density Survey*. Of the 1016 trees measured in the study site, only 78 (7.7%) of them were *J. bermudiana* trees: Ridge 1 had 59 individuals (11% of trees measured); Ridge 2 had 18 individuals (6% of trees measured); and Ridge 3 had 1 individual (0.5% of trees measured). *J. bermudiana* density decreased significantly across ridges (χ^2=7.8489, DF=2, $p<0.05$, Figure 6); these densities were likely due to the

monotypic stands of *J. bermudiana* on Ridge 1, the established individuals on Ridge 2, and the few colonizing individuals on Ridge 3.

Additionally, from the density survey using PCQM, the number of species recorded on each ridge differed slightly: 17 species were measured on Ridge 1; 14 species were measured on Ridge 2; and 11 species were measured on Ridge 3 (Table 1). However, the dominant species on each ridge differed, likely due to differing levels of disturbance by humans and the dual rainfall gradient. Ridge 1 was dominated by *Acacia confusa* (Formosa Koa, N=131, 24% of trees measured) and *Araucaria* species (N=123, 23% of trees measured). Ridge 2 was dominated by one endemic native species, *Metrosideros polymorpha* (Ohi'a lehua, N=60, 21% of trees measured) and one indigenous native species, *Osteomeles anthyllidifolia* (Ulei, N=60, 21% of trees measured). Ridge 3 was dominated by one invasive species, *Psidium cattleianum* (Strawberry Guava, N=72, 39% of trees measured) and one indigenous native species, *Osteomeles anthyllidifolia* (Ulei, N=30, 16% of trees measured). Only four tree species that are native to the study site were represented on all three ridges: *O. anthyllidifolia*, *Metrosideros* species, *Dodonaea viscose* (A'ali'i) and *Styphelia tameiameiae* (Pukiawe).

Field Germination Experiment. Despite 89.3% germination in the greenhouse experiment, *J. bermudiana* seeds scarified with the same sandpaper treatment and then planted in the study site resulted in extremely low germination rates. Of the 1080 seeds planted in cleared plots (i.e., middle subplots) across the study site, only 19 seedlings emerged (1.8%) and of the 1080 seeds planted in the standing vegetation plots (i.e., uncleared standing vegetation plots), only 3 seedlings emerged (0.28%). Additionally, 0% of the 351 intact seed cones germinated in the field.

Of the 19 seedlings that emerged from the cleared plots, there are no distinct patterns with respect to ridge or elevation. On Ridge 1, 3 seedlings emerged from two low elevation plots and 1 seedling emerged from a high elevation plot. On Ridge 2, all 11 seedlings were from two middle elevation plots. On Ridge 3, 4 seedlings emerged from one low elevation plot and 1 seedling emerged from one middle elevation plot. The 3 seedlings that were found in the standing vegetation plots had emerged from two plots in the lowest elevation plots on Ridge 1.

Seed Rain Study. The number of *J. bermudiana* seeds trapped in 2005 and 2006 was lower than expected (N=71) given the total area covered (20.78m^2) and total trap duration (4.5 months). However, *J. bermudiana* seeds were trapped across most of the elevational gradients on Ridge 1 (from 516m to 690m) and Ridge 2 (from 425m to 604m), but only on two distant elevations on Ridge 3 (517m and 694m) (Figure 7). Overall, there were generally more seeds trapped on Ridge 2 (N=40 seeds in 15 traps) compared to Ridge 1 (N=29 seeds in 13 traps) and Ridge 3 (N=2 seeds in 2 traps). Although these differences were not significant (χ^2=4.38, DF=2, p=0.1119, Figure 8), the 2 seeds trapped on Ridge 3 indicate that *J. bermudiana* seeds are at least present on the invasion front in the study site.

DISCUSSION

In the West Maui Mountains, the presence of *J. bermudiana* provides a unique opportunity to link the quality of avian seed dispersal with differing levels of invasion. *J. bermudiana*'s seed dispersers play a dual role in its invasion success; *J. bermudiana* relies on its dispersers to physically move its seeds across the landscape as well as increase its germination rates once seed deposition occurs. This study finds that although *J. bermudiana*'s main seed dispserser, *Z. japonicus*, is likely to move a large number of its seeds across the landscape (see Chapter 1), the overall heterogeneous environment of the West Maui Mountains make it difficult for *J. bermudiana* to establish successfully.

(1) How does J. bermudiana density compare to seed shadows in the study site? As expected, *J. bermudiana* density decreases from where *J. bermudiana* was initially introduced to where they are well established to where they are now starting to colonize (i.e., Ridges 1, 2, and 3, respectively). With respect to the seed rain study, substantially more seeds were trapped on Ridges 1 and 2 compared to Ridge 3. The seed rain data reflects this decreasing density; that is, more seeds were generally trapped in areas where

J. bermudiana adults were more likely present. This is not unusual, as seed shadows typically follow a leptokurtic pattern with seedling density decreasing exponentially with increasing distance from source trees (e.g., *J. virginiana*, Holthuijzen and Sharik 1984, 1985a). However, with less than 20 *J. bermudiana* individuals on Ridge 3, the 2 seeds trapped in an area of such low density suggest that *J. bermudiana* seeds are at least being introduced to new areas by its avian dispersers. Given the widespread abundance of *J. bermudiana*'s main seed disperser, *Z. japonicus*, in the study site (see Chapter 1), dispersal of seeds is highly likely to reach novel habitats across the landscape.

(2) How does germination differ under greenhouse conditions versus field conditions? In addition to dispersing seeds across the landscape, the seed dispersers in this system also likely increase germination rates of *J. bermudiana* seeds. As seen in the greenhouse experiments, seed treatments mimicking avian seed gut passage had significantly higher germination rates compared to intact seed cones. That is, removal of pulp from seed cones by the avian gut will positively affect germination rates of *J. bermudiana* seeds in the field. A similar result was found for the germination of *Actinidia chinensis* (kiwifruit) by *Z. lateralis*, where seeds passed though the avian gut reached 63.7% and intact seed cones resulted 0% (Logan and Xu 2006). The difference between acid and sandpaper treatments (i.e., crop and gizzard mimicked treatments, respectively) also suggests that seed treatment by different dispersers may affect germination rates in the field. For example, strict frugivorous birds are less likely to provide efficient seed treatment due to their less muscular gizzard and potential lack of abrasive sand and grit (Stanley and Lill 2002), thereby resulting in lower germination rates compared to birds that exhibit generalist feeding behaviors. In the field, *J. bermudiana* seeds are dispersed by *Z. japonicus*, who are omnivores that feed on fruit, nectar and insects (Guest 1973, Conant 1975). Since the gizzard of *Z. lateralis*, a facultative frugivore, has dimensions similar to those found in avian insectivores (Stanley and Lill 2002), I assume that the gizzard of *Z. japonicus* is comparable and therefore likely to positively affect germination rates in the field.

Despite effective seed treatment by *Z. japonicus*, however, the conditions in the field appear to be too harsh for seeds to have reach the germination and seedling survival rates found under greenhouse conditions. In the study site, only 1.8% of the seeds in cleared plots germinated into seedlings that survived to the following year compared to the 0.28% in standing vegetation. Since seedlings were monitored the following year, it may be the case that seeds had high germination rates and seedlings suffered high mortality after germination. In this system, secondary seed dispersal is unlikely (Woo, *unpublished data*), though more thorough studies on seed predation by several different species of ants in the study site might be worth pursuing in the future as ant predation has been documented for other *Juniperus* species (Montesinos et al. 2007). Though seeds may be deposited across the study site, it is highly likely that the interactions between the seeds and their environment play an extremely important role in successful germination and seedling survival.

(3) How might environmental gradients (i.e., water and light) affect J. bermudiana *seedling growth?* For the small subset of seeds that do germinate, *J. bermudiana* must also withstand the environmental gradients present in the West Maui Mountains. Greenhouse experiments suggest that *J. bermudiana* seedlings increase biomass and root-shoot ratios with more water, which can have implications on its distribution in the study site. Given the dual rainfall gradient in the West Maui Mountains, *J. bermudiana* is likely to have higher growth and, in turn, possibly higher survival in higher elevations and on windward ridges. However, greenhouse experiments also suggest that water is less of a significant resource for *J. bermudiana* compared to light. As a result, seedling growth may be more dependent on surrounding vegetation structure as opposed to the rainfall gradient. For example, tall thickets of the nitrogen-fixing *Dicranopteris linearis* (Uluhe/Falses Staghorn Fern) in areas of high rainfall may shade out any potential *J. bermudiana* seedlings. Research on a related species show that *J. ashei* seedlings grow at significantly higher rates on edge habitats, probably due to more light availability (Van Auken et al. 2004, Burkhardt and Tisdale 1976). The presence of high light availability—as opposed to rainfall—for *J. bermudiana* seedlings may therefore be a better predictor of its distribution and spread in the study site.

Results of the greenhouse experiments and field studies suggest that *J. bermudiana* has a hard time germinating and surviving in the study site, which might explain its slow spread since its introduction in the 1930s. In this study, avian seed treatment is likely to effectively introduce viable seeds across the landscape, but seedling emergence and survival is limited. The total number of seedlings surviving the following year was extremely low (N=19). However, it may be interesting to note that the majority of the seedlings (N=11) that did survive the following year in the study site were found in an area that balanced water and light availability, which is consistent with the findings of the greenhouse experiments. That is, the majority of the seedlings were found in middle elevational plots of the second ridge, an area where rainfall is not as abundant as the higher elevations but is also an area where bare ground is present, providing ample light availability. Similar results in the literature show that *J. thurifera* seeds also had extremely low seedling emergence in the field, survived better with more water availability, and had highest seedling densities in open areas (Montesinos et al. 2007). Although avian seed dispersal is beneficial to the invasion success of *J. bermudiana*, it is, ultimately, not enough to turn this exotic species into an invasive pest. *J. bermudiana* appears to need specific environmental conditions in order to germinate and survive, conditions that may be hard to accomplish consistently in the study site.

J. bermudiana is an example of an exotic species that is not likely to be 1 of the 10 established species that becomes an invasive pest. Although it has been introduced in the wild, it has been slow to establish in the West Maui Mountains and will not likely become aggressively invasive in the near future. The slow spread of *J. bermudiana* in the West Maui Mountains is ultimately limited by the establishment phase of the invasion process. However, since *J. bermudiana* has been introduced across Hawaii since the 1920s, future studies comparing the effects of different environmental conditions on seedling emergence and survival on different islands may shed some light on how this stage of the seed dispersal cycle can affect *J. bermudiana* invasion.

Implications of these results advise invasive species control efforts to focus on perhaps other more aggressive exotic species in the study site. However, if management for *J. bermudiana* were to be considered, efforts would be minimal: cutting down *J. bermudiana* adults with large seed crops will further slow the spread of this species in the West Maui Mountains as will early removal of *J. bermudiana* juveniles in areas with consistent rainfall and adequate light availability. The movement and seed cone removal of birds are less of a concern in this system compared to seedling establishment, though future work should look at how this may compare in other systems where *Juniperus* species pose a threat to surrounding vegetation (e.g., Ansley and Rasmussen 2005) or how *J. bermudiana* is spreading on the other islands of Hawaii.

TABLES

Table 1. Nomenclature, vernacular, family and invasion status of the 19 species recorded during 2006 PCQM density surveys. Data based on 127 sample point locations, with 8 tree species measured at each location (total N=1016). Total counts for each species are separated by ridge.

Species	**Common Name**	**Family**	**Status**	**N, Ridge 1**	**N, Ridge 2**	**N, Ridge 3**
Acacia confusa	Formosa Koa	Fabaceae	Exotic	131	4	-
Araucaria columnaris/ heterophylla	Cook/ Norfolk Island Pine	Araucariaceae	Exotic	123	-	-
Cryptomeria japonica	Japanese Tsugi Pine	Taxodiaceae/ Cupressaceae	Exotic	23	-	-
Dodonaea viscose	A'ali'i	Sapindaceae	Indigenous	6	23	11
Eucalyptus species	Eucalyptus	Myrtaceae	Exotic	22	5	9
Grevillea robusta	Silk/Silver Oak	Proteaceae	Exotic	4	17	6
Juniperus bermudiana	Bermuda Juniper	Cupressaceae	Exotic	59	18	1
Lantana camara	Lantana	Verbenaceae	Exotic	-	3	14
Metrosideros polymorpha	Ohi'a lehua	Myrtaceae	Endemic	16	60	17
Osteomeles anthyllidifolia	Ulei	Rosaceae	Indigenous	2	60	30
Psidium cattleianum	Strawberry Guava	Myrtaceae	Exotic	11	4	72
Rubus argutus	Blackberry	Rosaceae	Exotic	1	-	-
Schinus terebinthifolius	Christmas Berry	Anacardiaceae	Exotic	25	27	7
Styphelia tameiameiae	Pukiawe	Epacridaceae	Indigenous	59	25	10
Syzigium cuminii	Java Plum	Myrtaceae	Exotic	-	9	-
Thuja species	Cedar	Cupressaceae	Exotic	35	-	-
Wikstroemia monticola/ awahnense	‘Akia	Thymelaeaceae	Endemic	13	27	7
Unknown species	NA	NA	NA	14 (*2 spp.*)	6 (*1 spp.*)	-

FIGURES

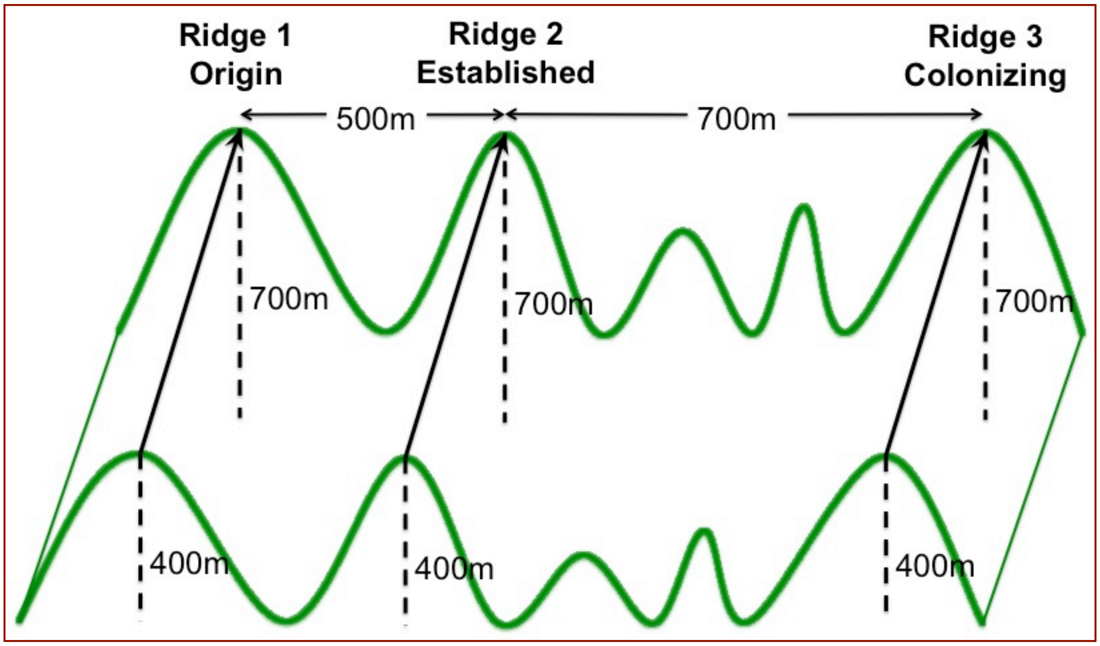

Figure 1. Diagram of study site in the West Maui Mountains of Maui, Hawaii. The study site consists of 3 upward-sloping ridges that are separated by deep gulches and differ in levels of *J. bermudiana* invasion.

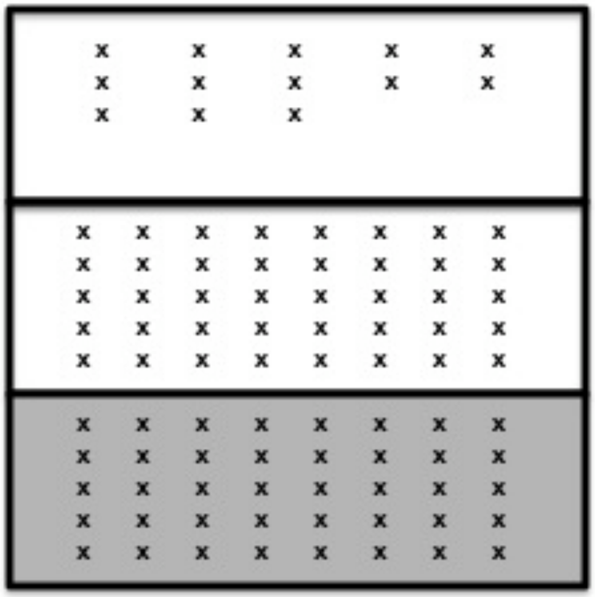

Figure 2. Diagram of one 1.5m x 1m field germination plot. White subplots indicate where vegetation was cleared; the one shaded subplot indicates standing vegetation (i.e., uncleared plot). Each "x" represents a seed that was scarified with sandpaper and planted, except for the first (i.e., top) subplot, where intact seed cones were sown.

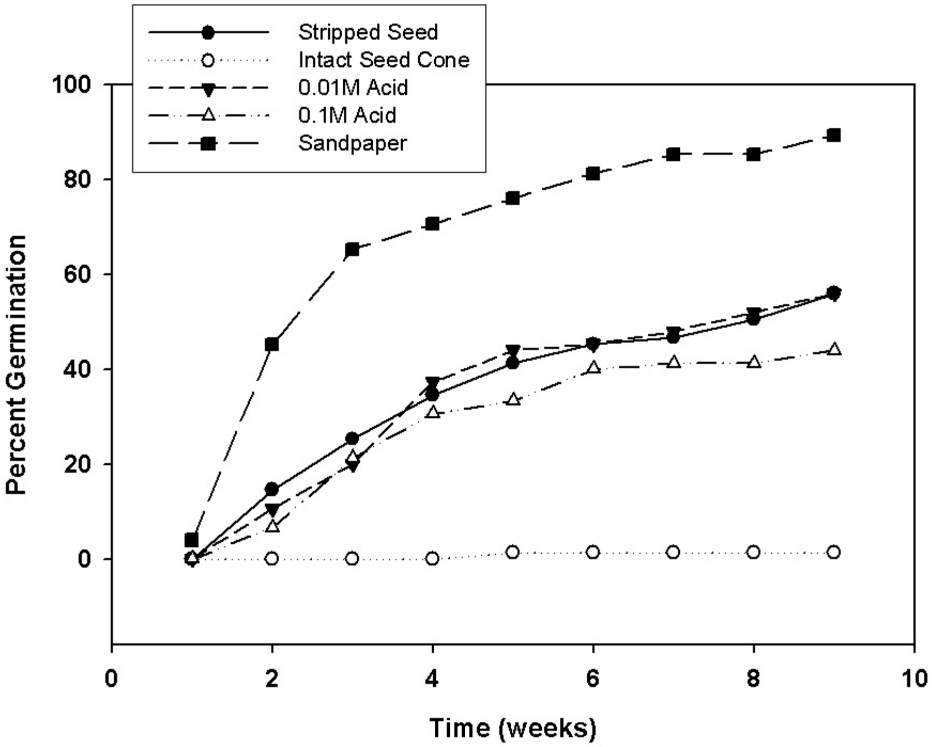

Figure 3. Percent germination of *J. bermudiana* seeds under varying treatments mimicking avian gut passage. Stripped seeds and intact seed cones served as controls. Percent germination was highest with seeds that were scarified with sandpaper (N=67).

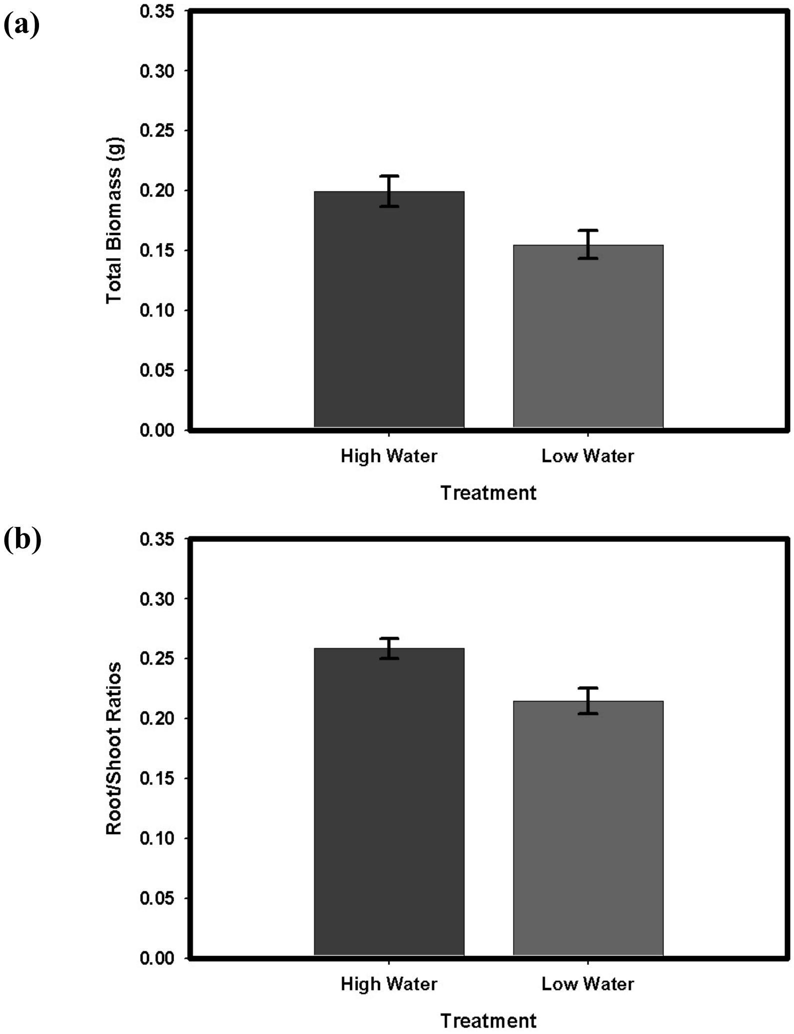

Figure 4. Effects of high and low water treatment on *J. bermudiana* (a) biomass and (b) root-shoot ratios. Plants receiving the high water treatment had significantly larger biomass ($p<0.05$) and root-shoot ratios ($p<0.005$) compared to plants receiving low water treatment.

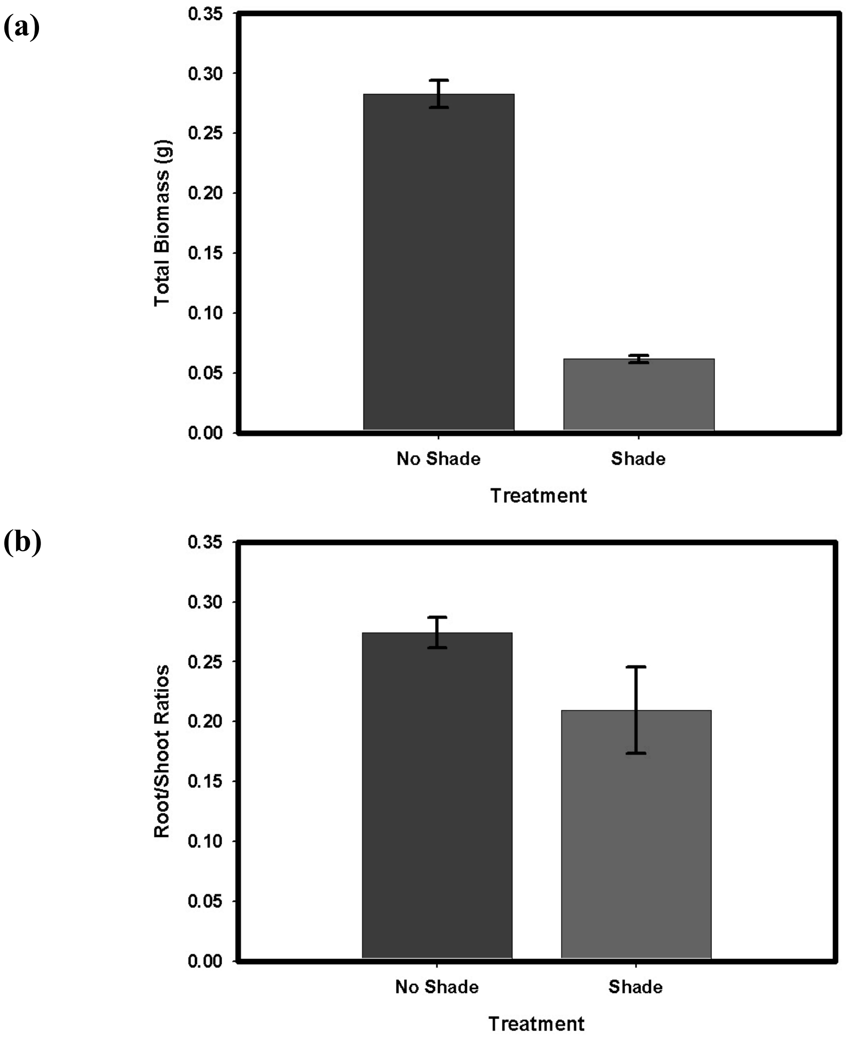

Figure 5. Effect of light treatment on *J. bermudiana* (a) biomass and (b) root-shoot ratios. Plants under ambient light (“no shade”) treatment had significantly larger biomass ($p<0.0001$) and root-shoot ratios ($p<0.005$) compared to plants under the shade treatment.

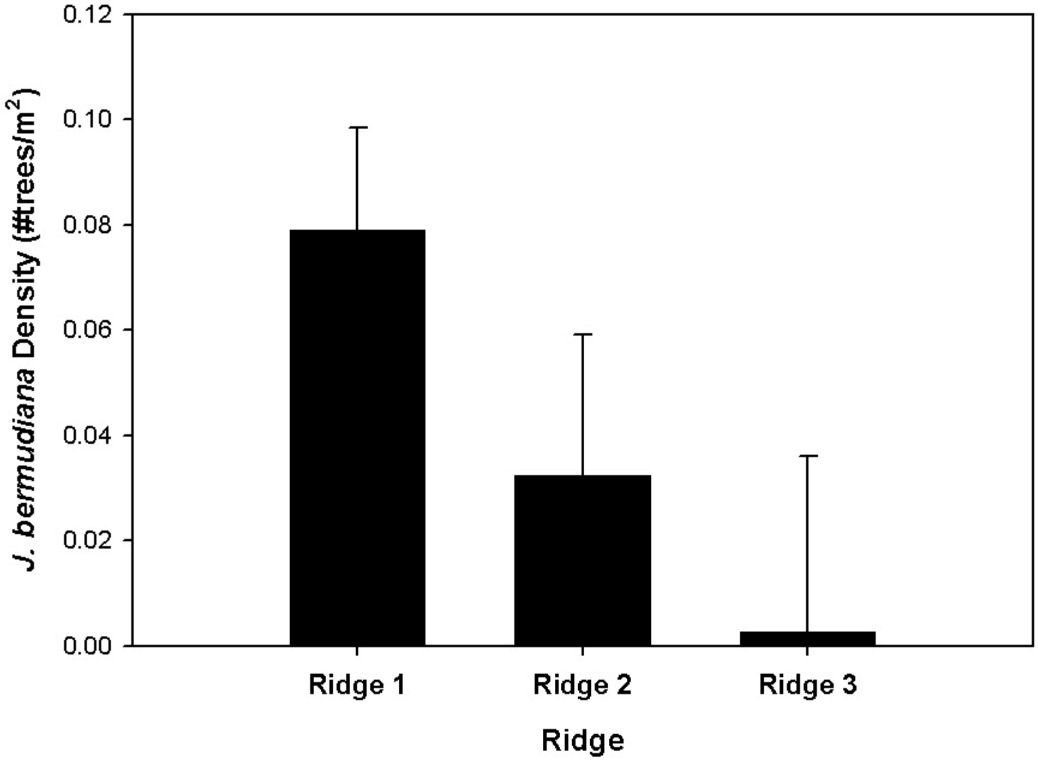

Figure 6. *J. bermudiana* density across three ridges in study site. *J. bermudiana* was most dense on Ridge 1 (N=59, 0.0791±0.0195 trees/m^2), followed by Ridge 2 (N=18, 0.0323±0.0268 trees/m^2) and, lastly, by Ridge 3 (N=1, 0.002630±0.0336 trees/m^2).

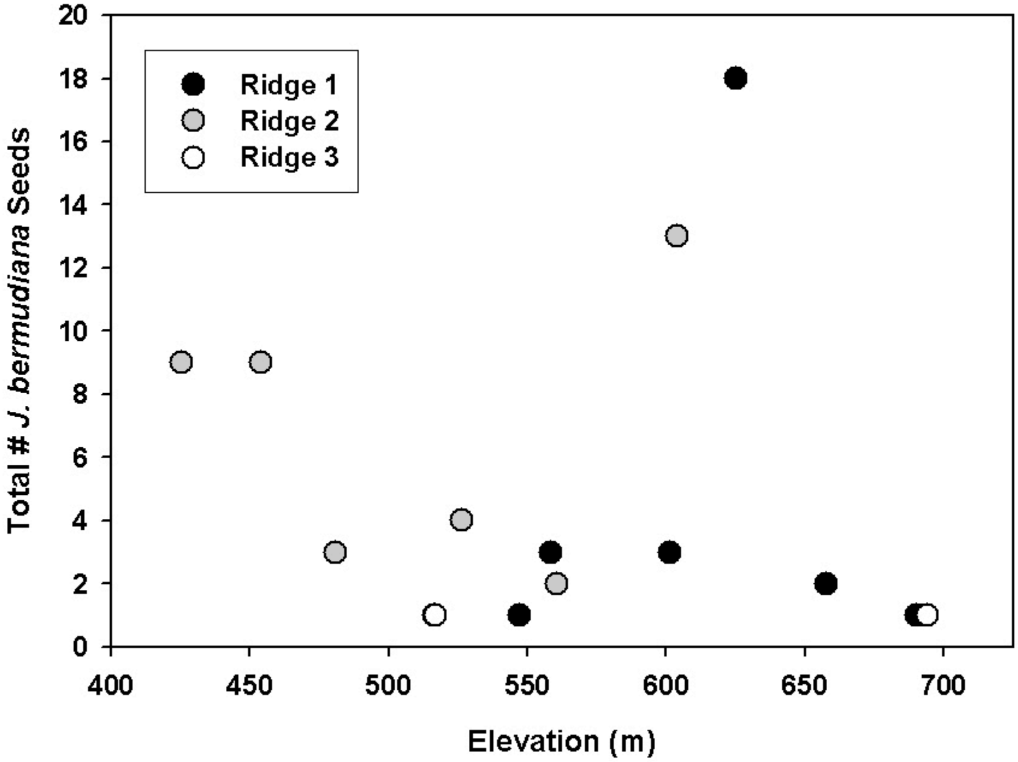

Figure 7. Total number of *J. bermudiana* seeds trapped across an elevational gradient on each ridge. Seed traps were placed every 200m along an elevational gradient on each ridge (N=10 on Ridge 1, N=10 on Ridge 2, N=7 on Ridge 3) but only certain elevations trapped *J. bermudiana* seeds (N=7 on Ridge 1, N=6 on Ridge 2, N=2 on Ridge 3).

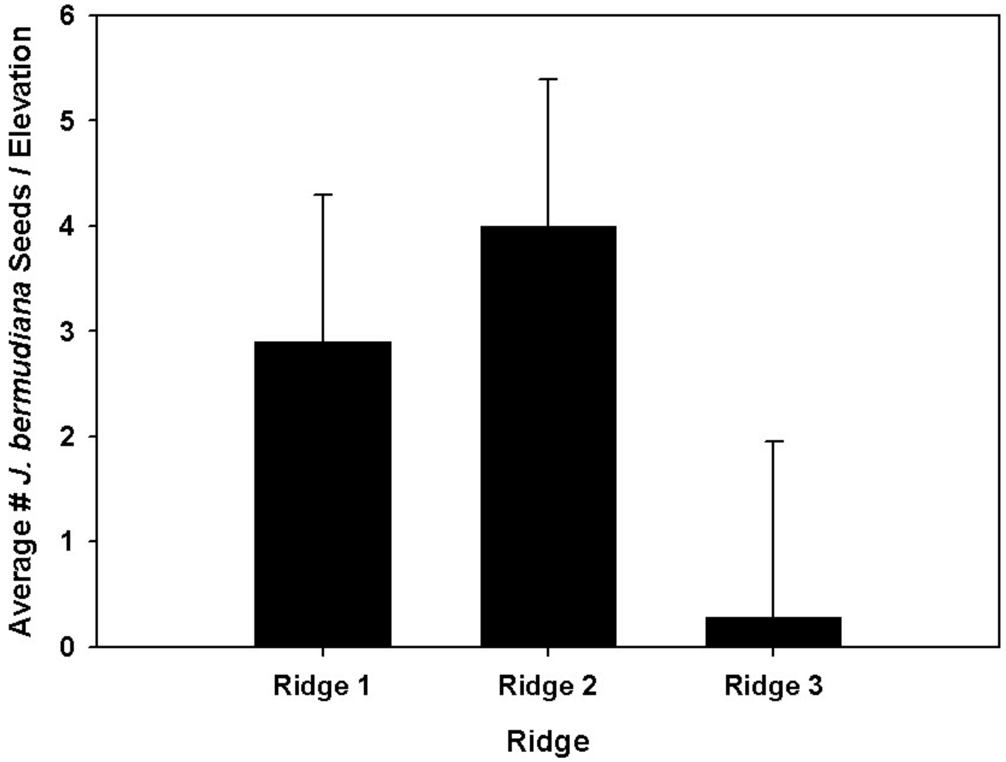

Figure 8. The average number of *J. bermudiana* seeds trapped across elevations did not significantly differ across ridges (p=0.1119). More seeds were, however, trapped on Ridge 2 (N=40 seeds in 15 traps) compared to Ridge 1 (N=29 seeds in 13 traps) and Ridge 3 (N=2 seeds in 2 traps).

III. Predicting the future spread of *Juniperus bermudiana* in Maui, Hawaii: A conceptual framework

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ABSTRACT

The growing concern of exotic plant introductions to novel habitats has increased the pressure to predict the effects of those species on a community and landscape level. The use of spatially explicit computer simulation models provides a method of predicting the distribution and spread of an exotic plant, particularly if the majority of parameters can be accurately estimated from data. Since many exotic plants depend on animal-mediated seed dispersal for invasive spread, this study focuses on developing a model that describes how data from greenhouse and field studies, coupled with data from the *Juniperus* literature can be used to parameterize the different processes of the seed dispersal cycle for use in a computer simulation model. In this study, the current development of this working model and future directions for this model are presented. This study is part of a three step process whose ultimate goals are to develop spatially explicit operational functions to parameterize each key process in the seed dispersal cycle, provide validation of the model so as to build confidence in model predictions, and conduct sensitivity analyses to better understand which processes in the seed dispersal cycle are most likely to influence exotic plant distribution and spread.

INTRODUCTION

Exotic plant introductions have increased dramatically over the past several decades. With the growing number of invasions on a global scale, the pressure to predict and manage these invasions has also increased. The use of spatial models in predicting the spread of invasive species dates back to Skellam (1951) and his use of reaction-diffusion (RD) models on the spread of muskrats in central Europe. To date, RD models are still the most common models in predicting spread of invasive species (With 2002, Higgins and Richardson 1996). Although RD models have been relatively successful for animal invasions (Levin 1992), this modeling approach has not been widely used for plant invasions (Higgins and Richardson 1996) because of their failure to address plant attributes, environmental heterogeneity, and stochasticity (Higgins et al. 1996). Incorporating spatial heterogeneity into models of invasions has only recently been highlighted in the literature (With 2002, 2004). Though some studies have successfully incorporated spatial environmental heterogeneity into their models in animal invasion distribution and spread (e.g., Turchin 1998, Revilla et al. 2004), an extension of these efforts should be made for exotic plants dependent on avian seed dispersal (Buckley et al. 2006). The use of spatially explicit computer simulation models will more likely lead to successful predictions of spread of an exotic plant on a landscape level. Unlike RD models, this modeling approach uses space and time as discrete variables thereby allowing the incorporation of spatial heterogeneity, stochasticity and local interactions.

The goal of this study is to establish the initial process of developing a modeling approach that incorporates the different processes involving the seed dispersal cycle and its effects on predicting the future distribution and spread of an exotic plant, *Juniperus bermudiana* (Bermuda Juniper). As described by Wang and Smith (2002), the seed dispersal cycle incorporates key processes from both seed dispersal studies (i.e., fruit production, fruit removal, seed dispersal) and plant demography studies (i.e., germination, seedling, sapling and adult recruitment). Conceptually, there is a three-step modeling approach used for this study: (1) the development of spatially explicit operational functions to parameterize each key process in the seed dispersal cycle; (2)

validation of the model to build confidence in model predictions; and (3) sensitivity analyses to better understand which processes in the seed dispersal cycle is most likely are influence exotic plant distribution and spread.

In particular, this chapter focuses on describing how data from the field and from the literature can be used to parameterize the different processes of the seed dispersal cycle for use in a computer simulation model. To date, few studies have successfully integrated empirical data with theoretical work in predicting invasive distribution and spread (see Murphy et al. 2008). Field data was collected on the *J. bermudiana* system in Hawaii (Chapters 1 and 2) and contributed to describing the processes of seed cone production, seed cone removal, seed dispersal, and germination. Because plant demography studies in the field failed to produce results, data from *Juniperus* studies in the literature formed the basis of describing the processes of seedling, juvenile and adult growth and survival. Model parameters of these data were incorporated into a spatially explicit simulation model, where all processes were linked and simulated on an annual basis (Figure 1).

Because this model is currently being developed, validation of the model and sensitivity analyses will not be reported. Parameter estimates are presented here, followed by a discussion of what considerations still need to be taken into account before validation and sensitivity analyses can occur. It is the goal of this model to predict the future distribution and spread of *J. bermudiana* in the West Maui Mountains and inform invasive species management and control; ultimately, however, the goal of this model is to better understand how the processes of seed dispersal can predict plant community structure across a landscape.

METHODS

Study system

J. bermudiana (Cupressaceae) was the dominant endemic tree in Bermuda until a catastrophic introduced scale epidemic killed 95% of the population in the late 1940s and early 1950s (D.B. Wingate, *personal communication*). Records show that as many as

6,500 *J. bermudiana* trees were introduced to forest reserves in all Hawaiian Islands by 1921 (Little and Skolmen 1989). *J. bermudiana* is fully naturalized and remains invasive on the mid-Atlantic island of St. Helena where it was introduced in the 1930s (Ashmole and Ashmole 2000). Although *J. bermudiana* is not at this point a major invasive pest in the West Maui Mountains, a similar fate could occur in Hawaii. *J. bermudiana* also depends on avian seed dispersal of its seed cones (each of which encase 1-3 seeds), both in its native range (D.B. Wingate, *personal communication*) and in Hawaii (see Chapter 1). My field observations in the West Maui Mountains have revealed *J. bermudiana* seed cones to be effectively dispersed by the widely abundant, pervasive and exotic *Zosterops japonicus* (Japanese White-Eye) (see Chapter 1 for more details).

Data for this study was conducted on privately owned land in the West Maui Mountains of Maui, Hawaii. Permission was granted to conduct research in both the Kapunakea Preserve (20° 55’ 30” N, 156° 38’ 13” W), owned by The Nature Conservancy of Hawaii, and in the Pu’u Kukui Watershed (20° 56’ 26” N, 156° 37’ 58” W), owned by Maui Land and Pineapple Company, Honolua Division. The West Maui Mountains, a volcanic system dating 1.3-1.6 million years old, is also slit by deep amphitheater-headed valleys (Stearns 1966), which result in distinct upward-sloping ridges across the entire mountain range. Data was collected on three specific ridges, on one of which *J. bermudiana* was first planted (in the Pu’u Kukui Watershed area, hereafter Ridge 1). The ridge leeward (i.e., south) of Ridge 1 (on the Kapunakea Preserve, hereafter Ridge 2) has many well-established *J. bermudiana* adults, while the ridge most leeward of the three ridges (also on the Kapunakea Preserve, hereafter Ridge 3) has fewer than 20 *J. bermudiana* adults. Ridge 3 is on the edge of the *J. bermudiana* distribution, and is therefore considered to be the potential invasion front for this species. The study site for all three ridges extends from 350m at the lowest elevation (bordering pineapple/sugar cane fields) to 700m at the highest elevation (bordering wet high elevational forests). The vegetation zone of most of the study site can be characterized as a mesic low elevational forest. Density surveys in the study site revealed a total of 19 different species (Table 1, Chapter 2) across the three ridges, with *J. bermudiana* density decreasing from Ridges 1 to 3 (see Chapter 2). The study site is also home to 14 exotic bird species and 1 endemic bird species; avian seed dispersal by *J. bermudiana*, however, is primarily dependent on the most dominant of these species, *Z. japonicus* (Table 1, Chapter 1).

Model description and parameter estimation

The model described in this chapter uses an annual time step, and a two-dimensional grid of sites represents space. To accommodate the entire study area in the West Maui Mountains, the model started with a very coarse grid cell size of 1600m^2. The entire grid space was 20 grid boxes x 20 grid boxes and consisted of five ridges differing in width (i.e., Ridges 1, 2, 3 with two additional ridges between Ridges 2 and 3) which were all separated by deep gulches differing in width (i.e. a total of four gulches). During each annual time step the model simulated the processes of the seed dispersal cycle as described in Wang and Smith (2002): seed cone production, seed cone removal, seed dispersal, germination, and seedling, juvenile, and adult growth and survival.

Elevation and germination probability for each grid cell was defined and static throughout the simulation. The number of *J. bermudiana* individuals in each stage class was characterized for each grid cell but these numbers were dynamic. That is, depending on the transition probabilities of each stage class and the outcome after each time step, these numbers were likely to change over time. Elevation for each grid cell on a ridge was determined by data from the field; elevation was measured along an elevational transect on Ridges 1, 2, and 3 and interpolated for the ridges between Ridges 2 and 3. Elevation for each grid cell in a gulch was approximated. Initial numbers for germination and transition probabilities are more clearly defined in the sections below on germination and seedling, juvenile, and adult growth and survival, respectively.

Seed cone production. Seed cone production for this model was limited to 12 weeks per year, which was the time *J. bermudiana* has been consistently observed to produce ripe seed cones (i.e., mid September to mid December in the study site; Woo, *personal observation*). Data from the number of seed cones per adult was collected from the *J. bermudiana* trees measured during the density surveys (see Chapter 2 for methods).

Of the 1016 trees measured from these surveys, only 78 *J. bermudiana* adults were measured and only 8 of those had ripe seed cones present. Because the total number of seed cones per adult tree (CPT) was assumed to depend on *J. bermudiana* density (JBD), a linear regression (JMP 5.1.2, SAS Institute, Inc.) was conducted on these 8 adults (R^2=0.6224; N=8 individuals; F=9.8903; $p<0.05$, Figure 2):

$$\ln(CPT/JBD)) = 10.355 - 7.388*(JBD) \tag{1}$$

which was transformed from the initial equation to yield:

$$CPT = 10.355*(JBD)*e^{(-7.388*JBD)} \tag{2}$$

Thus, if the total number of adults is known in each grid cell, the total number of seed cones can be calculated using the following equation:

$$\#\text{ cones/grid cell} = (\#\textit{ J. bermudiana}\text{ Adults})*CPT \tag{3}$$

Seed cone removal. Z. japonicus was found to be the most effective seed disperser for *J. bermudiana* seed cones with respect to forager abundance, visitation rates, seed handling and movement (see Chapter 1). Because *Z. japonicus* behaviors will have the most impact on the future distribution and spread of *J. bermudiana* in the landscape, modeling the process of seed cone removal was based only on *Z. japonicus* individuals during focal tree watches (see Chapter 1 for methods). We assumed that the total number of seed cones eaten per tree hour depended on the number of bird visits per tree hour, the time spent foraging per visit and the number of seed cones eaten per unit time.

The number of bird visits per tree hour was assumed to depend on the number of seed cones per tree (CPT) and on elevation (elev). The number of bird visits generally decreased with elevation (linear regression, R^2=0.1754, N=27 tree hours, F=5.3195, p=0.0297, JMP 5.1.2, SAS Institute, Inc.), except for areas with high *J. bermudiana* density (Figure 3). A multiple regression equation was constructed to determine how the number of bird visits per tree (BV) watch hour changes with seed cone availability and elevation (R^2=0.1098; N=35 tree watch hours; $F_{elevation}$=0.360, $p_{elevation}$=0.5526; $F_{cones/tree}$=0.332; $p_{cones/tree}$=0.5685; $F_{elevation*cones}$=0.184; $p_{elevation*cones}$=0.6708) using JMP 5.1.2 (SAS Institute, Inc.):

$$BV = -1.4685 + 0.01127*(elev) + 0.0009344*(CPT - 0.0000012*(elev*CPT)) \qquad (4)$$

The time spent foraging per visit was separated into two different classes of *Z. japonicus* behaviors that were likely to affect seed cone removal rates and seed dispersal movements. From failure time data of visitation rates during focal tree watches (see Chapter 1 for methods), *Z. japonicus* individuals were distinguished as either “movers” or “stayers,” where movers were defined as individuals that visited *J. bermudiana* adults for less than or equal to a 1-minute duration whereas stayers were defined as individuals that visited for more than a 1 minute duration. Average numbers for each group was used for the model. For individuals that visited for 1 minute or less, their average time was 0.732±0.250 minutes (N=153 individuals); for individuals that visited for more than 1 minute, their average time was 2.60±1.09 minutes (N=60 individuals).

Since no obvious pattern could be made out of the number of seed cones eaten per minute when *Z. japonicus* was foraging, the average rate from all observations (i.e., 3.303571±0.88291 seed cones gulped per minute, N=14 individuals; Figure 4) was used in the model. The total number of seed cones eaten per minute (CEPM), however, is a function of the number of seed cones available for each tree:

$$CEPM = 3.303571*(CPT/(k+CPT)) \qquad (5)$$

Finally, the probability of the number of seed cones eaten per hour in each grid cell was a function of the number of seed cones eaten per hour, time spent foraging (which depended on whether the bird was a mover or stayer), and the number of bird visits, divided by seed cone availability:

$$P(\text{eaten/hr})_{\text{stayer}} = (\text{each grid cell})*(\text{CEPM}*2.60*\text{BV}/(\text{CPT}+1\text{-grid cell}), \text{ and} \quad (6)$$

$$P(\text{eaten/hr})_{\text{mover}} = (\text{each grid cell})*(\text{CEPM}*0.732*\text{BV}/(\text{CPT}+1\text{-grid cell}) \quad (7)$$

Seed dispersal. Since the probability of seed cones eaten by *Z. japonicus* was based on an hour time frame, a new function was constructed to depict a more reasonable time step (1 week) for use within the dispersal kernel:

$$P(\text{eaten/wk})_{\text{stayers}} = 1-(1-P(\text{eaten/hr})_{\text{stayers}})^{(24\text{hrs}*7\text{days})} \quad (8)$$

$$P(\text{eaten/wk})_{\text{movers}} = 1-(1-P(\text{eaten/hr})_{\text{movers}})^{(24\text{hrs}*7\text{days})} \quad (9)$$

The bird follow data (refer to Chapter 1 for methods) measuring the distance traveled by *Z. japonicus* after a visit to a tree was also separated between movers and stayers. To keep consistent with the above definitions, movers were individuals that left an area and flew at least 20m within a 1-minute period, whereas stayers were individuals that remained in an area for at least a 1-minute period before flying at least 20m. A frequency distribution between the two groups show movers were more likely to contribute to long distance seed dispersal compared to stayers (Figure 5). With two separate movement patterns for *Z. japonicus*, two separate dispersal kernels were created to determine the distance seeds were moving around the grid space.

Maximum likelihood (ML) methods were used to estimate the distances traveled by each disperser group. That is, given the data observed for each group, estimates were found to maximize the likelihood of observing those data (Quinn and Keough 2002). More specifically, given the sample mean and variance of the distance traveled, the ML function will provide the likelihood of observing the data for all possible values of μ, the population mean for the distances traveled. As with many seed rain studies, an exponential distribution was first used to describe both dispersal kernels, using a single parameter (λ) with the following probability density function: $f(y) = \lambda e^{(-\lambda y)}$. The ML function for the distance traveled, then, is

$$P(d|\lambda) = \Pi_{(i=1:N)} \lambda e^{(-\lambda d_i)} \quad (10)$$

and the one-step dispersal probability (P(dispersal)) can then be transformed to:

$$\mathrm{P(dispersal)} = e^{-((\mathrm{d}i-M)^{\wedge}2)/2V} \tag{11}$$

where M and V are the observed mean and variance, respectively, for dispersal movement. For this model, bird follow data calculated these values to be $M=0.0418{*}e3$, $V_{movers}=1.928{*}e3$, and $V_{stayers}=1.825{*}e3$. However, because we are calculating this function across a two-dimentional grid space, we also needed to incorporate an n-fold convolution function, where the probability of distance traveled can be calculated in two steps (i.e., traveling to distance x in the first step and traveling to distance y-x in the second step). The probability of traveling to distance y, then, is the summation of these two-step probabilities for all possible x distances in the grid space. The resulting transition dispersal kernel used for this model was:

$$\mathrm{P(dispersal,}y) = e^{-((\mathrm{distyd-M})^{\wedge}2)/2\mathrm{V}} \tag{12}$$

where *distyd* is the distance from the first step to the second step across each cell in the grid space. Both dispersal probabilities were normalized across the grid space and the dispersal kernel was calculated from the product of P(dispersal), P(dispersal, y), and distances between grid cells.

To determine the ratio of stayers to movers, with respect to seed cone abundance, a logistic regression (JMP 5.1.2, SAS Institute, Inc.) was constructed ($R^2= 0.0197$, N=213 individuals, $\chi^2=4.996$, p=0.0254) for use in the model:

$$\mathrm{P(stay)} = (e^{(-1.3798+0.00004726*\mathrm{CPT})})/\ (1+(e^{(-1.3798+0.00004726*\mathrm{CPT})})) \tag{13}$$

Finally, the number of new seed cones entering a cell depended on the number of seed cones dispersed by stayers in each grid cell and was given by the product of #cones/grid cell, P(stay), $\mathrm{P(eaten/wk)}_{stayers}$, and the corresponding dispersal kernel.

Similarly, the number of new seed cones entering a cell also depended on the number of seed cones dispersed by movers in each grid cell, which was the product of #cones/grid cell, 1-P(stay), P(eaten/wk)$_{\text{movers}}$, and its corresponding dispersal kernel. The total number of seed cones entering any given grid cell, then, was the addition of seeds contributed by movers and stayers, multiplied by the 12 week period that *J. bermudiana* has ripe seed cones.

Germination. J. bermudiana seeds planted in the study site experienced substantially smaller germination rates compared to seeds planted under greenhouse conditions (see Chapter 2). No pattern was observed from the 22 seedlings that emerged from the field germination experiment; seedlings emerged on all ridges and at different elevations on each ridge. As a result, the germination probabilities for each grid cell remained static and set to a relatively high 1% germination rate across ridges and a 0% germination rate in each gulch. Because *J. bermudiana* adults were not present in the low elevations of deep gulches (Woo, *personal observation*), 0% germination was assumed in those grid cells. Additionally, although many intact seed cones fell beneath source trees (Woo, *personal observation*), intact seed cones had 0% and 1.3% germination in the field and greenhouse experiment, respectively, and were therefore not considered in this model. Further, secondary seed dispersal from intact seed cones was also assumed to be negligible (Woo, *unpublished data*).

Seedling, juvenile, and adult growth and survival. Because plant demography studies were not conducted with the *J. bermudiana* study system, growth and survival of different *J. bermudiana* stage classes—seedlings, juveniles and adults—were approximated from a combination of *J. bermudiana* field measurements and *Juniperus* demography studies from the literature. More specifically, stage classes were determined from height data measured during *J. bermudiana* density surveys (see Chapter 2 for sampling methods): *J. bermudiana* seedlings had a height of less than 2m; juveniles had a height between 2-5m; and adults had a height greater than 5m.

The study on the growth and survival of *J. ashei* seedlings by Van Auken and colleagues (2004) provided rough estimates of growth and survival for *J. bermudiana* seedlings. Given that it will take approximately 8 years to reach a height of 2m under greenhouse conditions (Woo, *unpublished data*), seedling rate of survival was estimated to be $0.05^{(1/8)}$ and seedling rate of growth was estimated to be 1/8. The probability of a seedling remaining in the seedling stage (P(S→S)) was calculated to be (rate of survival)*(1-(rate of growth)) and the probability of a seedling moving onto the juvenile stage (P(S→J)) was calculated to be (rate of survival)*(rate of growth). In short:

$$P(S\rightarrow S) = (\text{rate of survival})*(1-(\text{rate of growth})) = 0.05^{(1/8)}*(1-(1/8)) = 0.6017 \qquad (14)$$

$$P(S\rightarrow J) = (\text{rate of survival})*(\text{rate of growth}) = 0.05^{(1/8)}*(1/8) = 0.0860 \qquad (15)$$

The growth and survival of *J. bermudiana* juveniles were based on height data collected from the field and on Vasiliauskas and Aarssen's (1992) study on *J. virginiana*, respectively. Mean ages (year) and mean heights (m) from 20 stands in eastern Ontario from Vasiliauskas and Aarssen (1992) study on *J. virginiana* were regressed to estimate a growth rate for *J. bermudiana*. Using JMP 5.1.2 (SAS Institute, Inc), growth rate was approximately 0.1296 m/yr (R^2=0.780, N=40, F=134.712, p<0.0001) for the all height classes (Figure 6). The transition probability for juveniles to adults (P(J→A)) was calculated to be:

$$P(J\rightarrow A) = \text{growth rate}/\text{juvenile height class} = (0.1296\text{ m/yr}) / (5\text{m}-2\text{m}) = 0.0432 \qquad (16)$$

Juvenile mortality was calculated from the frequency of individuals surviving in sequential height classes starting at 8m (separated by 2-year intervals); the classes below 8m were not used (Figure 7). Height data from *J. bermudiana* density surveys (see Chapter 2 for methods) was regressed using JMP 5.1.2 (SAS Institute, Inc.). The resulting slope was 0.2176 (R^2=0.83832, N=6, F=20.740, p=0.0104, Figure 8). With an overall 0.1296 m/yr growth rate, the mortality of *J. bermudiana* can be approximated to be 0.088 individuals/year (i.e., slope – growth rate).

The survival of *J. bermudiana* adults were based on the approximation that adults reach maximum age at 100 years. Therefore, adult survival = (1-(1/100)) and was multiplied across the entire grid space to update numbers of adults after each time step. In the model, *J. bermudiana* adults are the only individuals that are density dependent.

Finally, three separate equations were used to update seedling, juvenile, and adult individuals in each grid cell:

$$\text{Total seedlings} = P(S \rightarrow S)*(\#\text{Seedlings}) + P(\text{germination})*(\#\text{New Seeds}) \tag{17}$$

$$\text{Total juveniles} = P(J \rightarrow J)*(\#\text{Juveniles}) + P(S \rightarrow J)*(\#\text{Seedlings}) \tag{18}$$

$$\text{Total adults} = P(J \rightarrow A)*(\#\text{Adults}) + (\text{Adult Survival})*(\#\text{Adults}) \tag{19}$$

After the total number of seedlings, juveniles, and adults in each grid cell were updated, the model looped back to the next time step, recalculating seed cone production, seed cone removal and so on until the final number of time steps for the entire loop were reached. Model simulations were coded in MATLAB 7.6 (MathWorks) and can be found at the end of the chapter.

CURRENT STATUS OF MODEL

The spatially explicit simulation model revealed *J. bermudiana* to explode uncharacteristically after 4 time steps. This suggests that there are a number of errors with the model. This is likely due to how the seed dispersal cycle is simulated within the model parameters. Some effort was made to fix some of these errors in the current model, but, unfortunately, there was not enough time to spend looking over the model in more detail. Although some issues were addressed, more time will be needed to find and correct some of the other errors in the program. Without reasonable model outputs to currently present, the discussion will be reserved to what future directions is needed with the current model.

DISCUSSION

Once a working model has been developed that makes biological sense for the *J. bermudiana* system, the model will likely also benefit from more rigorous estimates of parameters, particularly with the growth and survival data for *J. bermudiana* stage structure. Additionally, a finer grid size and a larger grid space that predicts outside the study site would better inform our understanding of *J. bermudiana* across the West Maui Mountains.

Validating this model is of crucial importance to its effectiveness. After a working model is produced, validation can be accomplished through the use of old aerial photographs of the study site, geographic information system (GIS) tools, and the working model to see if its initial distribution in the study site can predict its current distribution. If we assume *Z. japonicus* behaviors and environmental conditions to be static since *J. bermudiana* was first planted, then the distribution would be expected to be somewhat similar to how it is now. If validated, there will be more confidence to use this model to project into the future.

Conducting sensitivity analyses are also of particular usefulness. Several different parameters in this model are subject to manipulation, which can then be used to answer basic ecological questions on their effects on community structure. For example, germination rates and ratio of movers:stayers are two parameters that could be changed and tested fairly easily to see how numbers can affect *J. bermudiana* distribution in the study site. These types of analyses have important implications on the how vegetation structure can change depending on how seed dispersal processes are manipulated. This can inform basic community ecology and also restoration and conservation biology.

This model has the potential to predict *J. bermudiana's* invasion success. Perhaps, more importantly, this model also has the potential to test basic ecological theory with respect to seed dispersal, community assembly, and conservation biology. Closing the seed dispersal loop with a simulation model can provide a robust method in furthering our understanding of just how important specific processes of avian seed dispersal affect the successful invasion of *J. bermudiana* and other plant-bird systems.

FIGURES

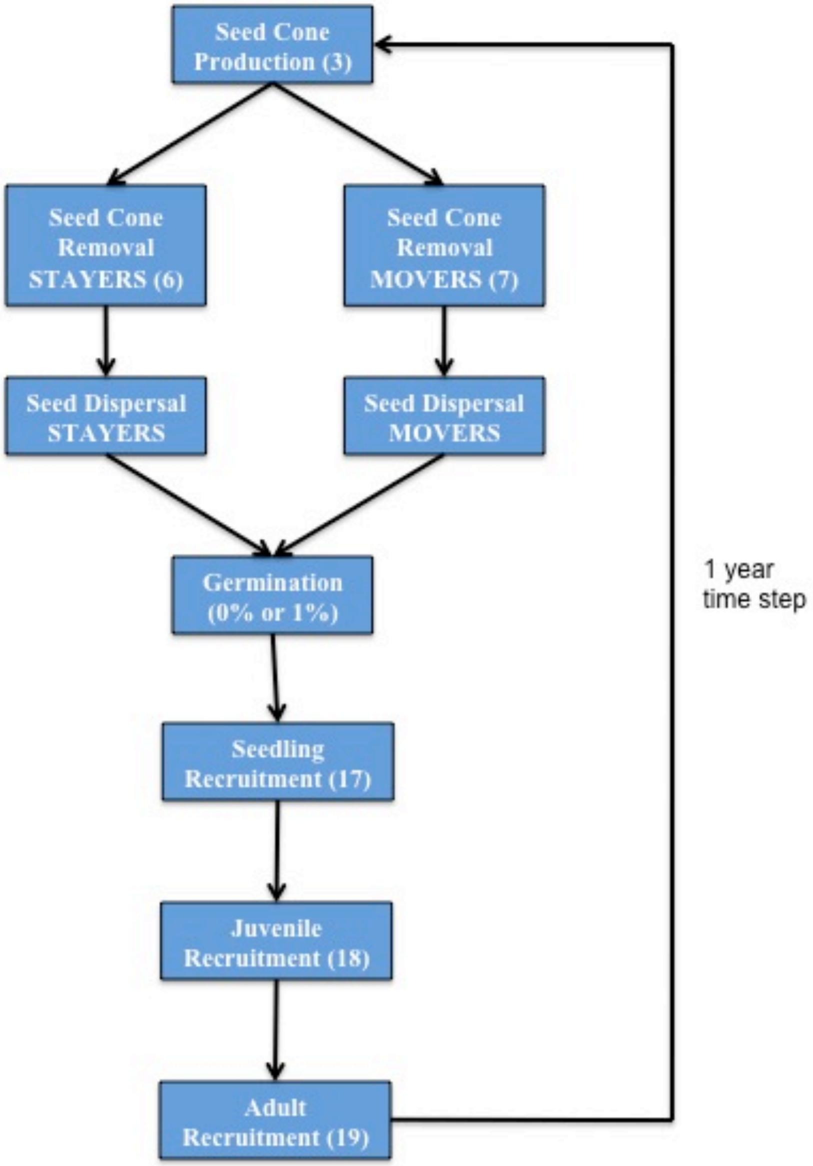

Figure 1. Diagram of the links between key processes of the seed dispersal cycle simulated each year in the spatially explicit computer simulation model for the *J. bermudiana* system. The numbers in parentheses refer to the final equations used in that process. Movers were defined as birds that left an area ≤ 1-minute period; stayers were defined as birds that left an area after staying for at least a 1-minute period (an area was either a *J. bermudiana* adult for seed cone removal rates and a 20m area for seed dispersal distances).

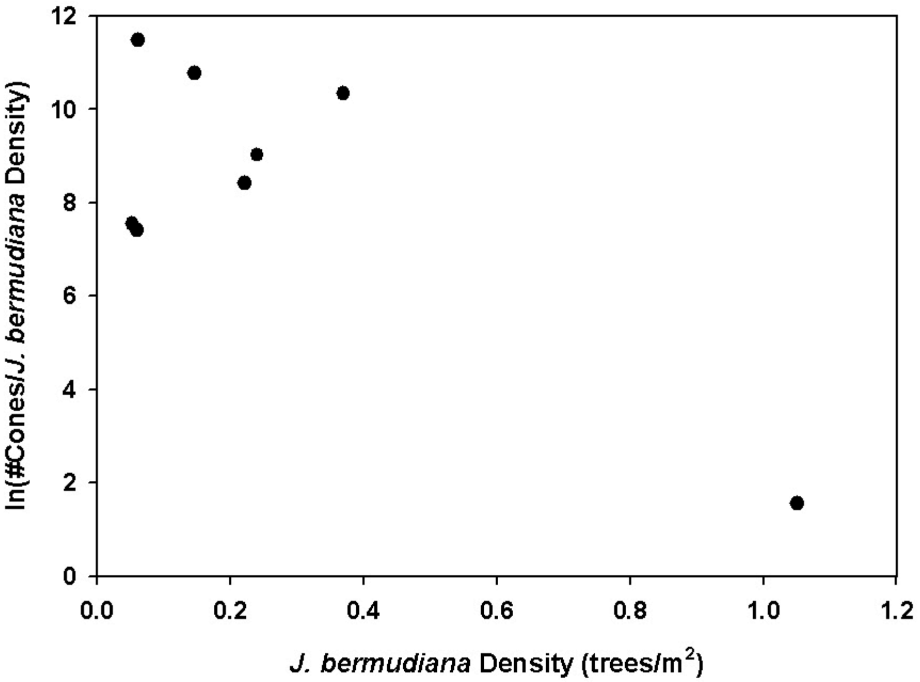

Figure 2. There was a significant relationship between cones per adult tree and *J. bermudiana* density (linear regression was on ln(#cones/*J. bermudiana* density) by *J. bermudiana* density on 8 individuals, R^2=0.622; $p<0.05$).

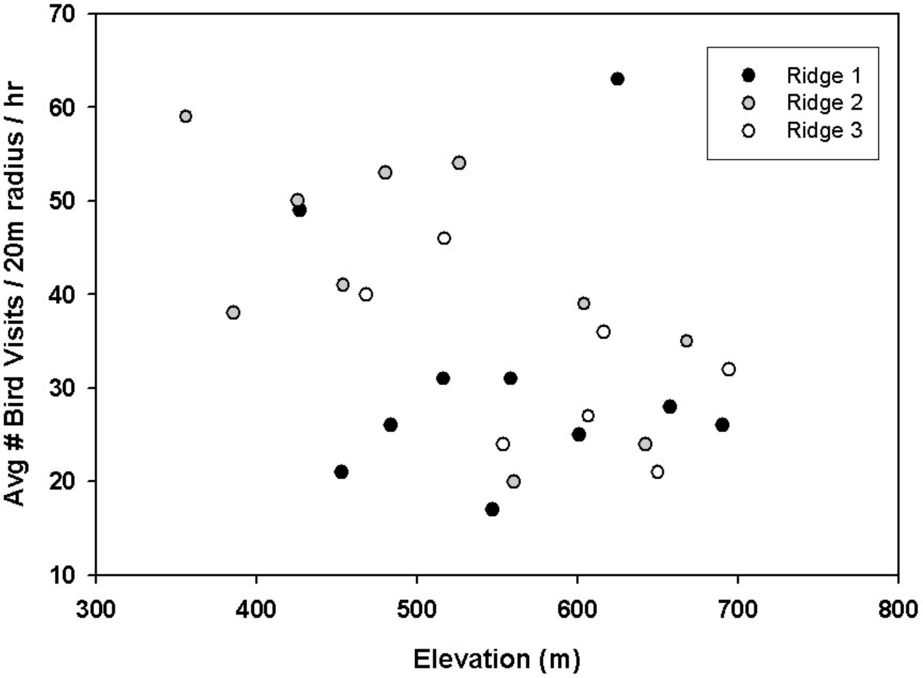

Figure 3. The total number of bird visits recorded during point counts surveys were scaled up to an hour. Bird visits generally decreased with elevation (linear regression, $R^2=0.18$, N=27 point count locations, $p<0.05$). The outlying point on Ridge 1 (i.e., 625m, 63 visits) was where *J. bermudiana* was first planted in high densities in the West Maui Mountains, likely resulting in the high number of bird visits.

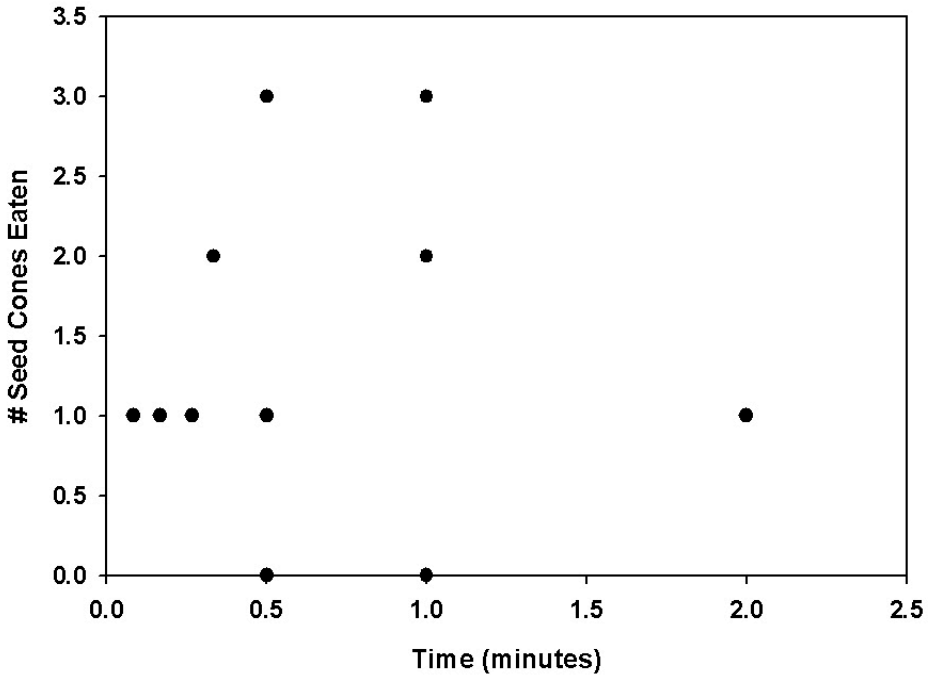

Figure 4. There were no obvious patterns for the number of seed cones eater per minute by *Z. japonicus*. The average rate from all observations was calculated to be 3.303571±0.88291 seed cones gulped per minute (N=14 individuals).

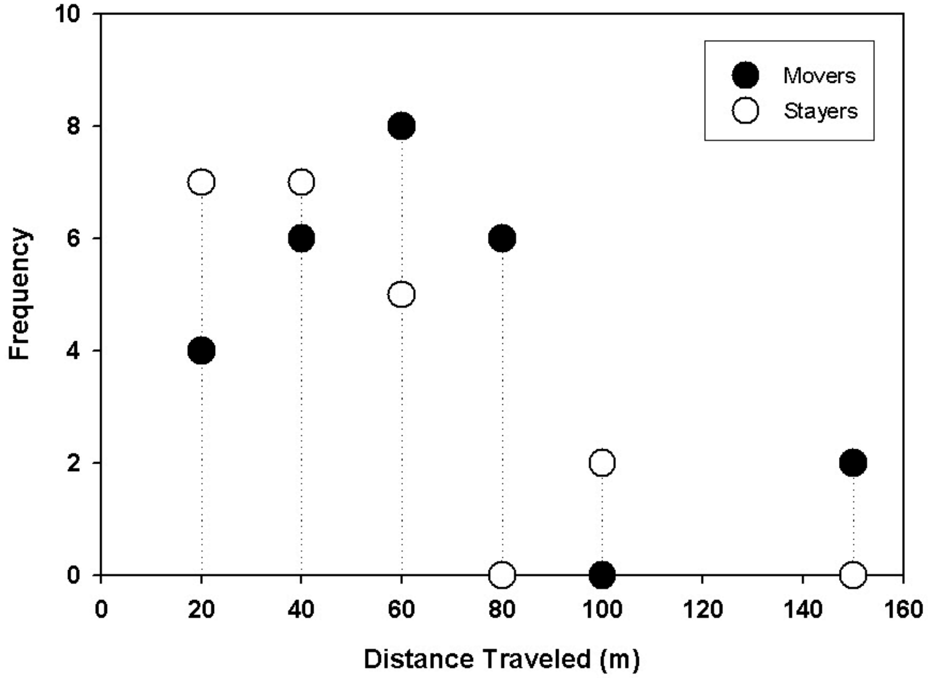

Figure 5. Frequency distribution of distance traveled between movers and stayers. Movers were individuals that left an area and flew at least 20m within a 1-minute period, whereas stayers were individuals that remained in an area for at least a 1-minute period before flying at least 20m. The average distance traveled with movers and stayers were 51.37±34.51m (N=28) and 40.82±20.11m (N=22), respectively.

Figure 6. Data from a study by Vasiliauskas and Aarssen (1992) show mean ages (year) and mean heights (m) from 20 stands of J. *virginiana* in eastern Ontario, separated by sex. Growth rate was approximately 0.1296 m/yr (linear regression, R^2=0.78, N=40, p<0.0001).

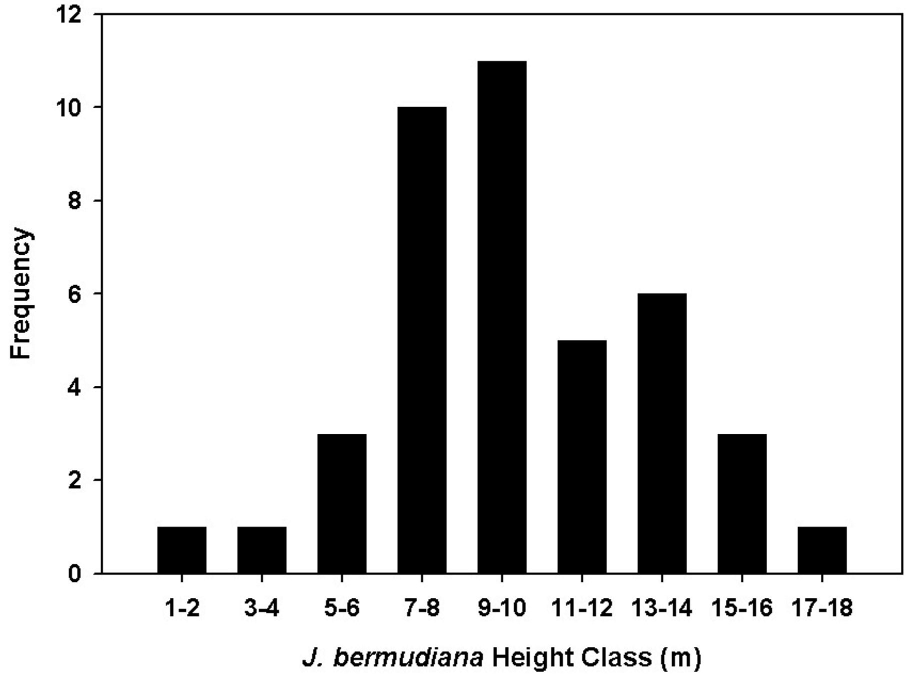

Figure 7. Frequency of *J. bermudiana* height classes from surveys, separated by 2m intervals. Growth and mortality of *J. bermudiana* trees were calculated from heights 7-18m. Heights 6m and below were not used to estimate *J. bermudiana* growth and mortality.

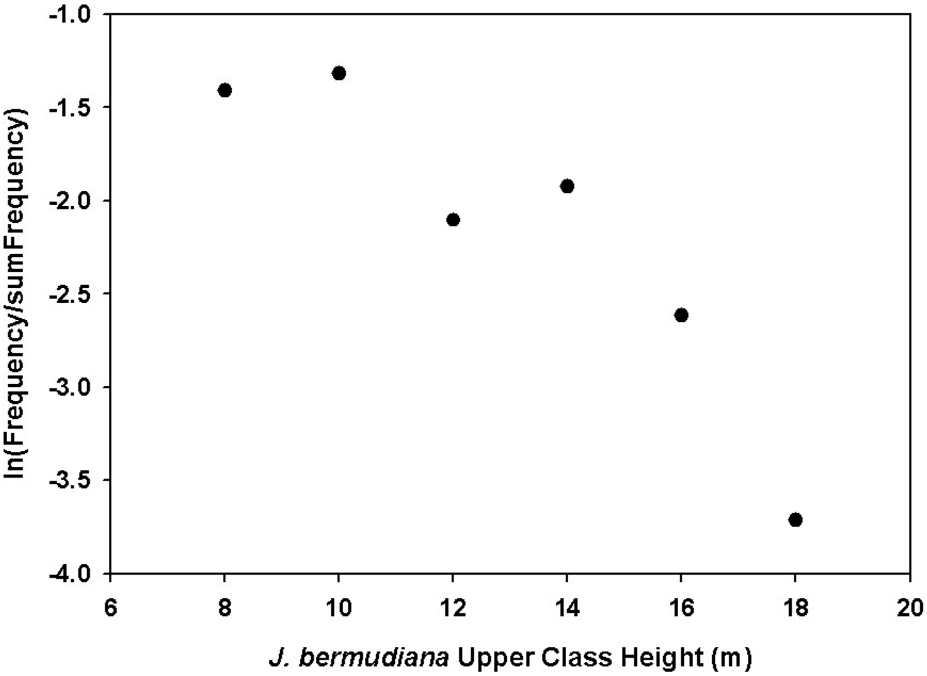

Figure 8. Height data from *J. bermudiana* density surveys was regressed using the natural log of the ratio of frequencies over the height classes. Growth and mortality of *J. bermudiana* trees had the resulting slope of 0.2176 (R^2=0.83832, N=6 height classes, $p<0.05$).

CODE FOR SIMULATION MODEL
for use in MATLAB 7

```
%parameter definitions

box_area=40*40;%square meters
a1=exp(10.36);b1=7.39 ;%slope & exponent for cones/tree
a2=-1.47 ;b2=.011 ;c2=.00093 ;d2=-.0000012 ;%regression parameters for visits/hr
a3=-1.3797 ;b3=0.00004726 ;%logistic regression for move/stay
max_eat_per_time=3.3;%cones eaten per hour
k=10;
T=10;%total # of time steps
disp_steps=24*7;%convert from hour to more reasonable time step within dispersal kernel (here week)
t_seed=12;%number of reproductive weeks in a year;
maxgerm=.01 ;%prob of germination in ideal habitat
lam=1/38.04;%1/avg distance of individuals that 'stay' near tree
time_stay=2.6;%min if stay>1 min
time_move=.73;%min if stay<=1 min
moves_til_poop=30./[time_stay time_move];
M=.0418109e3;V=1.92798e3;%mean and var for mover dispersal
Vstay=1.825e3;%variance in dispersal for stayers

%construct grids

load grid_data_small
[r,c]=size(Grid)
%Grid= ;%grid for habitat suitability
%Elev= ;%grid of elevations
New_seeds=0*Grid;%initialize w/ no seeds (?)
Seedlings=Grid.*round(100*rand(r,c));%numbers of seedlings in each box
Juveniles=Grid.*round(100*rand(r,c)) ;%numbers of juveniles in each box
Adults=Grid.*48 ;%numbers of adults in each box
Dgrid=Adults/box_area;%initial density
Pgerm=maxgerm*Grid;%grid for germination probability
Seedling_surv=.05^(1/8)*Grid ;%map of seedling survival probabiity
Seedling_grow=1/8*Grid ;%probability of transition from seedling to juvenile
Seed2seed=Seedling_surv.*(1-Seedling_grow);%move to loop if density dependent
Seed2juv=Seedling_surv.*(Seedling_grow);
Juv_surv=(1-.1)*Grid ;%map of juvenile survival probability
Juv_grow=.036*Grid;%map of probability of transition to adulthood
Juv2juv=Juv_surv.*(1-Juv_grow);
Juv2ad=Juv_surv.*(Juv_grow);
Ad_surv=(1-1/100)*Grid;%map of adult survivorship
```

```
%dispersal kernel

   x=[1:c]*box_area^.5;y=[1:r]*box_area^.5;%horizontal and vertical axes
   [gridx,gridy]=meshgrid(x,y);%cosntructs matrices of x and y - makes calculating
distances easy
   gridpts=500;%number of points on grid to generate dispersal kernel
   maxgrid=2*(c^2+r^2)^.5*box_area^.5;%maximum distance for possible dispersal
   d=linspace(0,maxgrid,gridpts);y=d;%dispersal axis
   dd=d(2)-d(1);%spacing of gridpoints on dispersal axis

   pd=exp(-.5*(d-M).^2/V);%one-step dispersal probability
   pd=pd'/sum(pd)/dd;%normalizes to area 1
   distyd=y'*ones(1,gridpts)-ones(gridpts,1)*d;%distance from first step to second
   pdy=exp(-.5*(distyd-M).^2/V);%transition kernel
   pdy=diag(1./sum(pdy,2))*pdy/dd;%normalizes rows to area 1

   for i=1:round(moves_til_poop(2));%loop calculates dispersal until seeds are dropped
      pd=pdy*pd*dd;
   end

   for i=1:r,for j=1:c,% loop interpolates distances to map of transition probabilities
     distmat=((i*box_area^.5-gridy).^2+(j*box_area^.5-gridx).^2).^.5;
     disp=reshape(interp1q(d',pd,distmat(:)),r,c);
     Pdist_move{i,j}=min(1,disp);
     Pdist_stay{i,j}=min(1,(2*pi*Vstay*moves_til_poop(1))^-.5*exp(-
.5*distmat.^2/(Vstay*moves_til_poop(1))));
%       subplot(2,3,2);imagesc(Pdist_move{i,j});colorbar;
%       subplot(2,3,5);imagesc(Pdist_stay{i,j});colorbar;
%       pause(.01)

   end;end

%Demographic loop starts here

for t=1:T
figure;
subplot(2,2,1);imagesc(Adults);colorbar
subplot(2,2,2);imagesc(Juveniles);colorbar
subplot(2,2,3);imagesc(Seedlings);colorbar
subplot(2,2,4);imagesc(New_seeds);colorbar
pause
t

  %growth & survival
```

```
  Seedlings=Seed2seed.*Seedlings+New_seeds.*Pgerm %updates seedling map
  Juveniles=Juv2juv.*Juveniles+Seed2juv.*Seedlings%updates juvenile map
  Adults=Ad_surv.*Adults+Juv2ad.*Juveniles %updates adult map
  %Dgrid=Adults/box_area;% recalculates adult density - ASSUMES ADULTS ARE
ONLY CAUSE OF DENS_DEP
  Dgrid=(Adults+Juveniles)/box_area %adult and juvenile density generate density dep

  %dispersal loop starts here

  New_seeds=zeros(r,c);
   cpt=a1*Dgrid.*exp(-b1*Dgrid)%cones/tree
   ctot=Adults.*cpt%total # cones
   bv=max(0,a2+b2*Elev+c2*cpt+d2*Elev.*cpt)%# bird visits
   pstay=exp(a3+b3*cpt)./(1+exp(a3+b3*cpt))
   %tpv=min(1,max(0,a3+b3*cpt));%time/visit
   eat_per_time=max_eat_per_time*cpt./(k+cpt)
   P_eaten_hr_stay=Grid.*(eat_per_time*time_stay*bv./(cpt+1-Grid))%P(eaten in 1 hr)
   P_eaten_hr_move=Grid.*(eat_per_time*time_move*bv./(cpt+1-Grid))%P(eaten in 1
hr)
   P_eaten_wk_stay=1-(1-P_eaten_hr_stay).^(disp_steps)%P(eaten in 1 wk)
   P_eaten_wk_move=1-(1-P_eaten_hr_move).^(disp_steps)
   for i=1:r, for j=1:c,%loop calculates dispersal of new seeds
        New_move=ctot(i,j)*pstay(i,j).*P_eaten_wk_stay(i,j)*Pdist_stay{i,j};
        New_stay=(1-pstay(i,j)).*P_eaten_wk_move(i,j)*Pdist_move{i,j}*ctot(i,j);
        New_seeds=New_seeds+New_move+New_stay;

          %  figure(3);
          %
subplot(2,2,1);imagesc(pstay(i,j).*P_eaten_wk_stay(i,j)*Pdist_stay{i,j});colorbar;
          %  subplot(2,2,2);imagesc((1-
pstay(i,j)).*P_eaten_wk_move(i,j)*Pdist_move{i,j});colorbar;
          %  subplot(2,2,3);imagesc(ctot);colorbar;

   end;end

   New_seeds=New_seeds*t_seed


%     figure(2);subplot(2,2,1);imagesc(P_eaten_wk_stay);colorbar;
%     subplot(2,2,2);imagesc(ctot);colorbar;
%     subplot(2,2,3);imagesc(P_eaten_wk_move);colorbar;
%     subplot(2,2,4);imagesc(New_seeds);colorbar;

end
```

EPILOGUE

As the number of exotic species being introduced globally increases, so too does the opportunity to conduct basic ecological research and the need for invasive species control and management. Research on biological invasions provide an exceptional way to serve this dual purpose, particularly when studying the stages of invasion of an exotic species that has not yet become an invasive pest. Furthermore, since an exotic species depends on its biotic interactions for successful invasion, research on an exotic species in the context of its community will only provide a more robust method of predicting invasion success.

This thesis had the goal of determining the impacts of the different stages of animal-mediated seed dispersal on the invasion success of an exotic plant. In particular, this thesis focused on the role plant-bird interactions played in the distribution and spread of *Juniperus bermudiana* (Bermuda Juniper), in the context of the seed dispersal cycle. Dependent on avian seed dispersal for invasion success and exhibiting three different levels of invasion in the West Maui Mountains, *J. bermudiana* served as a model system for my research. Since its introduction to the study site in the early 1930s, *J. bermudiana* has been slow to invade. By breaking down the seed dispersal cycle into measurable components, my research provides a clear and complete picture as to why *J. bermudiana* has been a lazy invader while exemplifying the utility of studying basic ecological principles in the context of invasive species.

More specifically, my behavioral work on the early processes of the seed dispersal cycle has identified how functional behaviors can detect which species will be the most effective seed disperser. Of the eight bird species observed to visit *J. bermudiana*, only three were observed to forage for *J. bermudiana* seed cones. Of those three foragers, only one (i.e., *Z. japonicus*) was considered an effective seed disperser of *J. bermudiana*. In addition to its widespread abundance and prevalence in the study site, the flock-feeding and seed handling behavior are likely to distribute *J. bermudiana* seeds across the landscape despite the presence of seed predators in this system. As a result, effective seed dispersal by *J. bermudiana* foragers is not limiting its invasion success in the study site.

Greenhouse and field experiments on the next stages of the seed dispersal cycle focused on the seed deposition, germination and seedling recruitment of *J. bermudiana* in the study site. Since uptake and movement of seeds were found to not be limiting in this system, this part of the study focused on determining whether the establishment phase of *J. bermudiana* was limiting its invasion success. Greenhouse experiments revealed that *J. bermudiana* is likely to have high germination, growth, and survival rates; however, field experiments revealed the opposite. This discrepancy between idealized versus realized conditions shows that *J. bermudiana* is not likely to overcome the harsh environmental conditions of the West Maui Mountains to become an invasive pest. *J. bermudiana* may not be limited in effective seed dispersal, but, rather, limited by successful establishment into novel habitats in the West Maui Mountains.

Simulation models were used as a platform to incorporate the last stages of the seed dispersal cycle (i.e., seedling, juvenile and adult recruitment) with the previous stages so as to close the seed dispersal loop. Since *J. bermudiana* demography was not explicitly measured in the field, estimates were made from data in the *Juniperus* literature. Using *Z. japonicus* foraging and movement behaviors, data on seed movement and germination, and estimates of *J. bermudiana* growth and survival in different stage classes, a conceptual model was presented in hopes of later predicting the distribution and spread of *J. bermudiana* in the West Maui Mountains. It is the goal of this study to not only continue to develop a working model, but to also validate and conduct sensitivity analyses on the model so as to better understand which factors are most likely to contribute to the invasion success of *J. bermudiana*.

Quantifying the different parts of the seed dispersal cycle and putting them back together as a whole seed dispersal loop is critical for a deeper understanding of how plant-bird interactions affect invasion success of an exotic plant. I used this approach with *J. bermudiana* in the West Maui Mountains and have found that measuring the different processes can help in understanding community structure as a whole while targeting stages that may be crucial in invasive species management. Completion of the simulation model will be essential to test basic principles in population and community ecology, particularly when considering species assembly and structure. By integrating behavioral studies, greenhouse and field experiments, and simulation modeling, I hope to provide a blue print for future studies in exotic plant-bird systems. Proximately, I would like to use this approach to inform *J. bermudiana* species control and management in the West Maui Mountains of Maui, Hawaii. Ultimately, however, I would like to extend this approach to other exotic plant-bird systems to create a comprehensive grasp of how these interactions can affect community structure both in ecological theory and in conservation application.

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