

The Biogeography of Ground Beetles (Coleoptera: Carabidae)
on the Islands of Lac la Ronge, Saskatchewan, Canada.

By

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Abstract

Islands offer unusual opportunities for studying theoretical concepts in ecology. I studied the role of island size and isolation in structuring assemblages of ground beetles (Coleoptera: Carabidae) on the islands and adjacent mainland of Lac la Ronge, Saskatchewan, Canada. Carabid beetles were collected on 30 islands (0.2 – 980.7 ha in size, 0.13 – 10.7 km from mainland) and five mainland sites using pitfall traps throughout the frost-free season. Carabid body size, wing length and seasonal activity information was obtained from the literature. In wing-dimorphic species, wing length was diagnosed by removing the elytra and subsequent dissections to determine the condition of flight muscles. Island size was an important factor affecting beetle assemblage, diversity, and population processes on islands. Island isolation did not negatively influence diversity at the scales examined in this study. Life history characteristics of species such as body size, wing length, and breeding period significantly influenced the distribution of beetles on islands. This work suggests that small islands experience greater turnover of carabids, particularly large-bodied flightless species, and that this may account for the island area effect observed in this island system.

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Table of Contents

Chapter 1: Introduction	1
Background and Rationale	1
Carabid Beetles on Islands	2
Thesis Objectives	4
Literature Cited	6
Chapter 2: A comparison of ground-beetle (Coleoptera: Carabidae) assemblages between boreal lake-islands and adjacent mainland	9
Introduction	9
Methods	10
Site Description and Island Characteristics	10
Sampling Protocol and Species Identification	12
Data Analysis	12
Results	13
Carabid Dominance and Diversity	13
Carabid Assemblages	17
Discussion	17
Conclusions	22
Literature Cited	22
Figures & Tables	26
Appendix	35
Chapter 3: Body size and wing length influence the distribution of ground beetles (Coleoptera: Carabidae) on boreal lake islands in central Canada	35
Introduction	35
Methods	37
Site Description and Sampling Protocol	37
Life History Traits	38
Data Analysis	38
Results	39
Life History Traits	39
Wing-Dimorphic Species	40
Discussion	41
Life History Traits	41
Wing-Dimorphism	44
Literature Cited	46
Figures & Tables	51
Chapter 4: Discussion	57
Main Results	57
Theoretical Implications and Conservation Planning	58
Future Research	59
Bibliography	61

List of Tables

Table 1.1 Number of islands within each island size category, their isolation index, raw species richness (S), and number of individuals captured per island (I). The most abundant species and their relative proportion of the total catch on the island are also given. † indicates average number of individuals per island class.....	26
Table 1.2 Summary of pooled species richness among island size classes, mainland, and isolation classes.....	27
Table 1.3 Summary of outputs for global regression models (interaction not included) including model parameters, standardized regression coefficients, and standard errors for raw species richness, rarefied species richness, and species evenness.....	27
Table 2.1 List of carabid species collected on the islands of Lac la Ronge, their wing type (m-macropterous, b-brachypterous, d-dimorphic), breeding period, mean body lengths (mm), and proportion of total catch (%).	51
Table 2.2 List of islands and the number of individuals (N), and proportion of macropterous species (% M_S) for each island. Number of <i>A. retractum</i> collected (N_R) and the proportion of macropterous males (σ) and females (ϕ) is also listed.	52

List of Figures

Figure 1.1: Map of islands (green) and mainland (white) of Lac La Ronge, Saskatchewan. Black circle indicate sampling locations for each site.	28
Figure 1.2: Relationship between total carabid catch rate and island area (\log_{10}) on the islands of Lac la Ronge (R^2 : 0.08, P : 0.14).	29
Figure 1.3: Rank-abundance curves for the 10 most abundant carabid species in each island class: very small (0.1 – 1.0 ha, $n = 6$); small (1.01 – 10 ha, $n = 9$); medium (10.01 – 100 ha, $n = 8$); large (100.01 – 1000 ha, $n = 7$).	29
Figure 1.4: Relationship between raw species richness (circles, solid line; R^2 : 0.05, P : 0.22) and rarefied species richness (triangles, dashed line; R^2 : 0.16, P : 0.03) and island area (\log_{10}). Raw species richness (mean: 11, standard error: 1.58) and rarefied species richness (mean: 7.99, standard error: 0.53) of mainland sites are shown on the right.	31
Figure 1.5: Relationship between species evenness and island area (\log_{10}). Species evenness for mainland sites is shown on the right (mean: 0.74, standard error: 0.04).	32
Figure 1.6: Relationship between rarefied species richness and (A) distance to mainland (R^2 : 0.07, P : 0.16) and (B) isolation index (R^2 : 0.05, P : 0.26) of carabids on the islands of Lac la Ronge.	32
Figure 1.7: Non-metric multidimensional scaling ordination illustrating the similarities in carabid beetle assemblage between island classes and mainland (ellipses: 95% C.I.) and the centroids of the 12 most abundant species, stress = 0.17.	33
Figure 1.8: Non-metric multidimensional scaling ordination illustrating the similarities between carabid assemblages on islands that are less isolated and more isolated, stress = 0.16. Ellipses represent 95% confidence intervals.	34
Figure 2.1: Relationship between \log_{10} island area and mean catch rate of large-bodied and small-bodied carabids (R^2 : 0.55, P : < 0.0001).	53
Figure 2.2: Relationship between \log_{10} island area and (A) proportion of macropterous species (R^2 : 0.50, P : < 0.001); and (B) proportion of spring breeding species (R^2 : 0.31, P : 0.001) on the islands of Lac la Ronge (regression line includes the two largest islands).	54
Figure 2.3: Changes in probability of <i>A. retractum</i> being macropterous (winged) with increasing island size (\log_{10}) for males and females.	55
Figure 2.4: Dorsal view of the half-winged <i>A. retractum</i> male phenotype (elytra removed).	56

List of Appendices

Appendix 1.1: wing type and mean body length obtained from Lindroth (1969) and Bousquet (2010).....	35
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Chapter 1: Introduction

Background and Rationale

The theory of Island Biogeography (MacArthur & Wilson 1963, 1967) was developed to explain factors that influence the number of species on islands. Shortly after its publication, its theoretical framework was applied to conservation planning and the design of nature reserves, which function as 'islands' within human-altered landscapes (Diamond 1975). This led to a vigorous debate within ecological circles as to whether a single large reserve or several small reserves (SLOSS) best conserve biological diversity (SLOSS debate, see Simberloff & Abele 1982; and Diamond 1976).

Based on Island Biogeography theory, a single large reserve should be better at preserving intact communities and maintaining viable populations, especially for vertebrates with large home-ranges (Diamond 1975). Opponents to the application of island theory to reserve design argued that several small reserves may be better because 'large' is a relative term and many species could still persist in small areas (Simberloff & Abele 1976). Furthermore, they argued that each of the small parcels may support species that aren't necessarily subsets of large islands, and spread the overall risk of catastrophic disturbance events (e.g. wildfire) (Simberloff & Abele 1976). Despite of the fact that natural systems are usually more complex than allowed in the debate, many of the concepts and ideas generated were useful, and continue to form the basis of conservation planning practices today. These include such concepts as the use of corridors or stepping stones, preference for unfragmented landscapes, and minimizing edge effects (Diamond 1975; Wilcox & Murphy 1985).

Publication of the theory of Island Biogeography (MacArthur & Wilson 1963, 1967), also led to widespread recognition that islands offer valuable features for ecological study. Because most island biotas are less species-rich than mainland areas, ecological interactions may be ‘less complicated’ on islands and easier to study (Vitousek & Benning 1995). Islands often form archipelagos, providing excellent opportunities for replication at the island-level (Wardle et al. 2002; Warren et al. 2014) and their isolation and discrete borders make them relatively independent, allowing them to be compared to other islands nearby (Wardle et al. 2002). For these reasons, islands frequently serve as model systems for testing hypotheses related to isolation, area and edge effects, and spatial arrangement of islands (Kotze 2008). Furthermore, the theoretical insights gained from studying island systems can help inform practical solutions to real-world problems as was illustrated in the design of ecological reserves.

Carabid Beetles on Islands

Carabid beetles (Coleoptera: Carabidae) are a suitable taxa for studying the effect of islands on biota because they are abundant and easy to collect (Lindroth 1985; 1986), diverse and well-known taxonomically (Lindroth 1969), and because they vary in dispersal capability based on wing length (Den Boer 1970). Carabid species are generally classified according to wing length into three categories: macropterous (fully-developed hind wings), brachypterous (apterous or reduced hind wings), and wing-dimorphic (individuals within the same species exhibit either macroptery or brachyptery; Den Boer 1970; Den Boer et al. 1980; Lindroth 1985, 1986). Macropterous species disperse via flight whereas brachypterous species are flightless and disperse to or between islands by drifting on the water surface or through human-assisted movements. Because macropterous, brachypterous, and wing-dimorphic species commonly occur in the same location (Ås 1984), proportions of macropterous vs. brachypterous species can

be used to compare dispersal and colonization strategies on islands (Den Boer 1970). Furthermore, the proportions of macropterous vs. brachypterous individuals within wing-dimorphic species can also provide valuable information regarding dispersal.

Carabids have been studied extensively on islands, especially in the Baltic Sea (see review by Kotze 2008 and references therein) and the Lake Mamry archipelago in Poland (Zalewski 2004; Ulrich & Zalewski 2006, 2007; Zalewski & Ulrich 2006, 2009). Together, these studies have made extensive contributions to our understanding of carabid beetles on islands, and insular faunas in general. Below, I briefly summarize the key findings of their research with a focus on information relevant to this thesis.

First, carabid assemblages on islands differ from their nearest mainland counterparts and are not a product of passive sampling phenomenon (Niemelä 1985; Kotze 2008; Zalewski et al. 2012). Niemelä et al. (1985) showed that some abundant species on mainland were scarce or absent on islands, and several species were more abundant on islands than on mainland. Thus, biological processes, such as autecological characteristics, availability of habitat, and/or competition influence structure of the carabid assemblage on islands (Niemelä et al. 1985; Niemelä 1988, Kotze et al. 2000; Kotze & Niemelä 2002; Zalewski & Ulrich 2006; Kotze 2008; Zalewski et al. 2012).

Second, dispersal from mainland and between islands in the Baltics (distances < 5km) occurs relatively easily (Kotze et al. 2000) possibly due to the ability of carabids to survive long periods drifting on the water surface. Studies have shown they can survive up to 5 days floating in brackish water (Palmén, 1944; Renault 2011) with no effect on fertility (Palmén, 1944) and 4

days completely submerged in freshwater (Renault 2011). Thus, it is possible for carabids to colonize islands by passively drifting on the water surface.

Third, the number of carabid species on islands tends to increase with island size (Niemelä et al. 1987; Nilsson et al. 1988; Kotze et al. 2000; Kotze & Niemelä 2002; Zalewski & Ulrich 2006) although evidence is divided as to whether this pattern is due to habitat diversity or area *per se* (Kotze 2008). Disentangling the ultimate causes of greater diversity on large islands is difficult because area and habitat diversity are related (Järvinen & Ranta 1987; Ås et al. 1997). Furthermore, researchers often deploy more pitfall traps on large islands (Niemelä 1987; Zalewski & Ulrich 2006, 2009) and thus any differentiation between the effects of area and habitat diversity are confounded by sampling intensity (Kotze 2008).

The islands of Lac la Ronge are similar in size and isolation to many islands in the Baltic Sea, but vary in several ways that could influence the distribution of carabids on islands. First, the islands of Lac la Ronge are geologically stable and haven't undergone significant change since their formation 10,000-14,000 years BP (Klassen 1994). In contrast, the gradual land uplift in Fennoscandia is slowly creating new islands, increasing island size and habitat complexity, and increasing overall connectivity between islands and the mainland in the Baltic region (Kotze 2008). Second, Lac la Ronge is a freshwater intra-continental lake whereas the Baltic Sea has low but variable salinity (Kotze 2008). Because carabids can survive up to twice as long floating on freshwater compared to seawater (Renault 2011), passive transport through drifting could allow carabids to travel further on Lac la Ronge than in the Baltic Sea. Hence, the processes that shape island communities may vary between these two island systems.

Thesis Objectives

In this work, I aimed to provide a comprehensive understanding of carabid beetle communities and factors influencing their colonization and establishment on islands. More specifically, I tested whether spatial features like island area and isolation can predict the number of species and assemblage structure of carabids on the islands of a lake in northern Saskatchewan. By sampling forested islands spanning an area and isolation gradient, I sought to determine the principal factors influencing the biogeography of carabid beetles in an island system, and to compare patterns observed in this study with those observed in other island systems.

In chapter 2, I compare island carabid assemblages with their nearest mainland counterparts. By exploring the influence of spatial features on carabid composition and diversity, I conclude that island area influences both the diversity and assemblage structure of carabid beetles, but the effects of isolation are less clear. Based on these findings, I suggest that island area has subtle effects on the population processes and inter/intraspecific interactions of carabid beetles.

In chapter 3, I explore how various autecological characteristics (body size, wing length, seasonal activity) are associated with carabid assemblages on the islands. By assessing their relationship with island size, I suggest that large-bodied, flightless species are underrepresented on small islands because they have greater resource requirements and lower immigration rates than small-bodied species capable of flight. Based on these findings, I conclude that certain autecological characteristics are associated with island size and are important factors influencing carabid assemblages on the islands.

In chapter 4, I summarize the research findings and discuss their implications for conservation planning and ecological theory. Furthermore, I briefly discuss additional questions and hypotheses generated from this dissertation and make recommendations for future research.

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Chapter 2: A comparison of ground-beetle (Coleoptera: Carabidae) assemblages between boreal lake-islands and adjacent mainland

Introduction

Since the publication of the theory of Island Biogeography (MacArthur & Wilson 1963, 1967), many authors have tested hypotheses about how area and isolation influence island biodiversity (Kotze 2008). A common approach is to compare biotic communities on islands with their nearest mainland counterparts (MacArthur & Wilson 1963, 1967; Niemelä et al. 1985; Kotze & Niemelä 2002). Island biotas are generally less species-rich than comparable mainland areas and this has been attributed to island characteristics such as island area, distance from mainland, and habitat diversity on islands (MacArthur & Wilson 1963, 1967; Järvinen & Ranta 1987; Niemelä et al. 1987; Ås et al. 1997).

Several hypotheses have been proposed to explain why diversity increases with island area (see Connor & McCoy 1979). For example, the ‘habitat diversity’ (Williams 1964) and ‘equilibrium theory’ (MacArthur & Wilson 1963, 1967) hypotheses invoke biological explanations for species-area relationships. The former proposes that as sampling area increases, the number of new habitats and species associated with those habitats also increases (Williams 1964). The latter explains that species number is a dynamic equilibrium between extinction and immigration rates, such that small, isolated islands have greater extinction rates and low immigration rates, respectively, and thus have lower diversity than found on large, more proximate islands (MacArthur & Wilson 1963, 1967). In contrast, the ‘sampling hypothesis’ posits that large islands have more species because they receive larger samples from the mainland species pool, simply because they provide larger interception targets (Connor & McCoy 1979). Under this hypothesis, species diversity on islands is strictly the product of a sampling phenomenon and is not the result of biological processes (Connor & McCoy 1979).

Niemelä (1985) tested and refuted the ‘passive sampling’ hypothesis for carabid beetles on Baltic islands. He showed that some species abundant on mainland were scarce or absent on islands, and several species were more abundant on islands than on mainland (Niemelä 1985). However, the islands of Lac la Ronge differ from the Baltic islands studied by (Niemelä 1985) in several ways such as species assemblages, salinity, distances between islands and mainland. Hence, the processes that shape island communities may differ between these two island systems.

In this study, I compared carabid beetle assemblages on forested islands of a boreal lake in Saskatchewan, Canada with those on adjacent mainland. The aims of this study are to 1) test the ‘passive sampling’ hypothesis for the island faunas by asking whether carabid diversity and species assemblage differ between islands and the mainland, and among islands of different sizes and isolation, and 2) compare the patterns observed on Lac la Ronge with those observed in other island systems.

Methods

Site Description and Island Characteristics

This study was conducted during summer 2013 in the vicinity of Lac la Ronge, Saskatchewan, Canada (55°06’ N, 105°01’ W). The lake lies on the southern edge of the Canadian Shield and includes >1400 islands that range in size from ≤ 0.1 – 980.7 ha (Fig. 1.1). Most islands are similar in shape, running south-west to north-east and located mainly in the central and northern reaches of the lake (Fig. 1.1). Although there are approximately 250 cabins on the islands, most are on small parcels of leased land with modification of additional island habitat prohibited. Consequently, the islands have not experienced significant habitat alteration or human impact.

I studied thirty islands and five forested mainland sites (Fig. 1). All islands are heavily forested but small sand beaches, marshes, and meadows occur on some. I focused my work on only forested areas to minimize variation caused by sampling different habitats. These areas were dominated by spruce (*Picea* spp.), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*), with trembling aspen (*Populus tremuloides*) less common. Jack pine (*Pinus banksiana*) was found in small numbers at mainland sites but rarely on the islands. Spruce was more common at mainland sites and large islands whereas balsam fir was more prevalent on small islands. Soil depth varied considerably across each site and the forest floor was covered by large mats of bryophytes and lichens (*Cladonia stellaris* and *Cladina* spp.). Patches of raspberry (*Rubus* spp.), skunk currant (*Ribes glandulosum*), dogwood (*Cornus sericea*), bunchberry (*Cornus canadensis*), twinflower (*Linnaea borealis*), and lingonberry (*Vaccinium vitis-idaea*) were common.

Island areas were determined using GIS software (Table 1; ArcGIS 10.3) and categorized as very small (0.1 – 1.0 ha), small (1.01 – 10 ha), medium (10.01 – 100 ha) and large (100.01 – 1,000 ha; Table 1). Island isolation was measured two ways: nearest distance to mainland and distance buffers. Nearest distance to mainland was measured using the ruler tool in GIS software (ArcGIS 10.3). Because of the ‘clustered’ nature of the islands on Lac la Ronge and the possibility of individuals immigrating from both mainland and neighboring-island species pools, I used buffers to develop an island isolation index for each island. In an effort to incorporate the effect of scales in the analysis, I used two distance buffers (5000m and 10,000m) to measure the proportion of water or land around the perimeter of each island. To do this, I converted a vector shapefile for Lac la Ronge and the surrounding area to a binary raster grid (1 – water; 0 – land) with a cell size of 5m. Then I used buffers to calculate the proportion of water within each buffer

and averaging between the two buffer distances. The resulting value was used as an isolation index for that island. For community analyses, islands were categorized as ‘more isolated’ (isolation index ≥ 0.8) and ‘less isolated’ (< 0.8) because this corresponded to a natural break with 15 islands in each category.

Sampling Protocol and Species Identification

Carabid beetles were sampled on each island using pitfall traps constructed from 1L round plastic containers with a smaller 0.5L inner cup (Spence & Niemelä 1994). Traps were placed in the ground so the lip of the container was level with the substrate. An opaque lid (15 x 15cm) was suspended 2-3cm above the trap to prevent debris and excess rainwater from clogging the trap (Work et al. 2002). Eight pitfall traps were distributed along a 120m transect at each site, with traps spaced at 15m intervals, starting 7.5m into each transect, to ensure that traps catches were independent (Digweed et al. 1995). Traps were run continuously from 2 June to 23 August (approximately the frost-free season at La Ronge, SK) and were emptied at ca. 14-17-day intervals, depending on weather that affected lake conditions, and re-filled each check with 2-3cm of propylene glycol. Samples were stored in 90% EtOH until identification.

Adult carabids were identified to species using Lindroth (1969) and Bousquet (2010). I included *Trachypachus holmbergi* Mannerheim (Trachypachidae) in the analysis because of its abundance in my study and its similarity and apparently close relationship to carabids (Lindroth 1969; Bell 1982). Voucher specimens are deposited in the Strickland Museum, Edmonton, Alberta, Canada, and with the collection of the Water Security Agency in Saskatoon, Saskatchewan, Canada.

Data Analysis

Species richness was standardized by trap-days to account for differences in trapping effort. Individual-based rarefied species richness was also calculated for each site using iNext software (Hsieh et al. 2013) to compare diversity standardized for the number of individuals collected. Regression, performed in R (R development Core Team 2013), was used to test the effect of island area and island isolation on species richness, rarefied species richness, and species evenness. Residuals for both the island area and island isolation models met the assumptions of normality (Shapiro-Wilk test) and equal variance. Rank-abundance curves were calculated using the BiodiversityR package in R (Kindt & Coe 2005).

Carabid abundances were standardized (total individuals per trap day) to account for traps that were lost. I compared carabid assemblages among island classes and mainland, and between island isolation categories using non-metric multidimensional scaling (NMDS) using Bray-Curtis distances. Stress and optimal number of dimensions were calculated using the vegan package in R (Oksanen et al. 2015), with stress values between 0.10 and 0.20 considered to indicate adequate representations of two-dimensional NMDS solutions (Clarke & Warwick 2001). Ellipses projected onto the ordination plot represented 95% confidence intervals for the mainland and island size categories. Centroids of the 12 most abundant species were calculated to estimate average locations of each species in the ordination space (Bergeron et al. 2011).

Results

Carabid Dominance and Diversity

In total, I collected 11,632 carabids representing 39 species (Appendix). All species collected on the islands are known in Saskatchewan (Hooper & Larson 2012; Bousquet et al. 2013), except *Pterostichus brevicornis* (Kirby). The two female individuals of this species collected from Love Island (55°04'48" N, 104°59'21"W) and Orr Island (55°07'13" N,

104°56'32"W; islands 23 and 26, respectively; see Appendix 1.1) are the first records from Saskatchewan. The two most abundant species, *Pterostichus adstrictus* Eschscholtz and *Calathus ingratus* Dejean, which were most abundant on 11 islands (Table 1) accounted for 46.8 % of catches, and together with the next 10 most abundant species [*Platynus decentis* (Say), *Agonum retractum* LeConte, *Stereocerus haematopus* (Dejean), *Synuchus impunctatus* (Say), *Pterostichus punctatissimus* (Randall), *Carabus chamissonis* Fisher von Waldheim, *Carabus taedatus* Fabricius, *Pterostichus pensylvanicus* LeConte, *T. holmbergi*, and *Agonum gratiosum* (Mannerheim)], accounted for 98.8% of the total catch. Total number of individual carabids caught per island and average number of individuals varied considerably and idiosyncratically among island classes (Table 1.1). Although average abundance was greater on the smaller islands (Table 1.1), variance was such that overall carabid catch rate showed no statistically significant linear relationship with island area ($R^2 = 0.08$, $P = 0.14$, Fig. 1.2).

Rank-abundance graphs revealed a distinct shift in relative abundances of species with increasing island area (Fig. 1.3). *Pterostichus adstrictus* was the dominant species on very small (0.1 to 1.0 ha) and small island (1.01 to 10 ha) classes, while relative abundances of *C. ingratus* increased to the point of dominating samples on medium (10.01 to 100 ha) and large island (100.01 to 1000 ha), as well as mainland sites. The small-bodied species (see Appendix 1.1), *A. retractum*, was among the five most abundant species on very small, small, and medium island classes, while declining to the ninth most abundant species on large islands. Similar patterns were observed for *T. holmbergi* which was among the top ten most abundant species in very small and small island classes, while decreasing in abundance on medium and large island classes and mainland sites. The opposite pattern was observed for large-bodied species. For example, *C. taedatus*, was relatively rare on very small and small islands, but was the ninth and

fifth most abundant species on medium and large island classes, respectively. Similarly, *Carabus chamissonis* was the third most commonly-collected species on large island classes, but only the ninth, fifth, and eighth most abundant on very small, small and medium island classes, respectively (Fig. 1.3).

Species presence varied considerably among islands. *Pterostichus adstrictus* and *C. ingratus* were found on all islands with *P. decentis*, *A. retractum*, *S. haematopus*, *S. impunctatus*, and *P. punctatissimus* also being quite common with > 80% prevalence. In contrast, *C. taedatus*, *A. gratiosum*, were only present on 37% of the islands and *T. holmbergi* was collected on only 30% of the islands, and was absent from mainland sites. *Carabus chamissonis* was present on most of the islands (80%) although four of the six islands where it was absent were less than two hectares in size. A similar pattern was observed in *C. taedatus* which, aside from a single individual collected on island 'LG' (Table 1.1), was absent from samples in the 14 smallest islands (≤ 7.5 ha). An opposite pattern was observed for the small-bodied, winged species, *A. gratiosum*, which was only found on islands less than 44 ha in size.

Raw species richness did not significantly differ with island area ($R^2 = 0.05$, $P = 0.22$; Fig. 1.4), although when diversity was standardized to a comparable number of individuals using rarefaction (see Buddle et al. 2005), richness significantly increased with island area ($R^2 = 0.16$, $P = 0.03$; Fig. 1.4). Likewise, evenness (Pielou's J') significantly increased with island area ($R^2 = 0.33$, $P = 0.0009$; Fig. 1.5). Overall, more species were collected from the islands than from adjacent mainland forests (37 vs. 17), although rarefied richness did not vary between island size classes and the mainland ($R^2 = 0.11$, $P = 0.49$). Total numbers of species were 22, 27, 24, 20, and 17 for very small, small, medium, large, and mainland, respectively (Table 1.2). Several open habitat species [*Amara erratica* (Duftschmid), *Amara littoralis* Mannerheim, *Amara patruelis*

Dejean, and *Bradycellus lugubris* (LeConte)] were collected in small numbers on the islands, probably reflecting small forest openings. These species undoubtedly occur in similar gaps on the mainland, but such openings were not included in any of the five mainland sites. Two species, *Amara sinuosa* (Casey) and *Blethisa multipunctata* (Linne), were found only on the mainland, but only a single individual of each was collected.

Rarefied species richness did not differ significantly with distance to mainland ($R^2 = 0.07$, $P = 0.16$; Fig. 1.6) or the island isolation index ($R^2 = 0.05$, $P = 0.26$; Fig. 1.6). Raw species richness increased with isolation, although this relationship was only significant for distance to mainland ($R^2 = 0.18$, $P = 0.02$; Fig. 1.6A) and not the island isolation index ($R^2 = 0.08$, $P = 0.14$; Fig. 1.6B). In general, there was no indication of an inverse relationship between species richness and isolation. In fact, there was a trend of the opposite pattern with species richness at 24 for less isolated islands and 35 for more isolated islands, respectively (Table 1.2). Furthermore, among the seven *Agonum* species collected in my study, only three [*A. retractum*, *A. gratiosum*, and *Agonum sordens* Kirby] were found on less isolated islands, while all seven were present on more isolated islands. A similar pattern was observed in *C. taedatus* which was missing from the 11 islands closest to mainland (nearest distance measure) and the eight least isolated islands (isolation index).

There was no evidence of an interaction between island area and either isolation measure for raw species richness, rarefied species richness, or species evenness. A global model was used to measure the effect of island area while accounting for the effect of isolation (and *vice versa*, see Table 1.3). Distance to mainland was used in the global model because it was a better predictor than the isolation index (see above). In general, distance to mainland only significantly affected raw species richness ($R^2 = 0.17$, $P = 0.048$), whereas island area was the best predictor

for both rarefied species richness ($R^2 = 0.18$, $P = 0.03$) and species evenness ($R^2 = 0.31$, $P = 0.003$, see Table 1.3).

Carabid Assemblages

A two-dimensional NMDS ordination arranged the carabid assemblages for mainland and island classes with an acceptable stress of 0.17 (Fig. 1.7). Species composition overlapped (95% confidence ellipses) markedly among mainland and large, medium, and small islands classes, but species composition differed notably for assemblages from very small islands.

Centroids for *C. taedatus*, *C. chamissonis*, *S. impunctatus*, and *P. punctatissimus* were concentrated in the mainland, large, and medium island classes, while centroids for *P. adstrictus*, *A. retractum*, *P. decentis*, *A. gratiosum*, and *T. holmbergi* were concentrated in small or very small island classes. Centroids for *P. pensylvanicus*, *S. haematopus*, and *C. ingratus* were clustered broadly to include mainland and all island classes. Island isolation was also represented by a two-dimensional NMDS solution (Fig. 1.8) with a similar stress of 0.16. The overlap of confidence ellipses shows that species composition was much less affected by isolation than by island size.

Discussion

Island carabid assemblages usually differ from their nearest mainland counterparts (Niemelä et al. 1985; Kotze & Niemelä 2002). I found support for this on only the smallest islands in my study. Islands less than one hectare differed distinctly from those of both large islands and mainland sites. Furthermore, as island size increased, the structure of the carabid assemblage on islands gradually approached that of the mainland. In contrast, carabid beetle assemblages on Baltic islands up to ca. 29 ha in size differed distinctly from the mainland

(Niemelä 1985; Kotze and Niemelä 2002). Below, I suggest three possible explanations for differences in the structure of the assemblage between the smallest islands, on the one hand, and large islands and the mainland on the other.

First, resources may be limited or shorter-lived on very small islands compared to larger islands and the mainland (MacArthur & Wilson 1963, 1967) and this may select against species with larger body sizes and consequently favor less competitive smaller-bodied carabids (Schoener & Janzen 1968). Relative abundances of large-bodied species, such as *P. punctatissimus*, *C. chamissonis*, and *C. taedatus*, were greatest on the mainland and medium-to-large islands, suggesting that these islands could support viable populations. However, only a single individual of *C. taedatus* was collected on only one of the 14 smallest islands (≤ 7.5 ha), suggesting that populations of this species are not sustainable on small islands. Similarly, of the six islands where *C. chamissonis* was apparently absent, four were less than two hectares in size, and both of the islands where *P. punctatissimus* was apparently absent were smaller than two hectares in size. In contrast, smaller-bodied species like *P. adstrictus*, *P. decentis*, and *A. retractum* were present on all of the very small-to-small islands and more abundant on these islands than on large islands and the mainland. Furthermore, two small-bodied species, *T. holmbergi*, and *A. gratiosum*, were each found on fewer than half of the islands, but the islands where they were present were mostly small islands (see Appendix 1.1).

Body size and the ability to fly are related in carabids such that large-bodied carabids tend to be flightless while smaller-bodied species are usually active flyers (Blake et al. 1994). Other studies have shown that mean carabid body size is correlated with site stability (Blake et al. 1994; Szyszko et al. 2000), and larger bodied, wingless species are typically found in more stable, continuous habitats (Szyszko et al. 2000; Šerić Jelaska & Durbešić 2009). In contrast,

smaller-bodied carabid species are found in more disturbed (Blake et al. 1994; Szyszko et al. 2000) or isolated patches (Šerić Jelaska & Durbešić 2009). Thus, apparent advantages of small body size on small islands may indicate that habitats on small islands are unstable or more unfavorable for large-bodied species.

Second, greater dispersal ability of winged carabids should allow them to exploit limited or short-lived resources on small islands through repeated colonization or migration off an island if conditions became unfavourable. Although isolation did not influence the structure of assemblage at the scales examined in this study (Distance to mainland 0.13 – 10.7 km, mean: 5.4, standard deviation: 3.4; Isolation index 0.47 – 0.90, mean: 0.79, standard deviation: 0.10), these methods only indicate whether carabids are capable of traveling distances required to colonize islands (and establish populations), not the relative frequency at which they do so. Thus, it is possible that both winged and wingless species can travel between islands, but that winged species do it more often, possibly due to accidentally being blown into the water mid-flight and colonizing islands by drifting on the water surface. For example, Karjalainen (2000) showed that of 996 carabids collected from drift material in the Gulf of Finland, 98.2% of individuals and 96.6% of species collected were winged. A significant aspect of colonization ability may therefore include the survival of carabids being blown into the water mid-flight, and immigration rates of small-bodied, winged species may result indirectly from their ability to fly. If, for example, large-bodied, wingless species both arrive less frequently and have greater turnover on smaller islands due to limited resources (see above), they should be less represented on smaller islands, as is consistent with my data.

Third, although I cannot exclude undetected influences of fine-scale variation in habitat quality on colonization and establishment for some species, it is possible that species interactions

play some role in determining the composition of island assemblages. Restrictions in ability of large-bodied species to maintain populations on small islands could provide a 'release' for some smaller-bodied species. For example, small-bodied species increase in abundance on small islands where large-bodied species are lower in abundance or absent. This is also reflected by greater species evenness on large islands, suggesting that the presence of large-bodied species maintains some form regulatory control over carabid assemblages, possibly through competition. Interspecific competition has also been proposed to explain the absence of *Pterostichus melanarius* on small islands in the Baltics, despite availability of suitable habitat on the islands (Kotze 2008) and the high ability of this species to expand into new areas (Niemelä & Spence 1991). Kotze et al. (2000) and Kotze (2008) suggested that its absence could be explained by direct competition with *Pterostichus niger*, a slightly larger-bodied, more active species that is numerically dominant on small islands. Unfortunately, interactions between species in this study are poorly understood. Future work, perhaps in the form of experimental introductions to islands could help determine why large-bodied species like *C. taedatus* are mainly absent or exist in relatively small populations on small islands.

Islands and mainland did not differ in diversity; however, rarefied species richness increased significantly with island area. I hypothesize that the positive island area-diversity relationship in this study may be due to higher extinction rates of large-bodied species on small islands. Although I cannot eliminate the effects of microhabitats on species diversity, my study focused on a single habitat type (conifer forest) and thus minimized the role of habitat diversity (Williams 1964) as an alternative explanation for positive SARs on the islands. Niemelä et al. (1985) also focused on a single habitat type on Baltic islands but failed to detect a significant

SAR. It is clear in this study that population processes are influencing the persistence of large-bodied species on small islands (see above).

I found different effects of isolation (nearest distance and buffers) on carabid species diversity on the islands of Lac la Ronge. In general, diversity increased with isolation, but this relationship was only significant for raw species richness and not island isolation index, or for other diversity measures (rarefied richness and evenness). These findings are unusual for two reasons. First, species richness is typically highest on islands closer to mainland (MacArthur & Wilson 1963, 1967). Second, connectivity measures using buffers are typically better predictors than nearest distance measures (Moilanen & Nieminen 2002; Driscoll & Lindenmayer 2009). Still, the fifteen least isolated islands (< 0.8 isolation index) harboured only 24 of the 39 species in my study, while the pooled number for the fifteen most isolated islands (> 0.8 isolation index) was 35 species. In contrast, Niemelä et al. (1988) showed that the number of carabid species was lowest on the most isolated Baltic islands.

The positive relationship between diversity and island isolation may be explained by the ability of carabids to survive up to twice as long floating on freshwater compared to seawater as demonstrated by Renault (2011) in flotation experiments. Lac la Ronge is a freshwater intra-continental lake, whereas the Baltics have low but variable salinity (Kotze 2008). Hence, the potential distance that carabids can travel in drift is greater on Lac la Ronge, possibly explaining the positive diversity-isolation relationship in this study.

It is also possible that the islands on Lac la Ronge function like a clustered system of stepping stones where colonization, both from mainland and between islands, occurs frequently. Kotze et al. (2002) compared diversity of clustered versus scattered islands in the Baltics and

revealed that scattered islands accumulated species more quickly than did clustered islands. Due to their proximity, clustered islands can have greater between-island colonization, whereas isolated islands are colonized primarily by propagules arriving from the mainland (Hanski & Gyllenberg 1997). This may explain why more isolated islands contained several species not found on less isolated islands. Alternatively, lower numbers of species on less isolated islands could arise because large-bodied species like *C. taedatus* are not present, and therefore do not keep populations of small-bodied species in check on these islands.

Conclusions

This study illustrates that the passive sampling hypothesis does not explain the species-area relationship observed for ground beetles on the islands of Lac la Ronge. Carabid assemblages on islands less than one hectare distinctly differed from large islands and the nearest mainland. Large-bodied species were both less abundant and occurred less frequently on small islands, suggesting that populations of these species may be more difficult to sustain. In contrast, relative abundances of small bodied species were greater on small islands; possibly due to a ‘release’ of regulatory processes in the absence of large-bodied species. Island isolation did not influence the structure of carabid assemblage and did not negatively influence species diversity at the scales examined in this study. Evidence of population processes on small islands, such as greater extinction rates and lower immigration of large-bodied species, likely contributes to the positive species-island area relationship observed on the islands of Lac la Ronge.

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Figures & Tables

Table 1.1 Number of islands within each island size category, their isolation index, raw species richness (S), and number of individuals captured per island (I). The most abundant species and their relative proportion of the total catch on the island are also given. † indicates average number of individuals per island class.

Island	Size (ha)	Isolation	S	I	Most abundant species (%)
<i>Very small islands</i>					
EW	0.2	0.76	9	142	<i>Pterostichus adstrictus</i> (43.0)
FI	0.5	0.90	14	589	<i>Pterostichus adstrictus</i> (56.9)
HB	0.5	0.85	15	341	<i>Calathus ingratus</i> (26.4)
LG	0.6	0.80	15	365	<i>Pterostichus adstrictus</i> (49.0)
AL	0.7	0.80	12	813	<i>Pterostichus adstrictus</i> (26.4)
GL	0.7	0.52	13	670	<i>Pterostichus adstrictus</i> (29.9)
				486.7†	
<i>Small islands</i>					
CI	1.2	0.79	10	146	<i>Agonum retractum</i> (43.8)
CU	1.5	0.89	12	452	<i>Pterostichus adstrictus</i> (50.7)
RI	1.6	0.87	15	351	<i>Pterostichus adstrictus</i> (35.3)
RB	2.5	0.90	14	407	<i>Carabus chamissonis</i> (27.0)
FU	2.6	0.62	15	460	<i>Calathus ingratus</i> (31.1)
CD	3.2	0.80	10	163	<i>Pterostichus punctatissimus</i> (32.5)
KS	3.4	0.88	14	399	<i>Calathus ingratus</i> (46.6)
MT	7.5	0.67	10	267	<i>Calathus ingratus</i> (22.5)
SD	8.2	0.86	9	232	<i>Calathus ingratus</i> (31.9)
				319.7†	
<i>Medium islands</i>					
DG	10.3	0.48	9	406	<i>Calathus ingratus</i> (43.3)
LO	15.1	0.80	12	443	<i>Calathus ingratus</i> (20.5)
NC	19.3	0.86	8	43	<i>Pterostichus punctatissimus</i> (32.6)
TB	19.5	0.86	16	718	<i>Pterostichus adstrictus</i> (29.2)
CC	21.1	0.69	8	74	<i>Pterostichus adstrictus</i> (27.0)
LQ	26.9	0.83	10	110	<i>Agonum retractum</i> (32.7)
KD	29.4	0.76	9	301	<i>Synuchus impunctatus</i> (37.9)
NT	43.2	0.81	14	85	<i>Platynus decentis</i> (24.7)
				272.5†	
<i>Large islands</i>					
UK	124.3	0.77	11	355	<i>Pterostichus adstrictus</i> (36.1)
JO	130.2	0.79	10	396	<i>Carabus chamissonis</i> (29.3)
LV	169.1	0.87	12	89	<i>Agonum retractum</i> (32.6)
BR	255.1	0.82	13	559	<i>Calathus ingratus</i> (32.9)

LZ	289.2	0.78	10	268	<i>Stereocerus haematopus</i> (20.9)
ROSS	534.8	0.75	11	119	<i>Pterostichus adstrictus</i> (26.9)
BI	980.7	0.87	13	255	<i>Synuchus impunctatus</i> (35.3)
				291.6†	
<i>Mainland</i>					
EF	-	-	13	325	<i>Calathus ingratus</i> (45.5)
FT	-	-	11	654	<i>Calathus ingratus</i> (34.1)
MS	-	-	12	309	<i>Calathus ingratus</i> (25.2)
NP	-	-	10	119	<i>Pterosthicus punctatissimus</i> (42.9)
SB	-	-	9	207	<i>Synuchus impunctatus</i> (55.6)
				323†	

Table 1.2 Summary of pooled species richness among island size classes, mainland, and isolation classes.

	Very small	Small	Medium	Large	Mainland	Less isolated	More isolated
Number of sites	6	9	8	7	5	15	15
Pooled species richness	22	27	24	20	17	24	35

Table 1.3 Summary of global regression models (interaction not included) including standardized regression coefficients (Std. Coeff), and standard errors (SE) for raw species richness, rarefied species richness, and species evenness.

Variable	Raw Species Richness			Rarefied Species Richness			Species Evenness		
	Std. Coeff	SE	P	Std. Coeff	SE	P	Std. Coeff	SE	P
distance.to.mainland	0.3277	0.12269	0.0129	0.09768	0.05853	0.1067	-0.004205	0.004085	0.312453
log10.area	-0.6957	0.43543	0.1222	0.4607	0.19463	0.0254	0.050576	0.013584	0.000916
trap.days	-0.015	0.01622	0.3627	-	-	-	-	-	-
intercept	19.02	9.03292	0.045	7.00677	0.41856	8.78E-16	0.714204	0.029212	2.00E-16
overall model	-	-	0.04786	-	-	0.0269	-	-	0.002553

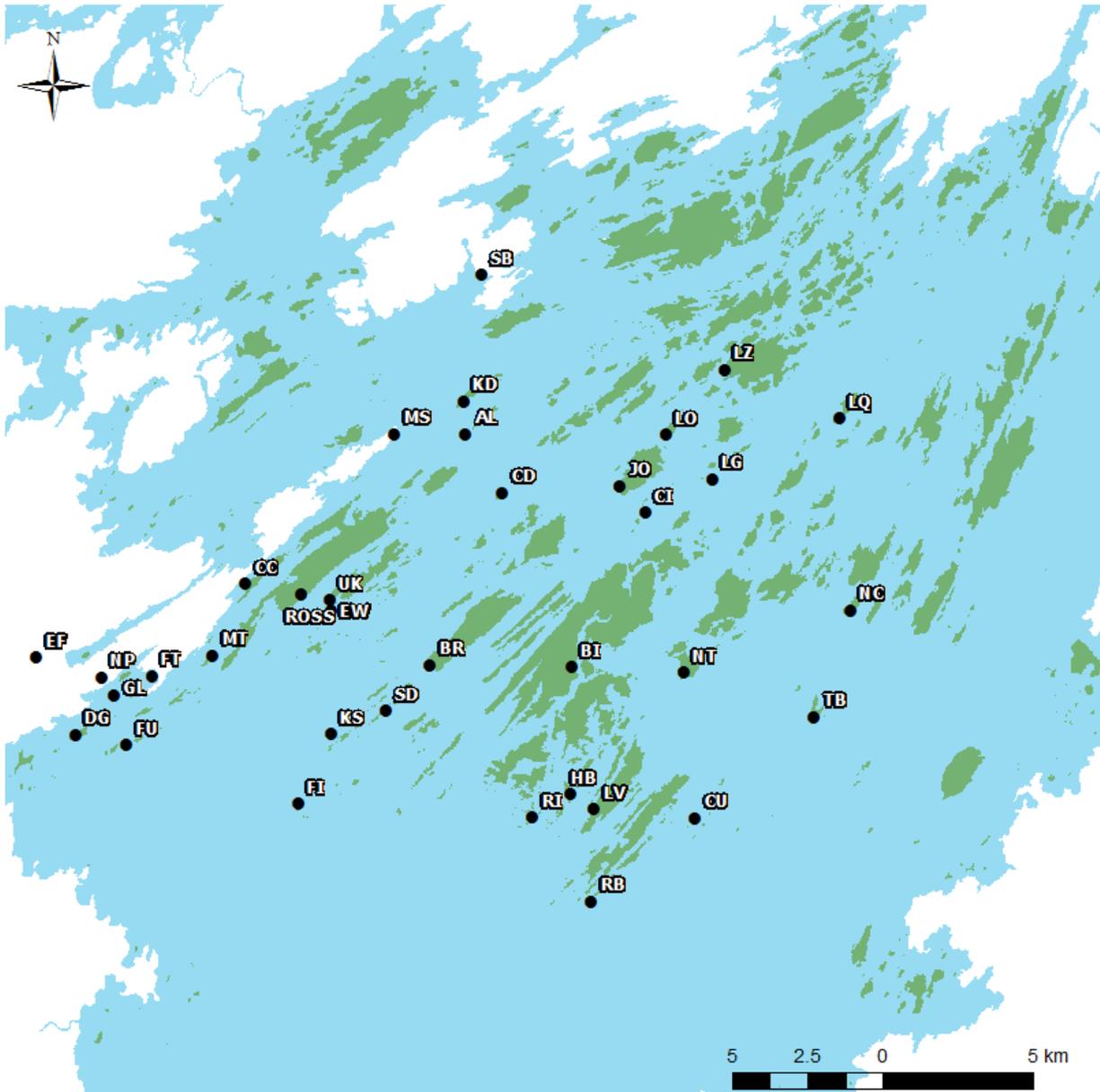


Figure 1.1 Map of islands (green) and mainland (white) of Lac La Ronge, Saskatchewan. Black circle indicate sampling locations for each site.

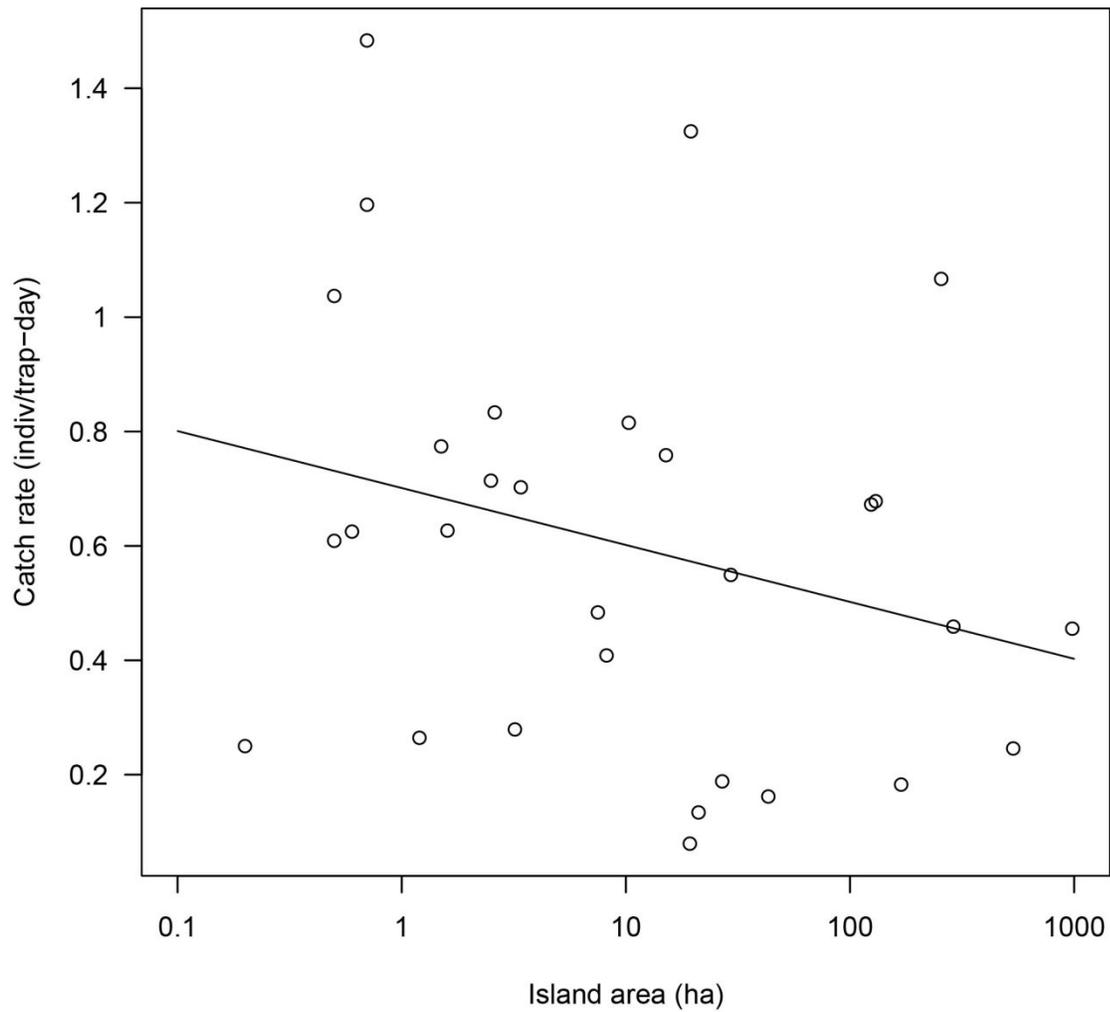


Figure 1.2 Relationship between total carabid catch rate and island area (\log_{10}) on the islands of Lac la Ronge (R^2 : 0.08, P : 0.14).

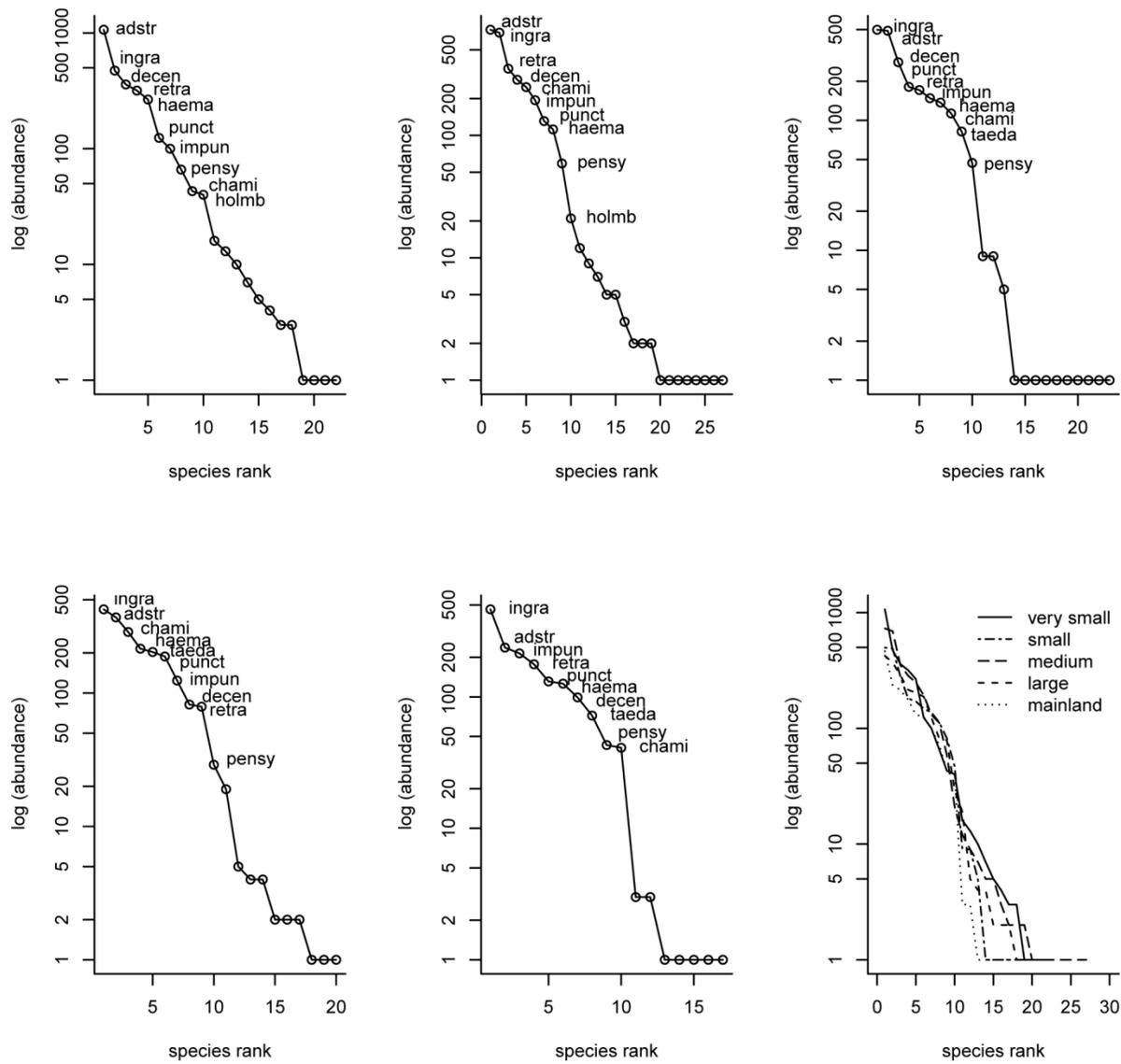


Figure 1.3 Rank-abundance curves for the 10 most abundant carabid species in each island class: very small (0.1 – 1.0 ha, n = 6); small (1.01 – 10 ha, n = 9); medium (10.01 – 100 ha, n = 8); large (100.01 – 1000 ha, n = 7).

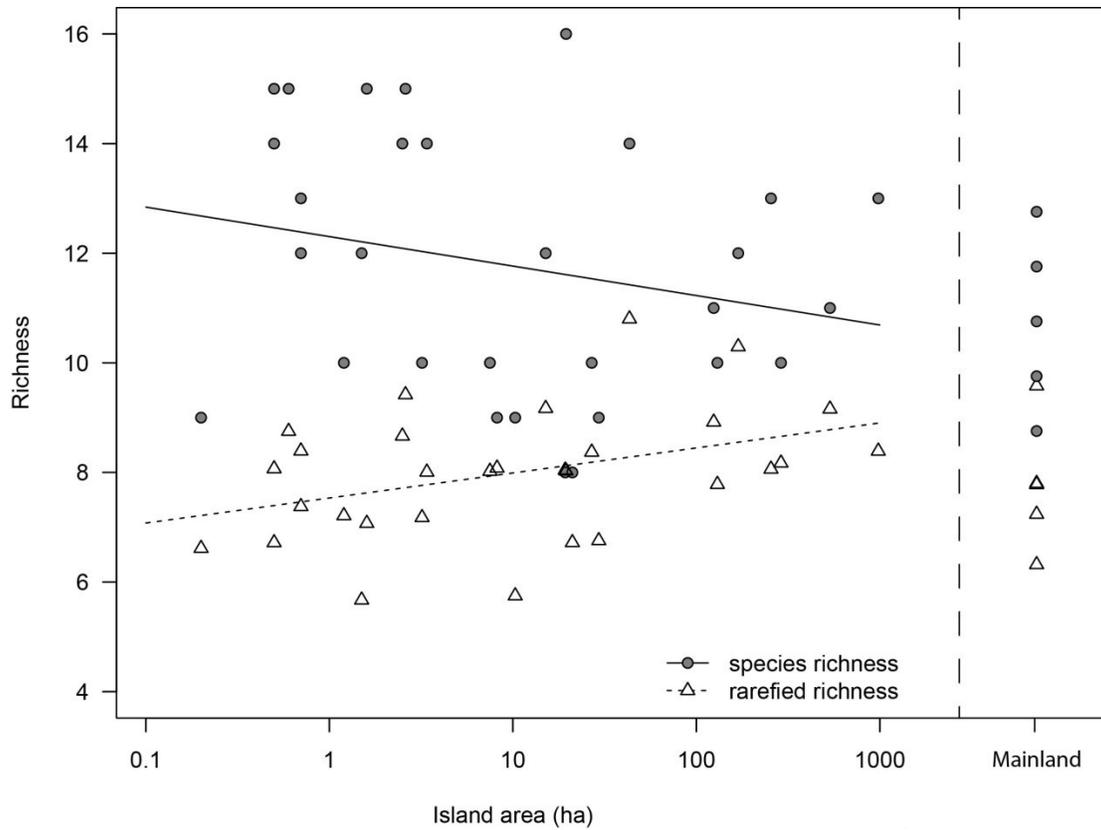


Figure 1.4 Relationship between raw species richness (circles, solid line; R^2 : 0.05, P : 0.22) and rarefied species richness (triangles, dashed line; R^2 : 0.16, P : 0.03) and island area (\log_{10}). Raw species richness (mean: 11, standard error: 1.58) and rarefied species richness (mean: 7.99, standard error: 0.53) for the mainland are shown on the right.

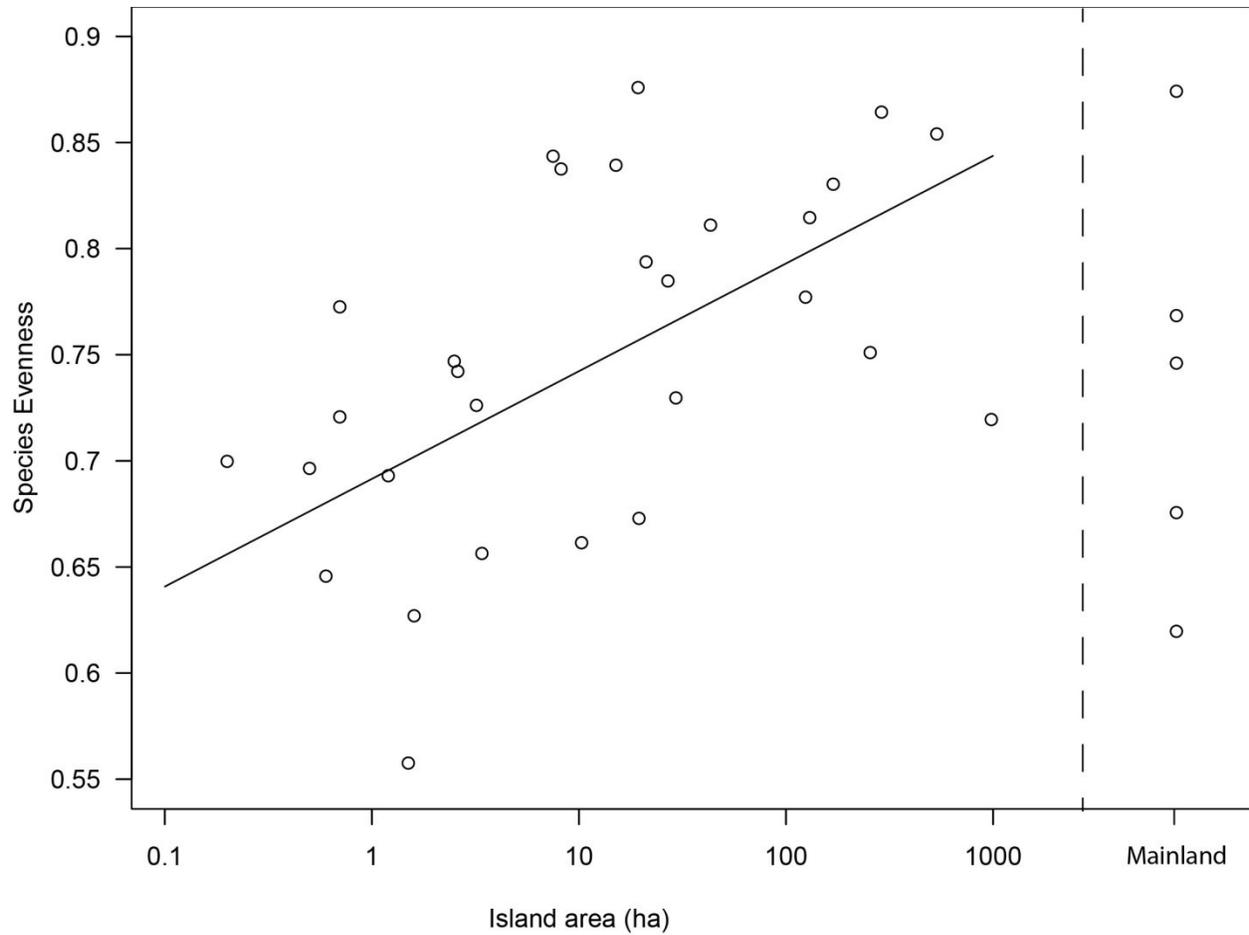


Figure 1.5 Relationship between species evenness and (\log_{10}) island area ($R^2: 0.33, P: < 0.001$). Species evenness for mainland sites is shown on the right (mean: 0.74, standard error: 0.04).

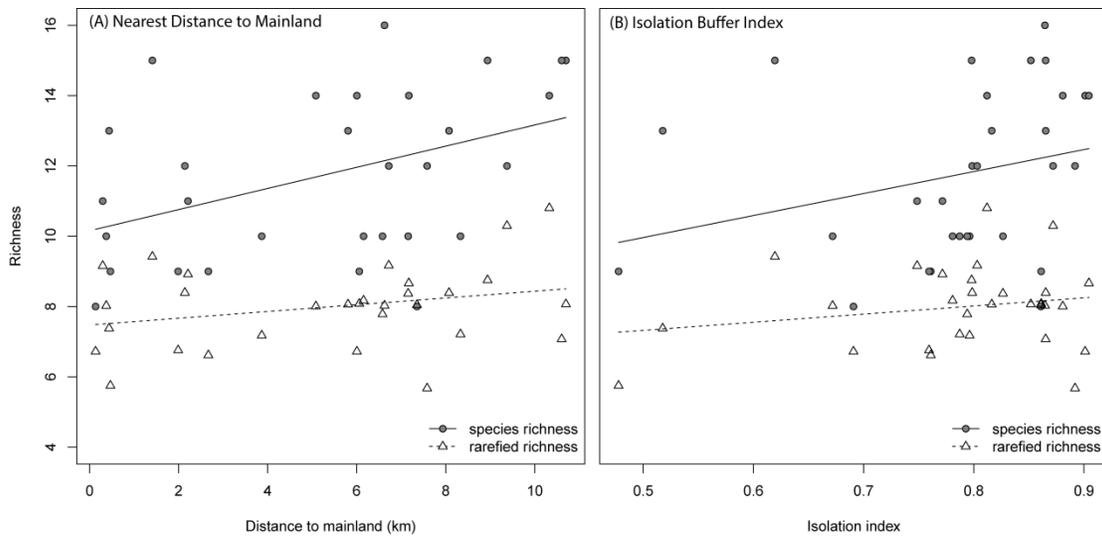


Figure 1.6 Relationship between carabid raw species richness and rarefied species richness for each measure of isolation: (A) distance to mainland and (B) isolation index.

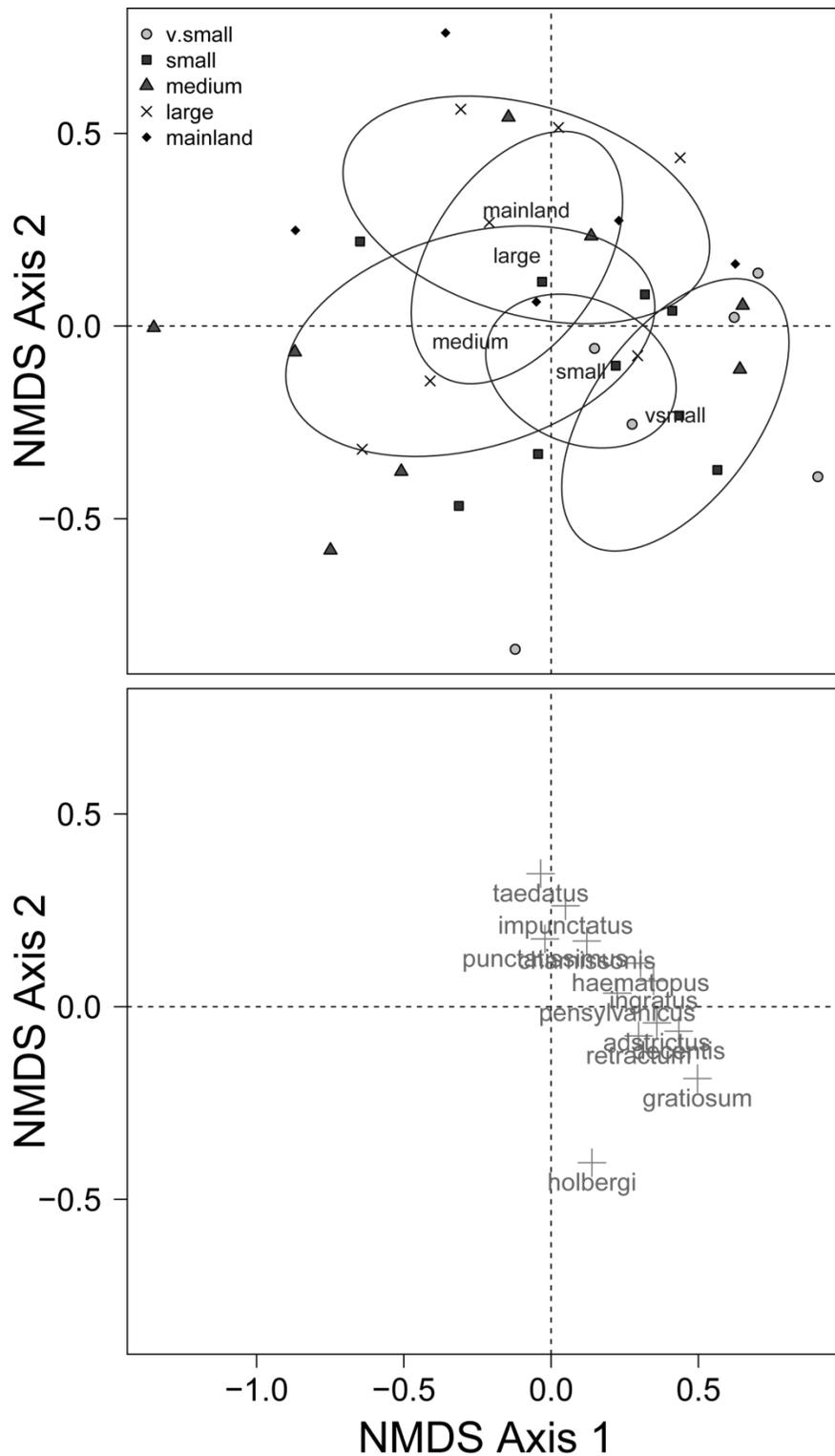


Figure 1.7 Non-metric multidimensional scaling ordination illustrating the similarities in carabid beetle assemblage between island classes and mainland (ellipses: 95% C.I.) and the centroids of the 12 most abundant species, stress = 0.17.

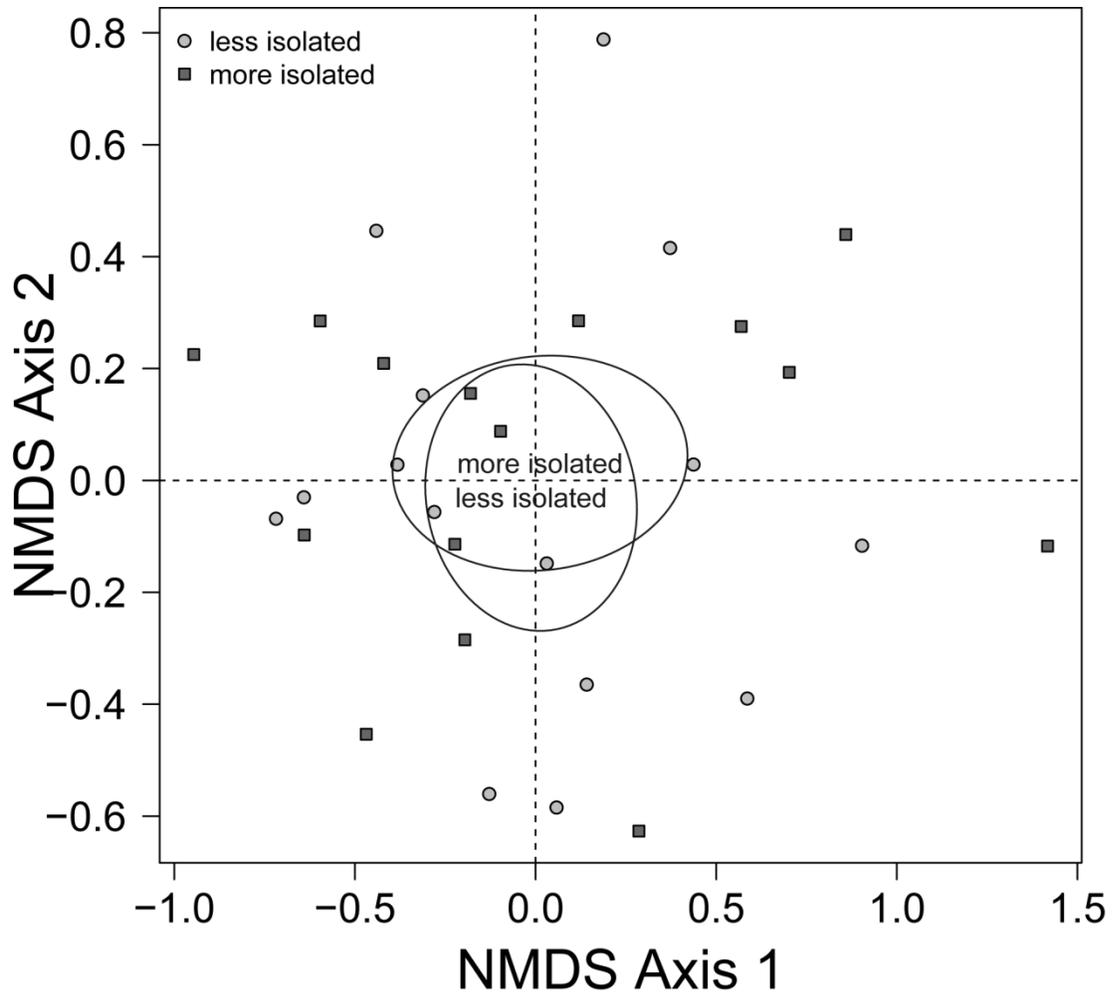


Figure 1.8 Non-metric multidimensional scaling ordination illustrating the similarities between carabid assemblages on islands that are less isolated and more isolated, stress = 0.16. Ellipses represent 95% confidence intervals.

Chapter 3: Body size and wing length influence the distribution of ground beetles (Coleoptera: Carabidae) on boreal lake islands in central Canada.

Introduction

In order for a species to successfully become established on an island, individuals must immigrate from source populations, locate suitable habitats, and reproduce in sufficient numbers to avoid extirpation (Kotze et al. 2008). These processes are influenced by the biological characteristics of particular species, such as variation in dispersal ability, niche-breadth, fecundity, and ability to compete for resources (Kotze et al. 2008).

Body size is perhaps one of the most well-studied attribute of island faunas because it influences many characteristics associated with immigration potential, ecological interactions, and resource requirements (Lomolino 2005). For example, body size influences metabolic rate and minimum resource requirements (McNab 1988, 1999) so that islands with low resource availability should favor smaller body size. Likewise, smaller-bodied species of carabid beetles (Coleoptera: Carabidae) are more common in disturbed habitats (Blake et al. 1994; Szyszko et al. 2000; Ribera et al. 2001; Niemelä et al. 2002; Braun et al. 2004; Magura et al. 2006; Elek & Lövei 2007) or isolated patches (Šerić Jelaska & Durbešić 2009), whereas large-bodied carabids are usually more dominant in stable, late-successional, and contiguous habitats (Szyszko et al. 2000; Šerić Jelaska & Durbešić 2009). These observations may reflect trade-offs in resource requirements, duration of development, and dispersal ability which all vary with body size (Den Boer 1970; Blake et al. 1994).

Carabid dispersal is directly influenced by wing length (Den Boer 1980). Individuals of species that are entirely macropterous (functional long hind wings) may disperse via flight while those of species that are entirely brachypterous (non-functional short hind wings) or apterous

(hind wings lost) disperse only by walking or passively drifting on water (Blake et al. 1994). Some carabid species are wing-dimorphic, meaning individuals may or may not possess fully developed wings (Den Boer 1970; Den Boer et al. 1980; Lindroth 1985, 1986). In such species, colonization of new areas typically occurs via the macropterous morph and once established, populations commonly shift towards dominance of the wingless form (see Niemelä & Spence 1991; Bourassa et al. 2011). This pattern appears to reflect local reproductive advantages associated with loss of flight (Ås 1984; Roff 1986; Spence & Spence 1988; Desender 2000; but see Carter 1976; Langor & Larson 1983; Desender 1989; Aukema 1991), emigration of macropterous individuals (den Boer 1970), and dominance of the gene that codes for the flightless morph (Aukema et al. 1996). For example, the introduction and subsequent spread of *Pterostichus melanarius* Illiger across western Canada (Niemelä & Spence 1991; Bourassa et al. 2011) fits this explanation. At the margins of its expanding range, the proportion of macropterous *P. melanarius* was much higher than at established sites only 81 km away (60-70% vs. 20%, respectively; Niemelä & Spence 1991). Similarly, from studies of lake islands on which most established populations of dimorphic species gradually shifted from being macropterous to dominated by flightless individuals. In fact, Zalewski (2004) proposed using frequencies of macropterous individuals to estimate the age of island populations.

Carabid species are classified as either spring or autumn breeders. Spring breeders overwinter as adults and reproduce during early summer, while autumn breeders, at least in temperate and boreal regions of Canada, overwinter as larvae and complete development the following spring or summer (Bousquet 2010). Although classifying carabid reproduction in this way oversimplifies the complexity of carabid life-cycles (see Bousquet & Pilon 1980), Zalewski

(2004) suggests that autumn breeders are more prone to extinction on islands because overwintering larvae are less tolerant to fluctuating environmental conditions than adults.

In the current study, I explore how life-history traits like body size, wing length, and breeding period are associated with patterns of relative abundance in carabid assemblages on islands in Lac la Ronge, Canada. I test the following hypotheses: 1) carabid body size is inversely related to island size, and 2) small islands have higher proportions of macropterous species, because these have higher immigration rates than do wingless species (Karjalainen 2000), and 3) small islands have a higher proportion of spring-breeding species. I compared catch rates of large-bodied and small-bodied species, and the proportion of macropterous species and spring-breeding species of carabid beetles among islands spanning an island size gradient. Furthermore, I compared the frequency of macroptery among three wing-dimorphic species, *Calathus ingratus* Dejean, *Synuchus impunctatus* (Say), and *Agonum retractum* (LeConte) and considered differences among islands of different size.

Methods

Site Description and Sampling Protocol

This study was conducted on islands in Lac la Ronge, Saskatchewan (55°06' N, 105°01' W); a large (1,413 km²) freshwater lake in the boreal forest of central Canada. During the summer of 2013, I sampled forested sites on thirty islands, ranging in size from 0.2 – 980.7 ha (Table 1.1, Chapter 1). Transects of eight pitfall traps, containing 2-3cm of propylene glycol to preserve specimens, were deployed at each site, for a total of 240 pitfall traps (see Chapter 1). Traps were positioned 15m apart in order to ensure independence of captures (Digweed et al. 1995) and a small plywood lid (15 x 15cm) was placed above the trap to exclude rainwater and

debris. Each trap was visited a total of five times at 14-17 day intervals throughout the frost-free season (2 June to 23 August) to collect samples and replenish the preservative.

Life History Traits

Adult carabids were identified to species using Lindroth (1969) and Bousquet (2010) and classified as ‘small-bodied’ (< 11.9 mm) or ‘large-bodied’ (> 12.0 mm) based on size records from the literature. Species were classified with respect to wing length as either (1) macropterous, i.e., hind wings fully developed; (2) flightless, either brachypterous or apterous; or (3) dimorphic (see Šerić Jelaska & Durbešić 2009). Wing length in dimorphic species was diagnosed by removing the elytra, and subsequent dissections to determine the condition of the flight muscles (see Langor & Larson 1983). This was done because flight not only depends on fully developed wings but also the functional muscles associated with flight (den Boer et al. 1980; den Boer 1990; Desender 2000; Matalin 2003) which may be histolyzed after a pre-reproductive flight period (Van Huizen 1979; Desender 2000; Matalin 2003) or may never develop (Nelemans 1987).

Information about breeding periods of species considered here was obtained from the literature (Lindroth 1969; Bousquet 2010). Because the life-cycle of *Cicindela longilabris* can last up to three-years (Bousquet 2010) and is not easily classified as spring or autumn breeder, I omitted this species from the seasonal-activity analysis.

Data Analysis

Linear regression was used to test whether body size and proportions of macropterous or spring-breeding species were related to island size. Residuals for wing length and seasonal-activity models met the assumptions of normality (Shapiro-Wilk test) and equal variance. Data

for analyzing the effect of area on body size were standardized by catch rate (total individuals per trap day) to account for missing or disturbed traps and then square-root transformed to meet assumptions of normality (Shapiro-Wilk test) and homogeneity of variance. Logistic regression, using the *stats* package in R (R development Core Team 2013), was used to test whether area and sex affected the probability of individuals being macropterous in *A. retractum*; the only dimorphic species to show significant variation in wing-morph ratios.

Results

Life History Traits

In total, 10,018 carabids were collected representing 37 species. Catch rates of small-bodied species were inversely related to island size while catch rates of large-bodied species significantly increased with island size ($R^2 = 0.55$, $P = < 0.0001$, Fig. 2.1). Furthermore, the body size model indicated that there was a significant interaction between body size and island area ($P = 0.0015$). These observations support my first hypothesis and suggest that body size strongly influences the relative abundances of carabids on islands.

Of the 37 species collected in this study, 64.8% (24) were strictly macropterous, compared to only 13.5% (5) that were flightless (Table 2.1). Overall, 21.6% (8) of species were wing-dimorphic. Proportion of macropterous species varied between 100% on islands 'FI' (0.5 ha) and 'CU' (1.5 ha) to 40% on the island 'NC' (19.3 ha; Table 2.2). Proportion of macropterous species significantly decreased with island area ($R^2 = 0.50$, $P = < 0.0001$, Fig. 2.2a). Taken together, these observations indicate that the ability to fly predicts the distribution of carabid beetles on the islands, supporting my second hypothesis.

Spring-breeding species accounted for 61.1% (22) of the species included in the analysis. Proportion of spring-breeding species was inversely related to island area ($\beta = -4.10 \pm 1.16$, $R^2 = 0.31$, $P = 0.001$, Fig. 2.2b), although this trend was influenced by the two largest islands, ‘ROSS’ and ‘BI’, which had exceptionally low proportions of spring breeders (see Fig. 2.2b). In a similar analysis performed without the two largest islands ($n = 28$), the proportion of spring-breeding species was marginally significant with island area ($\beta = -2.09 \pm 1.14$, $R^2 = 0.11$, $P = 0.08$).

Wing-Dimorphic Species

Of the eight dimorphic species in this study, three species [*Calathus ingratus* Dejean, *Synuchus impunctatus* (Say), and *A. retractum*] were present on nearly all of the islands and were collected in sufficient numbers to analyze patterns of wing length variation (Table 2.1). *Calathus ingratus* and *S. impunctatus* were predominantly wingless with, respectively, only 0.71% ($n = 990$) and 0.65% ($n = 153$) of individuals examined being macropterous. Individuals collected from mainland sites around Lac la Ronge demonstrated that the rate of macroptery in both *C. ingratus* (0.4%, $n = 247$) and *S. impunctatus* (0%, $n = 27$) were low.

In contrast, 23.8% ($n = 917$) of all *A. retractum* collected on the islands were macropterous, with significantly higher rates of macroptery among females (28.2%) compared to males (6.9%) (Odds ratio = 5.31, 95% CI [4.72, 5.89], $P = <0.001$; Fig. 2.3). Rates of macroptery among female *A. retractum* on islands were also greater than the nearest mainland (7.8%, $n = 141$) but this pattern was not observed in males, which did not significantly differ in rates of macroptery between islands and mainland (9.4%, $n = 32$). Furthermore, the probability of being macropterous in *A. retractum* was inversely related to island area for females (Odds ratio = 0.723, 95% CI [0.508, 0.938], $P = 0.004$; Fig. 2.3) but not for males (Odds ratio = 0.772, 95% CI [-0.014, 1.558], $P = 0.52$; Fig. 2.3). I also performed this analysis for females without islands that

had fewer than five individuals of *A. retractum*, and thereby had the potential to bias the relationship due to few observations. The model was still significant (Odds ratio = 0.731, 95% CI [0.522, 0.940], $P = 0.003$).

Female *A. retractum* were either macropterous or wingless, although a few males had a third, half-winged and likely flightless form (Fig. 2.4). Only two individuals of this phenotype were recorded (island 'CI', 1.2 ha, Table 2), but four additional specimens were found on the mainland as part of a separate study (site 'FT', Chapter 1). These numbers suggest that the frequency of the half-winged morph in *A. retractum* populations is low (< 1%).

Dissections of *A. retractum* showed that roughly half ($n = 30$) of the macropterous males and females possessed fully functional wing-muscles and thus were likely able to fly at the time of collection.

Discussion

Life History Traits

These results support the prediction that 1) body size of carabid communities increases and 2) the proportion of macropterous species significantly decreases with island area. I also found a higher proportion of spring-breeding species on small islands, although the strength of this relationship depended on results from the two largest islands (>500 ha). The positive relationship between body size and island area appears to reflect a combination of high relative abundance of small-bodied species and low abundance or absence of large-bodied species on small islands (see Chapter 1). As discussed in Chapter 1, competitive 'release' may explain why small-bodied species increase in abundance on small islands with reduction in large-bodied species.

The reduction of large-bodied species on small islands may relate to their greater resource demands (McNab 1988, 1999; Blake et al. 1994). If food availability on islands is positively related to island area (McNab 2002), small islands should favor smaller-bodied species that require fewer resources. Šustek (1987) suggested that small body sizes in carabids may be related to low primary productivity, although habitats with high productivity, like intensively managed grasslands, still favor small body sizes (Blake et al. 1994). Instead, Syzszko et al. (2000) suggested that small body size in carabids was related to soil organic matter, which is basal to the soil food web from which much carabid food is drawn. Soil data were not collected in the present study, although studies of boreal lake islands in Sweden (Wardle et al. 1997; Wardle et al. 2002; Wardle et al. 2003) demonstrate that long-term absence of fire on small islands can lead to less productive soil because late-successional plant species produce poorer quality litter and more phenolics that retard soil processes (Wardle et al. 1997). Although connections to carabids are obscure, further work about such relationships could provide new insights about potential resource limitations for carabids on islands.

Many studies have shown that carabid community structure shifts towards small-bodied species in highly disturbed or unstable habitats, including intensively managed grasslands (Blake et al. 1994), recently harvested forests (Szyzko et al. 2000; Šerić Jelaska et al. 2011), fragmented forests (Šerić Jelaska & Durbešić 2009), and areas increasingly affected by urbanisation (Niemelä et al. 2002; Weller & Ganzhorn 2004; Magura et al. 2006; Elek & Lövei 2007). Intraspecific reductions in body size have also been observed in the darkling beetle, *Asida planipennis* (Coleoptera: Tenebrionidae), on small islands of the western Mediterranean (Palmer 2002). Together, these studies suggest that small body size is favoured in degraded environments

and that in general, large-bodied species are less adapted or unable to survive highly disturbed or unstable habitats.

Underrepresentation of large-bodied species on small islands due to limited resources may also be exacerbated by their more-limited ability to disperse. Because large-bodied species are typically flightless on these islands (i.e. *C. taedatus*, *C. chamissonis*, and *P. punctatissimus*), they must have colonized primarily via drifting on the water surface. Consequently, they likely have lower immigration rates than in macropterous species. Limited available data on immigration of carabids suggest that macropters dominate in drift material (Karjalainen 2000). Resource limitations on small islands causing greater extinction rates of large-bodied species, and lower frequency of arrival of flightless species likely explain why higher proportions of macropterous species occur on small islands. Although populations of large-bodied species may be occasionally found on small islands, these may represent ‘sink’ habitats for large-bodied species in the context of metapopulation dynamics. Furthermore, because immigration of large-bodied flightless species is lower, populations of these species are not ‘rescued’ from local extinction.

It is also important to note that high numbers of large-bodied carabid species do occur in some disturbed habitats. For example, large-bodied European exotics like *C. nemoralis* (21-26 mm), *C. granulatus* (16-24 mm), and *P. melanarius* (12-19 mm; Bousquet 2010) dominate the ground beetle assemblages of urban centers in western Canada (Niemelä et al. 2002; Bourassa et al. 2011). It is not clear why these species are so profoundly abundant (Niemelä et al. 2002; Bourassa et al. 2011), nevertheless, the ability of these large-bodied species to proliferate in highly disturbed urban centers shows that resource availability may vary depending on the

species, that disturbance does not always favor smaller body sizes, and that other factors, such as release from natural enemies, may explain proliferation of exotic species in new habitats.

Species that breed during autumn and overwinter as larvae are thought to be more vulnerable to fluctuations in environmental conditions (Zalewski 2004). Assuming that small island environments are less stable, spring breeding species should be more prevalent on these islands, as is consistent with this study (see Fig. 2.2B). However, when the two largest islands are omitted thus considering islands smaller than 500 ha in size, this relationship is only marginally significant ($R^2 = 0.11$, $P = 0.08$). I offer two explanations for this trend. First, this weak relationship may be confounded because seasonal activity is tied to other life history traits (body size, wing length). Alternatively, the trend may have some biological significance. For example, carabids overwintering on islands may be more exposed to strong winds and erratic freeze-thaw cycles than those overwintering on mainland. Assuming large islands have smaller perimeter-area ratios (less edge) than small islands, large islands may be less exposed to extreme weather conditions and therefore more favourable for autumn breeders overwintering as larvae.

Wing-Dimorphism

Of the three most abundant dimorphic species collected in this study, *C. ingratus* and *S. impunctatus* were predominantly flightless (< 1% macroptery) and exhibited about the same degree of macroptery as on the adjacent mainland. I propose two explanations for the very low frequency of macroptery in these species. First, islands may have been colonized by macropterous forms and with sufficient time, local selection against flight has shifted island populations to almost a completely flightless form. This so-called ‘parachute-effect’, (Niemelä & Spence 1999) has been observed in other studies of colonization (Lindroth 1949; Den Boer 1970; Haeck 1971; Desender 1989; Laroche & Larivière 1990; Niemelä & Spence 1991, 1999;

Aukema et al. 1996; Desender et al. 1998) and appears to result from a combination of local reproductive advantages of the flightless form (Ås 1984; Roff 1986; Spence & Spence 1988; Desender 2000; but see Carter 1976; Langor & Larson 1983; Desender 1989; Aukema 1991), local emigration of macropters (Den Boer 1970), and dominance of the gene that codes for the wingless form (Aukema et al. 1996). Low proportions of the macropterous form in *C. ingratus* and *S. impunctatus* might suggest that island populations are relatively stable (Zalewski 2004), but in the absence of information about rates of selection, estimates of population age are not possible.

Second, it is also possible that the low frequency of macroptery in source populations of *C. ingratus* and *S. impunctatus* means that islands are colonized primarily by individuals of the flightless morph. Even if occasional flight occurs, the low numbers of individuals with wings in source populations suggests that colonization of distant islands by flight will be infrequent. In this scenario, greater dispersal ability of the macropterous form is likely outweighed by dominance of the flightless form in source populations. Furthermore, assuming simple Mendelian-inheritance of the winged trait, at least for *C. ingratus* (see Aukema 1995 for inheritance of other *Calathus*), mating between colonizing macropterous individuals and flightless morphs of well-established populations would favor production of flightless offspring.

Probability of macroptery in *A. retractum* was significantly higher in females suggesting that inheritance of the winged trait is sex-linked. Carter (1976) also noted the apparent rarity of winged *A. retractum* males and higher proportions of macropterous females (42% and 46% macroptery in 1971 and 1972, respectively) in the Kananaskis Valley, Canada. Significant variation in frequency of macroptery between sexes in this study (28.2% in females vs. 6.9% in

males) and in Carter's (1976) suggests that inheritance of the winged trait in *A. retractum* is not straight-forwardly Mendelian.

Probability of being macropterous in *A. retractum* was also significantly higher on small islands, but only among females. These findings provide additional support for the hypothesis that greater dispersal ability allows for exploitation of limited or short-lived resources on small islands (see Chapter 1 discussion). Because females are more likely to be winged, and presence of functional flight muscles suggests that they can fly, they may benefit from increased dispersal ability. The relatively low proportion of macroptery in females on mainland (7.8%) compared to islands (28.2%) also supports this conclusion.

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Figures & Tables

Table 2.1 List of carabid species collected on the islands of Lac la Ronge, their wing type (m-macropterous, b-brachypterous, d-dimorphic), breeding period, mean body lengths (mm), and proportion of total catch (%).

Species List	Wing Type	Mean Body Length (mm)	Breeding Period	% of Total Catch
<i>Agonum affine</i> Kirby	m	8.6	spring	0.02
<i>A. corvus</i> (LeConte)	m	8.8	spring	0.01
<i>A. gratiosum</i> (Mannerheim)	m	7.8	spring	0.33
<i>A. melanarium</i> Dejean	m	9.0	spring	0.14
<i>A. propinquum</i> (Gemminger & Harold)	m	7.2	spring	0.01
<i>A. retractum</i> (LeConte)	d	6.9	spring	9.20
<i>A. sordens</i> (Kirby)	m	5.9	spring	0.18
<i>Amara erratica</i> (Duftschmid)	m	7.6	spring	0.01
<i>A. littoralis</i> Mannerheim	m	8.0	spring	0.01
<i>A. patruelis</i> Dejean	m	8.7	spring	0.03
<i>Bembidion bimaculatum</i> (Kirby)	m	6.4	autumn	0.01
<i>Bradycellus lugubris</i> (LeConte)	m	6.7	spring	0.02
<i>Calathus ingratus</i> Dejean	d	8.8	autumn	20.8
<i>Carabus chamissonis</i> (Fisher von Waldheim)	b	14.5	spring	6.90
<i>C. taedatus</i> Fabricius	b	21.5	spring	3.00
<i>Calosoma frigidum</i> Kirby	m	22.0	spring	0.02
<i>Cicindela longilabris</i> Say	m	16.0	3 year cycle	0.01
<i>Cymindis cribricollis</i> Dejean	d	9.7	autumn	0.25
<i>C. unicolor</i> Kirby	b	8.8	autumn	0.06
<i>Elaphrus clairvillei</i> Kirby	m	9.1	spring	0.02
<i>Harpalus fulvilabris</i> Mannerheim	d	10.0	autumn	0.14
<i>H. laevipes</i> Zetterstedt	m	11.3	autumn	0.01
<i>Loricera pilicornis</i> (Fabricius)	m	7.8	spring	0.05
<i>Miscodera arctica</i> Mannerheim	m	8.0	autumn	0.08
<i>Patrobus foveocollis</i> (Eschscholtz)	d	9.8	autumn	0.04
<i>P. septentrionis</i> Dejean	m	10.0	autumn	0.02
<i>Platynus decentis</i> (Say)	m	11.5	spring	10.0
<i>P. mannerheimii</i> (Dejean)	m	12.1	spring	0.01
<i>Pterostichus adstrictus</i> (Eschscholtz)	m	11.3	spring	26.5
<i>P. brevicornis</i> (Kirby)	b	5.5	autumn	0.02
<i>P. pensylvanicus</i> (LeConte)	m	10.8	spring	2.00
<i>P. punctatissimus</i> (Randall)	b	16.5	autumn	6.20
<i>Stereocerus haematopus</i> (Dejean)	m	11.0	autumn	7.30
<i>Syntomus americanus</i> (Dejean)	d	3.1	spring	0.12
<i>Synuchus impunctatus</i> (Say)	d	10.0	autumn	5.70
<i>Trachypachus holmbergi</i> Mannerheim	m	4.8	spring	0.80
<i>Trechus apicalis</i> Motschulsky	d	4.3	autumn	0.04

Table 2.2 List of islands and the number of individuals (N), and proportion of macropterous species (%M_S) by island. Number of *A. retracts* collected (N_R) and the proportion of macropterous males (♂) and females (♀) is also listed.

Island number	Island	Area (ha)	N	%M _S	N _R	<i>Agonum retracts</i>	
						♂	♀
1	EW	0.2	142	80.0	22	0	64.7
2	FI	0.5	589	100	17	0	53.3
3	HB	0.5	341	80.0	72	27.3	37.7
4	LG	0.6	365	72.7	21	0	33.3
5	AL	0.7	813	71.4	133	2.9	44.9
6	GL	0.7	670	77.8	53	7.7	12.5
7	CI	1.2	146	71.4	62	10.0	25.0
8	CU	1.5	452	100	94	6.9	12.3
9	RI	1.6	351	90.9	18	0	35.3
10	RB	2.5	407	81.8	29	0	16.7
11	FU	2.6	460	80.0	31	0	18.5
12	CD	3.2	163	71.4	4		
13	KS	3.4	399	81.8	39	9.1	39.3
14	MT	7.5	267	66.7	13	25.0	22.2
15	SD	8.2	232	60.0	59	0	4.1
16	DG	10.3	406	66.7	61	12.5	28.3
17	LO	15.1	443	50.0	28	0	17.6
18	NC	19.3	43	40.0	1		
19	TB	19.5	718	75.0	31	0	32.0
20	CC	21.1	74	60.0	1		
21	LQ	26.9	110	71.4	36	20.0	32.3
22	KD	29.4	301	66.7	9	50.0	28.6
23	NT	43.2	85	70.0	4		
24	UK	124.3	355	71.4	16	0	46.2
25	JO	130.2	396	57.1	5	0	20.0
26	LV	169.1	89	55.6	29	0	10.5
27	BR	255.1	559	60.0	5	0	25.0
28	LZ	289.2	268	57.1	2		
29	ROSS	534.8	119	50.0	8	0	33.3
30	BI	980.7	255	50.0	14	0	15.4
Sum			10018		917		

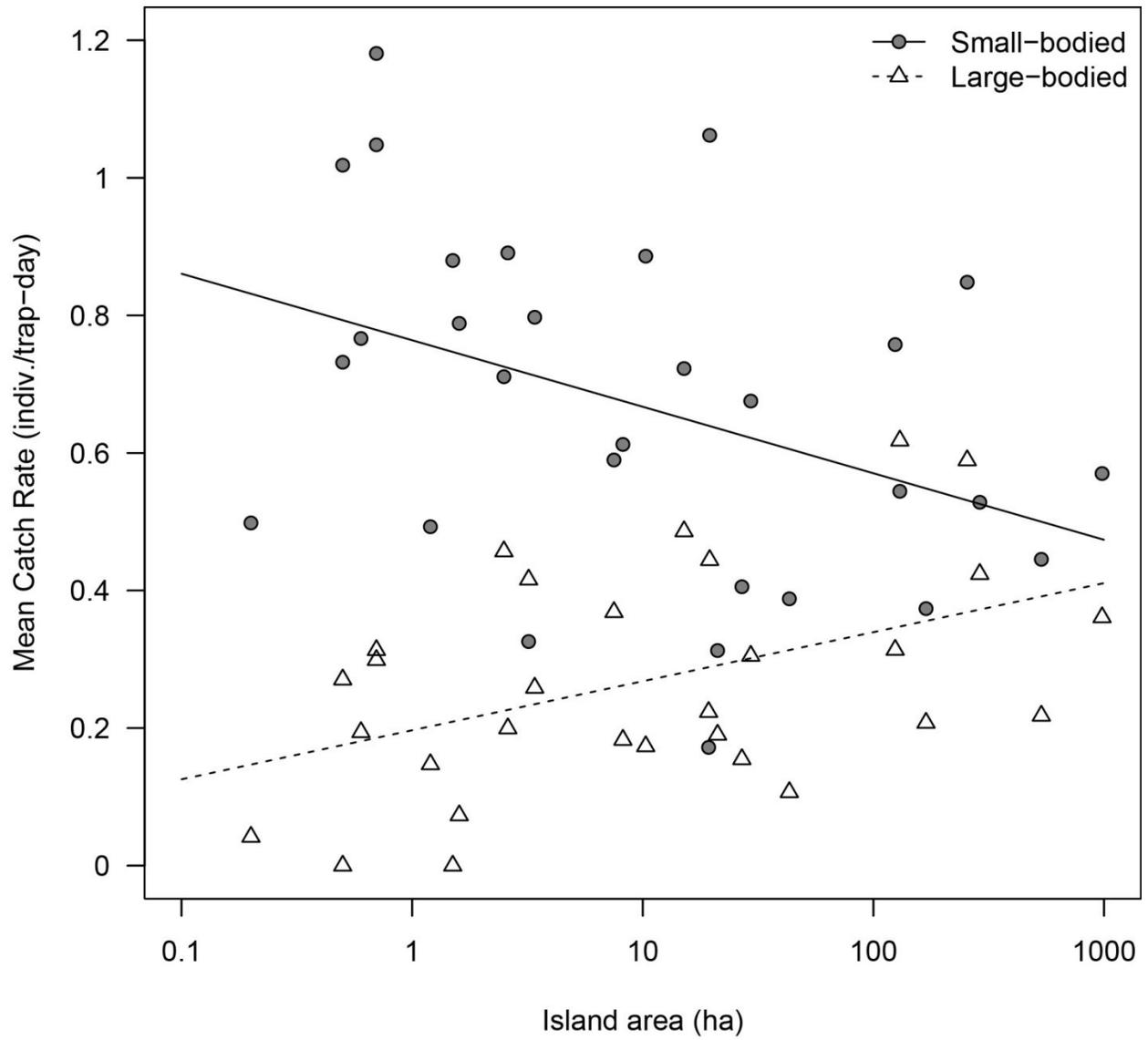


Figure 2.1 Relationship between \log_{10} island area and mean catch rate of large-bodied and small-bodied carabids ($R^2: 0.55, P: < 0.0001$).

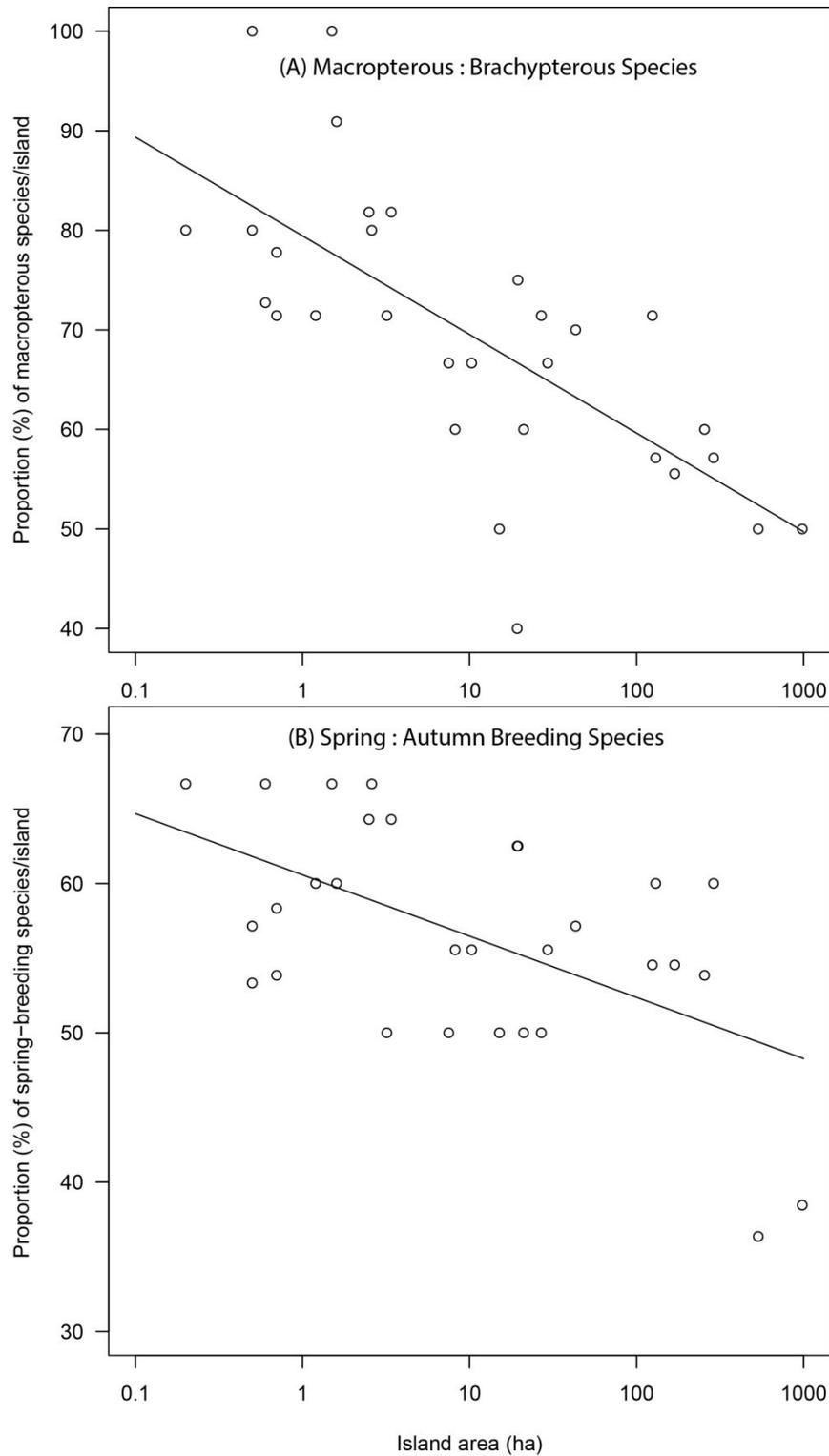


Figure 2.2 Relationship between \log_{10} island area and (A) proportion of macropterous species ($R^2: 0.50, P: < 0.001$); and (B) proportion of spring breeding species ($R^2: 0.31, P: 0.001$) on the islands of Lac la Ronge (regression line includes the two largest islands).

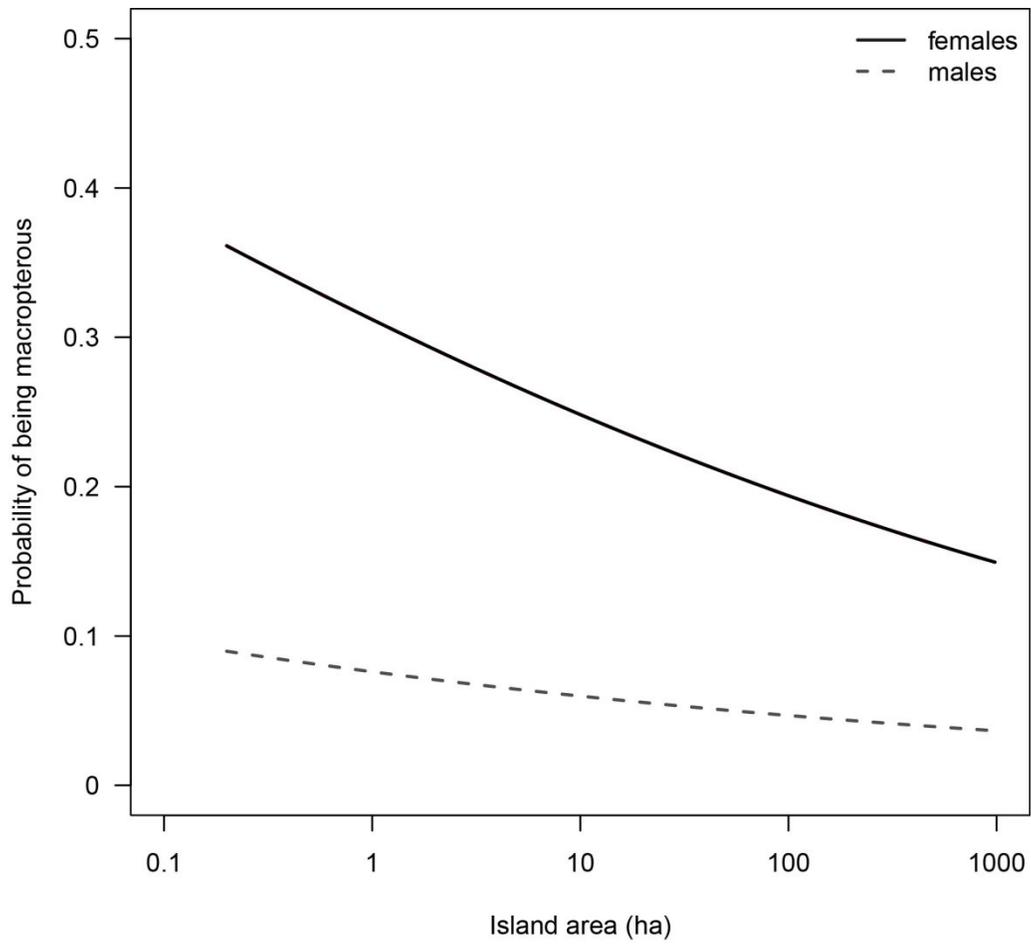


Figure 2.3 Changes in predicted probability of *A. retractum* being macropterous (winged) with increasing island size (\log_{10}) for males and females.



Figure 2.4 Dorsal view of the half-winged *A. retractum* male phenotype (elytra removed).

Chapter 4: Discussion

Main Results

My research supports the notion that study of carabid beetles on islands is useful for understanding how spatial features like area and isolation influence biodiversity. I showed that carabid assemblages and diversity on the islands of Lac la Ronge are influenced by area and that diversity does not decrease with isolation. From these findings, I infer that the population processes in carabids, and possibly other insects, are likely influenced by the interaction of island size with life history traits of particular species. This in turn, suggests hypotheses that open up many possibilities for new investigations. In the discussion below, I aim to summarize my findings and relate them in a broader sense to the study of island biogeography and conservation planning.

In chapter 2, I showed that rarefied species richness significantly increased with island area. Contrary to expectations from theory, however, richness either increased or was not influenced by isolation. Carabid assemblages were distinct on islands smaller than one hectare but gradually approached the structure of mainland assemblages with increasing area. Small islands were characterized by high abundances of small-bodied species and lower numbers or absence of large-bodied species like *Carabus taedatus*. Based on these findings, I suggest that the passive ‘sampling hypothesis’, which proposes that large islands have more species because they intercept larger sample from the species pool, does not adequately explain the diversity patterns observed among islands in Lac la Ronge. I infer that population processes such as greater extinction rates of larger-bodied species and the concomitant competitive release of smaller bodied species on small islands contributes to the positive species-area relationship observed in this chapter.

In chapter 3, I compared life history traits like carabid body size, wing length, and seasonal activity among boreal lake-islands spanning an island size gradient from 0.2 to 980.7 ha. I showed that catch rates of small-bodied species were inversely related to island size, and that small islands had a higher proportion of winged species and spring-breeding species. I also showed that the ratio of macroptery to brachyptery in the dimorphic species, *A. retractum*, was significantly higher on small islands. I suggest that large-bodied species are underrepresented on small islands due to greater resource requirements associated with large body size and lower resource availability on small islands. Under-representation of large-bodied species may also be exacerbated by lower immigration rates of large-bodied species, which tend to be flightless and therefore colonize islands by passively drifting on the water surface.

Theoretical Implications and Conservation Planning

The research conducted in this dissertation supports the notion that area is an important determinant of diversity. Small islands support lower carabid diversity and distinctly different carabid assemblages than large islands and mainland. Thus, acknowledging the obvious differences between true islands and habitat ‘islands’ (*i.e.* patches), management practices aimed at conserving maximum carabid diversity should embrace areas greater than one hectare as being more useful. This recommendation is consistent with research on retention patches in forest management, which suggest that the smallest retention patches should be greater than 0.5 hectares (Pyper 2009). However, small islands in Lac la Ronge supported several species not found on large islands, and thus, smaller patches may also be valuable. Therefore, conserving boreal lake islands across a range of sizes is probably best.

Clear association between autecological traits and island size indicate the importance of considering species characteristics in conservation planning. For example, large-bodied,

flightless species are more sensitive to island size because they have greater resource requirements and most likely lower immigration rates compared to species that can fly. Thus, while the focus is often on preserving the greatest number of species, it is also important to consider individual species, both for their conservation value but also the specific characteristics that make them vulnerable to factors like fragmentation or isolation.

The cause of positive species-area relationships is commonly debated in ecological circles. The research in this dissertation shows that the passive ‘sampling hypothesis’ (Connor & McCoy 1979) does not adequately explain the observed patterns of diversity on Lac la Ronge. Although it is difficult to rule out potential effects of microhabitat on diversity, population processes on the islands, resulting from influences like greater turnover rates of large-bodied species and/or competitive release of small-bodied species may, in part, explain the patterns of diversity observed in this study in ways reminiscent of the ‘equilibrium theory’ of Island Biogeography (MacArthur & Wilson 1963, 1967).

Future Research

As is often the case in science, the research conducted in this M.Sc. thesis raises a number of interesting questions and hypotheses. Future work, as outlined below, would likely advance our understanding of the island biogeography of carabid beetles on Lac la Ronge.

1) The effects of isolation (or lack thereof) examined in this research is surprising. However, as noted in Chapter 1, the methods I used to measure isolation (nearest distance and distance buffers) only indicate whether carabids can travel the distance to or between islands, not the relative frequency that they do so. Thus, it would be useful to know the relative frequency at which carabid immigrate to the islands and whether this frequency is at all influenced by wing

type. This information is important with respect to the ‘equilibrium theory’ hypothesis (immigration rate is inversely related to isolation) but also metapopulation dynamics and the potential for immigrants to ‘rescue’ island populations from local extirpation.

2) Most island studies of carabids have typically focused on broader habitat types (i.e. forest vs. pasture, Niemelä et al. 1987; Niemelä 1988; Niemelä et al. 1988; but see Zalewski et al. 2012) despite the response of carabids to fine scale variations in microhabitat (Niemelä et al. 1992a; Niemelä et al. 1992b). Although this dissertation focused on a single habitat type, the question remains whether fine scale habitat features that vary due to island size influences abundance and diversity of carabid beetles on islands.

3) The large-bodied wingless species, *C. taedatus*, is found on most large islands and mainland sites but is nearly absent from the 14 smallest islands in this study. Experimental introductions of *C. taedatus* to small islands could help determine whether dispersal and/or unsuitable habitat on small islands prevent this species from maintaining viable populations on small islands. Much could be learned from such experiments, both about probability of persistence and effective propagule sizes for establishment.

4) If small-island environments are unfavourable for large-bodied species because of limiting resources, the question remains: what resource(s) are limited on small islands? Blake et al. (1994) and Szyzko et al. (2000) suggested that soil organic matter is an important determinant of carabid biomass; however, I did not collect soil data as part of this study. Future work in this direction could help to determine why large-bodied species are underrepresented on small islands.

5) The apparent sex-linked inheritance of the winged trait in *A. retractum* is worth investigating. Possible explanation for higher proportions of macropterous females on small islands includes exploitation of short-lived or limited resources by individuals capable of flight. Alternatively, flightless *A. retractum* may both arrive less frequently and have higher extinction rates, and thus are less common compared to macropterous forms. Aukema (1995) showed that in *Calathus melanocephalus*, the inheritance is simple Mendelian, but that expression of the winged form can be influenced by temperature and food supply. Understanding the factors that control expression of the winged trait in *A. retractum* would help resolve these questions.

In conclusion, my results provide both practical and theoretical information that is useful in understanding island faunas on boreal lake islands, and which have implications and possible application in conservation planning. In this work, I have demonstrated that the study of islands and carabid beetles helps facilitate a deeper understanding of factors that influence biodiversity and the distribution of species.

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