

**COMMUNITY AND REGIONAL SCALE PATTERNS OF
NATIVE AND EXOTIC PLANT SPECIES IN SAND BEACHES OF
VANCOUVER ISLAND, BRITISH COLUMBIA**

by

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Abstract

I compared the distribution and abundance of native and exotic plant species at two spatial scales using vegetation data from eighteen beaches on the west coast of Vancouver Island, BC. I found that native and exotic plant species have similar patterns of distribution and abundance at both community and regional scales. This suggests that despite some biological differences between native and exotic species they share common ecological patterns.

Within sand beach plant communities, I found that spatial patterns of native and exotic plant species richness were similar; both were low near the shore, reached a maximum approximately 50 m inland, and then declined in the dunes behind. The results support the generalization that increased invasibility from exotic species is associated with sites of high native species richness within plant communities. This pattern is a major conservation concern because it indicates that sites with the highest biological diversity are at the greatest risk from exotic species invasion. Native and exotic species richness peaked in plots with the most fertile soils.

At a regional scale, native and exotic plant species also have similar ecological patterns. Regional distribution–local abundance relationships, which were analyzed using data from sand beaches together with seven other plant communities, for native and exotic plants species in regional patch networks were statistically coincident or similar. As well, the proportions of native and exotic species in patch occupancy classes were statistically equal in all regional patch networks. Most native and exotic species were both regionally rare and locally sparse. Collectively, the results indicate that the distribution and abundance of native and exotic plant species are not independent at a regional scale.

I also described and named seven sand beach plant associations from the west coast of Vancouver Island: 1) *Cakile edentula* - *Atriplex gmelinii* Sparse Vegetation; 2) *Leymus mollis* spp. *mollis* - *Lathyrus japonicus* Herbaceous Vegetation; 3) *Festuca rubra* - *Fragaria chiloensis* Herbaceous Vegetation; 4) *Ammophila arenaria* Herbaceous Vegetation; 5) *Arctostaphylos uva-ursi* Dwarf Shrubland; 6) *Eurhynchium oreganum* / *Gaultheria shallon* Shrubland; and, 7) *Poa macrantha* Sparse Vegetation. All are of potential conservation concern because the limited development of beach vegetation in coastal British Columbia.

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CHAPTER 1

GENERAL INTRODUCTION

The introduction and spread of exotic plant species has changed patterns of diversity in many plant communities (Lonsdale, 1999). Estimates indicate that over 2,800 new vascular plant species (or 23.9% of all vascular plants) have been introduced to Canada since European settlement began (Vitousek *et al.*, 1997). There is concern that the exotic species invasion will worsen leading to an “invasion meltdown” as natural ecosystems are incrementally changed by the continuing introduction of new species (Simberloff and Von Holle, 1999; Levine and D’Antonio, 2003). The rapid spread of exotic species has been identified as one of the most significant global changes caused by anthropogenic influences (Vitousek *et al.*, 1996).

In this thesis I compare the distribution and abundance of native and exotic plant species at two spatial scales. I argue that native and exotic plant species have similar patterns of distribution and abundance at community and regional scales. This suggests that despite biological differences between native and exotic species (Kolar and Lodge, 2001), they share common ecological patterns (Thomson *et al.*, 1995). Shared spatial patterns between native and exotic species likely reflect similar responses to biotic and abiotic processes and factors that control plant community composition (Stohlgren *et al.*, 1999). Most of the statistical analyses in my research use vegetation data collected from eighteen beaches on the west coast of Vancouver Island. Seven additional plant community datasets were used for analyses of regional scale patterns.

I used sand beaches to study patterns of exotic plant invasion for several reasons. Beaches occur at the intersection of marine and terrestrial realms (Ranwell, 1972; Brown and McLachlan, 1990). Patterns of vegetation development are structured by the effects of marine-related disturbance processes (e.g., tides, ocean spray) and the successional development of soil (Ranwell, 1972; Hesp, 1991; Wilson and Sykes, 1999). Sand beaches in British Columbia are useful model ecosystems for invasion ecology research because they show distinctive spatial patterns at community and regional scales, and have a high proportion of exotic plant species. The prevalence of exotic plants in beaches is likely caused by the combined effects of suitable environmental conditions for colonization and establishment, and the dispersal of new species by wind, currents, and human activities. In general, little comprehensive research has been conducted on plant community development of Vancouver

Island beaches and this thesis will also be an important contribution to understanding the ecology of these dynamic ecosystems.

Spatial Patterns of Vegetation Development

Describing and interpreting patterns of species distribution is a fundamental focus of ecology: "we are interested in where organisms are found, how many occur there, and why" (Krebs, 1972).

Variation in species distribution and abundance occurs at a variety of spatial scales which is reflected in the broad range of research strategies (Turner, 1989; Wiens, 1989; Bellehumeur and Legendre, 1998). Plant competition may reflect processes at a local scale (e.g., 1 m² vegetation plot; e.g., Tilman and Kareiva, 1997), whereas understanding the influence of environmental variation on species richness, composition, and community structure may focus on community, landscape, or regional scale patterns (Thomson *et al.*, 1996; Dale, 1999; Dungan *et al.*, 2002).

Within sand beaches, vegetation development is distinctly zonal (Oosting and Billings, 1949; Doing, 1985). Sand beach vegetation on Vancouver Island can be divided into a sparsely-vegetated lower beach zone, a grass-dominated upper beach zone, and a dune zone that is both species-poor and sparsely-vegetated (Kuramoto, 1965). A variety of distinctive plant associations occur in these three zones, and the second chapter focuses on identifying re-occurring vegetation communities.

Sand beaches, like other frequently disturbed, ecotonal plant communities, support a disproportionately high number of exotic species (Sobrino *et al.*, 2002; Grosholz, 2002). This characteristic, combined with spatially-compressed environmental gradients, make them useful for comparing similarities or differences in the ecological behaviour of native and exotic plant species along environmental gradients (e.g., soil pH, distance).

Sand beaches in coastal B.C. also have a distinctive regional scale pattern. They are generally isolated within a matrix of rock- and cobble-dominated shoreline (Holland, 1964). This spatially patchy regional structure makes them useful for studying macroecological patterns because they provide a simplified regional structure for studying population distribution. Macroecology seeks to describe and understand ecological patterns that exist at regional, continental, or global scales (Brown and Maurer, 1989; Brown, 1995; Gaston and Blackburn, 2000).

Are Native and Exotic Species Ecologically Different?

Much of the current research emphasis of invasion ecology has focused on the premise that exotic species are ecologically different from native species. Exotic species are often portrayed as ‘super-organisms’ that rapidly move across landscapes using superior competitive and dispersal abilities. While there is some support that fewer pathogens in new habitats (Keane and Crawley, 2002; Mitchell and Power, 2003) or genetic variation (Blossey and Notzold, 1995; Lee, 2002; Leger and Rice, 2003) differentiate exotic from native species, there is also evidence from observational studies that their ecological behaviour is similar to native species (Lonsdale, 1999; Stohlgren *et al.*, 1999). My research asks a fundamental question for invasion ecology: do native and exotic species share similar ecological patterns at different scales?

Thesis Structure

The thesis is divided into four chapters. This chapter has briefly introduced the research topics, highlighted the themes that unify these topics, and described the usefulness of beach plant communities for studying spatial patterns of vegetation. Chapter 2 describes, classifies, and relates beach plant associations based on their floristic composition and environment. Chapter 3 compares the spatial variation in exotic and native plant species richness to community scale environmental gradients in beach plant communities. Chapter 4 examines regional scale patterns of exotic plant species invasion by comparing distribution and abundance relationships of native and exotic plant species in eight regional plant community networks.

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CHAPTER 2

DESCRIPTION AND CLASSIFICATION OF PLANT ASSOCIATIONS IN SAND BEACHES OF THE WEST COAST OF VANCOUVER ISLAND

INTRODUCTION

Sand beaches support distinctive plant communities that are adapted to the unique environmental conditions along marine shorelines (Ranwell, 1972; Hesp, 1991; Maun, 1994). In British Columbia beach plant communities are dominated by grasses, forbs, and low shrubs that grow in a narrow band between the upper limit of tidal inundation and the lower limit of conifer forest. Plant community development occurs along a gradient inland from the shoreline with distinctive zonal patterning characteristic of beaches (Oosting and Billings, 1949; Doing, 1985; Wilson and Sykes, 1999). Closest to the shore, a sparsely vegetated lower beach zone that is colonized by plant species that are adapted to wave disturbance, oceanspray, and nutrient-poor soils, is characteristic (Gagne and Houle, 2002). Farther inland, a more species-rich upper beach zone develops that often has a well-defined foredune ridge. Higher soil stability, reduced wave disturbance, and increased nutrient availability characterize the physical environment of the upper beach zone (Salisbury, 1959; Ranwell, 1972; Wilson and Sykes, 1999). A third zone of dunes commonly occur inland of the upper beach. Dunes are sparsely vegetated areas of open sand and typically support a small number of plant species with adaptations for dry, nutrient-poor soils (Kellman and Roulet, 2002; Cain *et al.*, 1999).

On the west coast of Vancouver Island, sand beach plant communities are uncommon because of the limited occurrence of coastal areas with sand-dominated substrates. Sand beaches in this region are often separated by long distances of rock- and cobble-dominated shoreline that support floristically and physiognomically different plant communities. Because of their limited occurrence and fragmented distribution pattern, the conservation significance of both plant associations and plant species in sand beaches is high. However, lack of basic ecological information has limited the inclusion of beach plant associations and species in provincial or international conservation databases. Some previous research has been aimed at describing and classifying sand beach plant associations of western Vancouver Island beaches, but most has focused on few sites or with limited sampling. Kuramoto (1965) completed a comprehensive study of plant associations at Wickaninnish Beach, in what is now Pacific Rim National Park Reserve, that focused on classification of plant associations. He described seven plant associations using the Braun-Blanquet approach. More recently, Hebda *et al.* (1997) characterized beach vegetation as part of a broad vegetation

classification of Brooks Peninsula located on northwest Vancouver Island. Plant associations were not described, although a beach vegetation type was included in a physiognomically-defined herbaceous vegetation category. Additional studies documenting aspects of beach vegetation composition or physiography on the west coast of Vancouver Island include Bell (1972); Bell and Harcombe (1973); and Neumann (1995). More broadly, Pacific Coast beach vegetation was studied by McDonald and Barbour (1974) and Breckon and Barbour (1974), and more comprehensively in Washington, Oregon, or California by Kumler (1969), Wiedemann (1966), Wiedemann (1984), Barbour *et al.* (1976); Holton and Johnson (1979), and Christy *et al.* (1998).

In this chapter, I classify, describe, and relate plant associations found in sand beaches on western Vancouver Island based on their floristic composition and environment. I also compare the plant associations to the results of previous classification studies from the Pacific coastal region, and discuss the rarity of specific beach plant associations based on their distribution and abundance on the west coast of Vancouver Island. The purpose is twofold. First, this chapter provides an overview of the different plant associations as background information for understanding vegetation patterns in sand beaches in the region. Chapter 3 deconstructs these patterns by looking at environmental factors that may influence species richness in sand beaches. Second, and more importantly, the results provide basic information with which to identify and assign significance to the regional rarity of these distinct plant associations. British Columbia, like most jurisdictions in North America, uses plant associations as a standard unit for conservation planning (Jennings *et al.*, 2002, BC CDC, 2002). However, only one beach plant association is currently recognized by the B.C. Conservation Data Centre (*Carex macrocephala* Herbaceous Vegetation) and it is unclear if its description is based on adequate sampling and interpretation. The poor representation of non-forested plant associations in provincial conservation databases reflects the lack of basic information about them. New information on beach plant associations will aid in identifying associations that require higher priority in conservation planning. Similarly, exotic species invasions, recreational disturbance, and global climate change (e.g., sea-level rise, increased storm intensity) have the potential to cause widespread change to sand beaches. Collecting baseline information on their composition and structure will allow for monitoring programs to measure changes in vegetation over time.

METHODS

Study Area

Vegetation composition and environmental conditions were measured in eighteen sites between Cape Scott (50.77 N; 128.41 W) and Port Renfrew (48.57 N; 124.40 W) on the west coast of Vancouver

Island, British Columbia (Figure 2.1 and Table 2.1). This is a physiographically and climatically uniform region with coastal lowland vegetation dominated by temperate coniferous rain forest (Meidinger and Pojar, 1991; Franklin and Dyrness, 1998). Most of the coastline is composed of rock, cobble, or gravel with an abrupt transition between algal intertidal communities and forest. Unlike the outer coast of Washington and Oregon where coarse sand is the dominant coastal substrate, sand beaches are spatially isolated and regionally rare. They occur where sand has been eroded from glacial outwash deposits and transported and deposited into low energy sites (Holland, 1964; Thomson, 1981). Sand beaches typically occur in groups because of shared physiographic conditions. The majority of study sites are crescent beaches (0.5 to 5 km in length) terminated by rock headlands (see Figure 2.3a (Ahous Bay, Vargas Island) and Figure 2.3b (Schooner Cove, Pacific Rim National Park Reserve). Rarely, spits occur in the lee of islands (e.g., Clayoquot Island, Clayoquot Sound; Figure 2.3c) or where paired beaches create tombolos (e.g., Guise Bay, Cape Scott; Figure 2.3d).

Study sites were selected qualitatively from a group of approximately twenty-five sand beaches based on environmental comparability (beaches were > 500 m long, substrates were sand-dominated, and vegetation development was between 10 and 200 m wide) and practical issues of accessibility and jurisdiction. Many sites are protected as provincial or national parks.

Field Sampling

Linear transects were established perpendicular to the shoreline and plant composition and abundance were measured in plots along each transect using a stratified-random sampling design. A total of 612 plots was sampled. Transect length ranged from 5 to 225 m depending on the distance between the seaward extent of beach vegetation and the forest margin. The unvegetated portion of the lower beach nearest the intertidal zone was excluded from the transect measurement. Distance between transects varied from 50 m to 250 m apart depending on beach length and vegetation complexity. Plots (2 m by 2 m square) were placed at random distances within physiognomically homogenous vegetation zones along each transect (Figure 2.2). Sampling intensity was approximately 1 plot per 10 m of transect length. Transect start points were recorded with a handheld GPS unit (NAD83 in decimal degrees using a Garmin XP12 unit) which will allow for future monitoring of vegetation change. Field sampling was undertaken between May and September 2001.

Plant Community Data – A list of vascular plants, bryophytes, and lichen species was compiled for each plot and percent plant cover (0.1 to 100%) was estimated for each species. Voucher specimens were collected for taxa that could not be identified in the field or were of potential conservation

value. Identification was undertaken at the University of British Columbia or Royal British Columbia Museum herbaria. Dr. A. Ceska and F. Lomer assisted with identification of vascular plants and O. Lee and Dr. W. Schofield assisted with identification of bryophytes. Taxonomy and nomenclature follows Douglas *et al.* (1998-2002) for vascular plants, Anderson *et al.* (1990) for bryophytes and Goward (1999) for lichens. As a result of taxonomic uncertainties or lack of adequate voucher specimens, lichen species were grouped as follows: *Cladonia* species were placed into one of three morphologically defined groups, and *Peltigera* species were grouped at the generic level. All specimens were deposited at the University of British Columbia herbarium. Total plant cover was calculated as a synthetic variable by summing cover values for each species in the plot, expressed as a percentage. Total bryophyte and lichen cover was calculated as a second synthetic variable. Total species richness was calculated as the total number of plant species per plot.

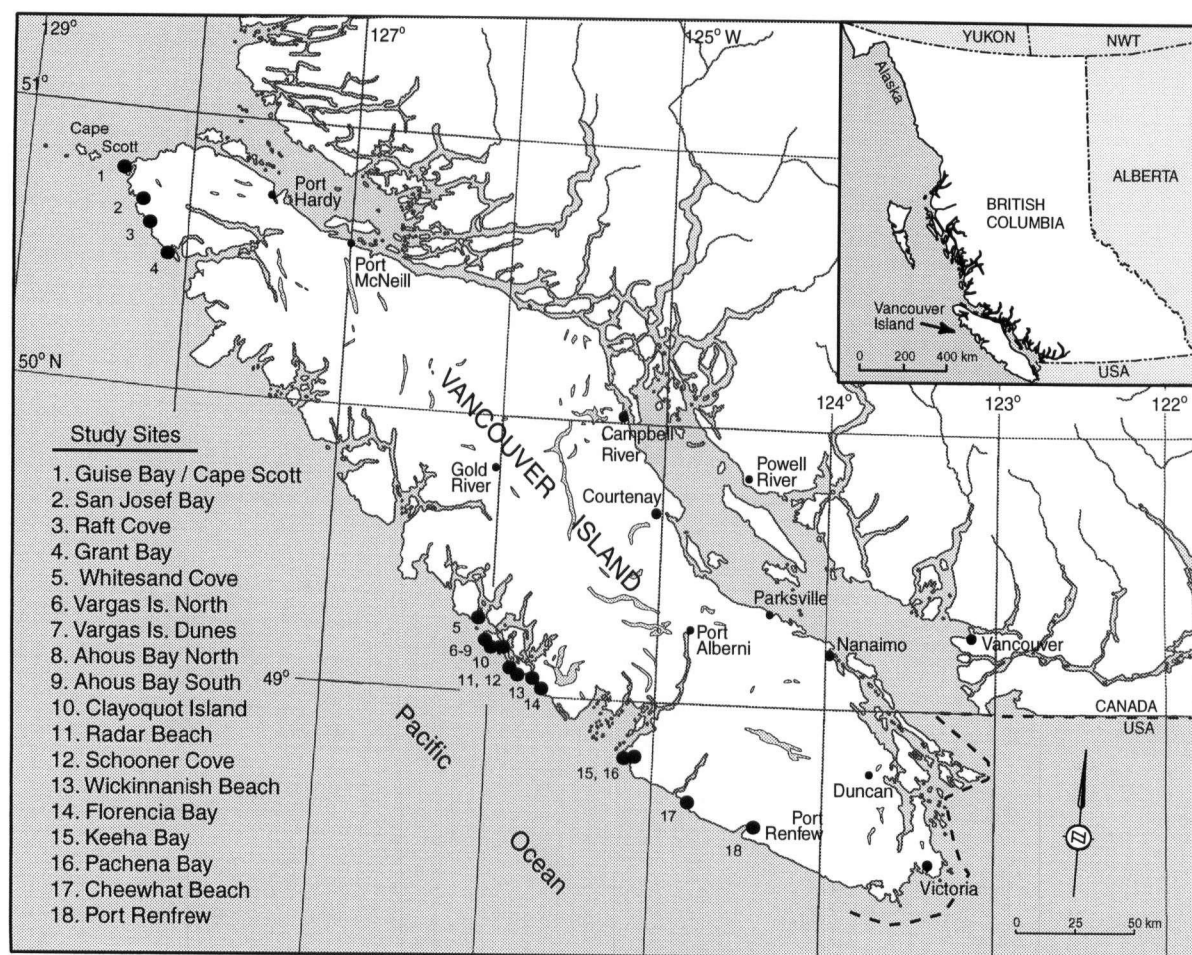


Figure 2.1. Location of sand beach study sites on the west coast of Vancouver Island.

Spatial Location – The location of each plot was measured from the seaward extent of vegetation using a 50 m tape, measuring staff, and clinometer (Figure 2.2). Elevation was converted to chart

datum by estimating the elevation of the most recent tide line using WXTide, a tide height prediction program.

Soil Chemistry – I collected one 200 ml sample of shallow surface soil (5–10 cm below the surface) from each plot. Soil analysis methods and detailed results are summarized in Chapter 3.

Table 2.1. Summary of sampling site information (North to South).

Site Name	Location ¹		Ownership / Jurisdiction ²	Total Area ³ (ha)	General Description
	Lat (N).	Long (W).			
Guise Bay	50.77	128.41	Prov. Park	13.9	tombolo; extensive dunes
San Josef Bay	50.67	128.28	Prov. Park	2.3	crescent beach
Raft Cove	50.59	128.23	Prov. Park	2.3	crescent beach
Grant Bay	50.48	128.10	Crown Land	2.4	crescent beach
Whitesand Cove	49.26	126.06	Prov. Park	1.7	crescent beach; small dune
Vargas North	49.20	126.03	Prov. Park	3.0	crescent beach
Vargas Dune	49.19	126.03	Prov. Park	3.6	crescent beach; dunes
Ahous Bay North	49.19	126.01	Prov. Park	2.8	crescent beach; small dune
Ahous Bay South	49.18	126.01	Prov. Park	8.6	crescent beach
Clayoquot Island	49.16	125.92	Private	16.7	spit; dunes
Radar Beach	49.08	125.85	Nat. Park	2.4	crescent beach; dunes
Schooner Cove	49.07	125.80	Nat. Park	7.9	crescent beach; dunes
Wickaninnish Beach	49.03	125.69	Nat. Park	17.5	crescent beach; dunes
Florencia Bay	49.00	125.63	Nat. Park	7.0	crescent beach
Keeha Bay	48.79	125.12	Nat. Park + IR	3.7	crescent beach; small dune
Pachena Bay	48.79	125.18	Nat. Park + IR	1.3	crescent beach
Cheewhat Beach	48.66	124.81	Nat. Park + IR	1.7	crescent beach; small dune
Port Renfrew	48.57	124.40	Nat. Park + IR	5.1	crescent beach

¹ Decimal degrees.

² IR = Indian reserve.

³ Total area measured as beach length x average transect length or from air photo interpretation.

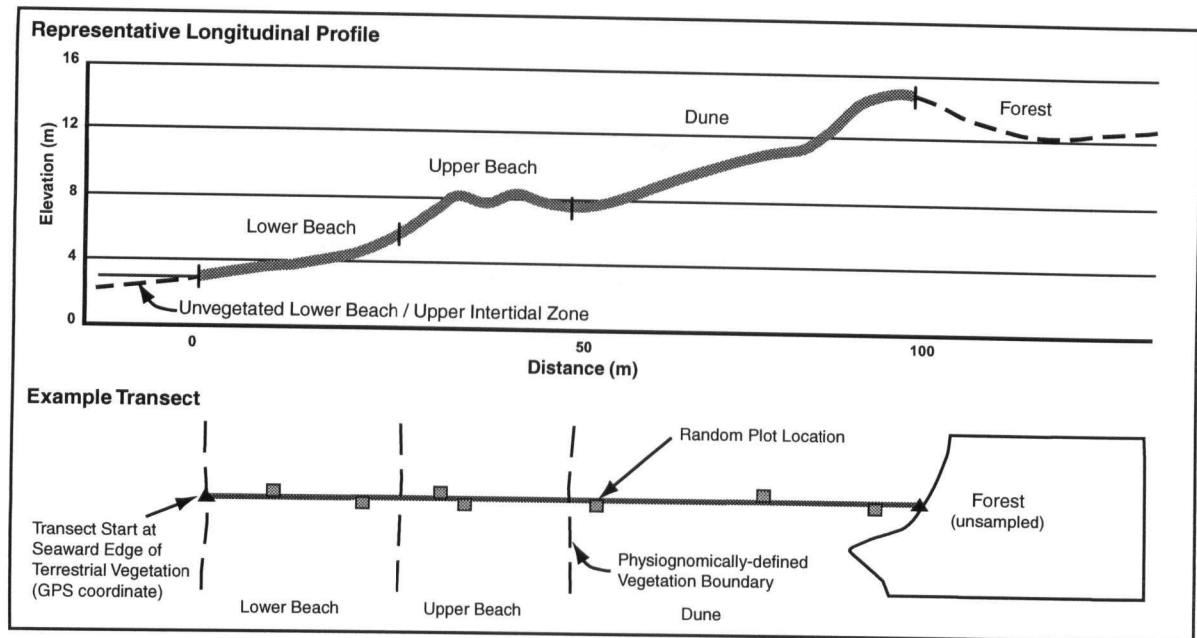


Figure 2.2. Generalized transect sampling method for sand beaches.

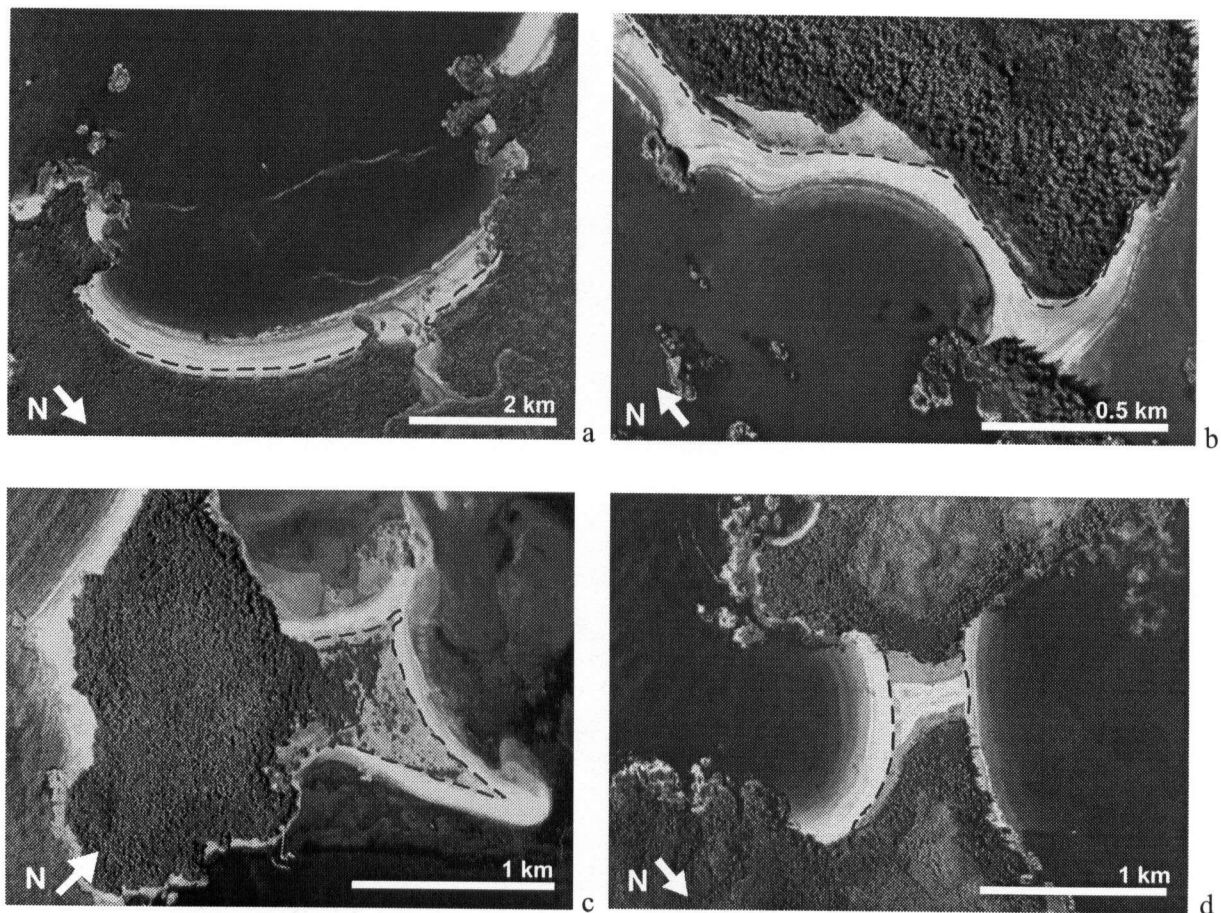


Figure 2.3. Representative sand beach sites on the west coast of Vancouver Island: a) Ahous Bay, Vargas Island; b) Schooner Cove, Pacific Rim National Park Reserve; c) Clayoquot (Stubbs) Island, Clayoquot Sound; d) Guise Bay, Cape Scott. Sampled areas are within the red-dashed line. All air photos from BC Government; 1995-1996.

Data Analyses

Three methods were used to describe, classify, and relate plant associations¹ based on floristic composition and abundance. I used TWINSpan (Hill, 1979) to identify preliminary groups of plots based on floristic differences. TWINSpan provides a divisive, hierarchical classification that uses indicator species defined in ordination space to differentiate groups (Hill, 1979; Jongman *et al.*, 1987). While its underlying statistical assumptions have been repeatedly questioned (see van Groenwoud, 1992, Lee and McDonald, 1993, McCune and Grace, 2002), the ecological interpretability of the species groups is often useful and TWINSpan continues to be a common tool of ecologists. TWINSpan was run on the full set of 612 plots using the default pseudo-species cut-levels (0%, 2%, 5%, 10%, 20% cover) and default settings (6 divisions, minimum group size 10, maximum group size 50) in PC-ORD 4.12 (McCune and Medford, 2001).

To refine and distinguish the final plant associations, I used hand-sorting to identify diagnostic species or groups of species for each association. The objective was to define a diagnostic species or set of species that are frequent and abundant in one association, and infrequent and sparse in all other associations. Each TWINSpan-defined group was sorted based on the mean frequency and mean cover of each species. Only species that occur in more than 40% (e.g., mean cover class III (40 to 60% frequency)) of plots within a group were retained for possible inclusion in the synoptic table as diagnostic species. Some TWINSpan groups were clearly-defined plant associations and required minimal hand-sorting, while others were amalgamated or split into two or more units. Specifically, four lower beach units described by TWINSpan were amalgamated into one association defined by the presence of *Cakile edentula* and *Atriplex gmelinii*. The initial units were defined by *Cakile edentula*, *Atriplex gmelinii*, *Rumex maritimus*, and *Honkenya peploides* respectively and could be considered subassociations of the *Cakile edentula* – *Atriplex gmelinii* association. A broad group of successional-mature plots with similar bryophyte and lichen assemblages were split into three associations by hand-sorting. Subassociations were not described in this study.

Potential diagnostic species were amalgamated into a synoptic table. Species that were common to more than one unit were removed. The final synoptic table only includes species that meet the formal phytosociologic definitions of *differential species*². This procedure identifies plant associations that

¹ A *plant association* is a recurring plant community that is defined by a characteristic range in species composition, specific diagnostic species, and a range in habitat conditions and physiognomy or structure (Jennings *et al.*, 2002). The term *plant community* is considered a broader term without formal requirements for defining or naming.

² *Differential species* have greater than 2 mean presence or mean cover classes higher than other units in the diagnostic table (Pojar *et al.*, 1987).

are compatible with both traditional Braun-Blanquet definitions (see Pojar *et al.*, 1997) and the National Vegetation Classification System that is used by Canadian and American conservation agencies (Grossman *et al.*, 1998; Jennings *et al.*, 2002). Plant association names follow the conventions of the National Vegetation Classification System and are based on one or two differential species and interpretation of their physiognomy (Grossman *et al.*, 1998; Jennings *et al.*, 2002). Common names of associations are not provided here but are easily converted from the scientific names (e.g., *Ammophila arenaria* Herbaceous Vegetation = European beachgrass Herbaceous Vegetation).

Nonmetric multidimensional scaling (NMS) was used to examine relationships among plots and among plant associations. NMS iteratively searches for a multidimensional solution with the least difference (or stress) between distance or dissimilarity in the original dataset and those generated for the same plots in the reduced ordination space of the final solution. As a data reduction tool in ecology, it is considered the ordination method of choice because of mathematical robustness and biological meaningfulness (McCune and Grace, 2002). NMS analysis was undertaken in PC-ORD following the recommendations in McCune and Grace (2002). Two NMS analyses were undertaken each consisting of an initial test and a final analysis with a target dimensionality. First, an analysis of all 612 plots was undertaken in which the final stress and instability was evaluated for solutions in one to six-dimensions. This used the Sorenson distance measure, a random starting configuration, and 25 runs with real data. I compared the stress of the solutions to those generated by random configurations of the data using 25 Monte Carlo simulations. Based on this initial test, a three-dimensional solution was selected and a final analysis was rerun for only this dimensionality using a single run with the same distance measure, the same starting configuration, and 250 iterations to assess stability. The second analysis followed similar steps with the same settings but used a subset of 257 plots for which more complete environmental data was available. Environmental variables were regressed against the NMS solution to identify the strength and direction of their relationship with floristic variation.

Environmental characteristics of each plant association were also described. Variation in spatial location (distance inland and elevation), species richness per plot, total plant cover per plot, and soil chemistry (pH, specific conductivity, total carbon, total nitrogen) were summarized using box plots that depict the mean and quantiles (10%, 25%, 75%, 90%).

RESULTS

One hundred and fifty four plant species were present in the 612 plots used to describe and classify plant associations. Of these, 112 (72.7%) were native species and 42 (27.3%) were exotic species. Twenty-three (20.5%) of the native species were bryophytes or lichens. All of the exotic species were vascular plants.

Seven plant associations were identified. General floristic, physiognomic, and soil chemistry characteristics are summarized in Table 2.2 and representative photographs are presented in Figure 2.4. A synoptic table of diagnostic species for the associations is provided in Table 2.3. Diagnostic values are also noted using the categories and definitions proposed by Pojar *et al.* (1987).

Plant association rarity was measured as both plant association frequency (percentage of total plots for each association (N/612 plots)) and regional occurrence (total number of sites in which the plant association was present (N/18 sites)). Table 2.4 summarizes information on the distribution of plots, plant associations, and total species by sampling site including information on rarity by percentage of plots and regional occurrence. Based on the percentage of plots in which the association was found, the *Arctostaphylos uva-ursi* association was the rarest association (5.8 % of plots, 9 sites) followed by the *Eurhynchium oreganum* / *Gaultheria shallon* association (6.5% of plots, 12 sites), and the *Festuca rubra* – *Fragaria chiloensis* association (8.4% of plots, 10 sites). Summary values for the remaining community types were (in order of rarity): *Poa macrantha* association (16.9% of plots, 8 sites), *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* association (14.2% of plots, 16 sites), *Ammophila arenaria* association (16.9% of plots, 9 sites), and *Cakile edentula* – *Atriplex gmelinii* association (31.4% of plots, 18 sites).

Table 2.2. Summary descriptions of floristically-defined plant associations including characteristic species and environmental characteristics.

Plant Association	General Description of Vegetation and Soil Chemistry ¹	Characteristic Species ²
Association 1: <i>Cakile edentula</i> – <i>Atriplex gmelinii</i> Sparse Vegetation	Common, sparsely vegetated, species-poor, lower beach community; high disturbance from waves and tides; generally fine sand substrates. Vegetation characteristics: mean percent cover 8.7%; mean percent bryophyte and lichen cover 0.0%; mean species richness: 2.2 species. Soil chemistry characteristics: mean soil pH 8.07; %N 0.004; %C 0.100	<i>Cakile edentula</i> *, <i>Cakile maritima</i> *, <i>Atriplex gmelinii</i> , <i>Honkenya peploides</i> , <i>Rumex maritimus</i> , <i>Leymus mollis</i> spp. <i>mollis</i> .
Association 2: <i>Leymus mollis</i> spp. <i>mollis</i> – <i>Lathyrus japonicus</i> Herbaceous Vegetation	Common, native upper beach community; may have declined because of development of <i>Ammophila arenaria</i> Herbaceous Vegetation association. Vegetation characteristics: mean percent cover 40.5%, mean percent bryophyte and lichen cover 7.8%; mean species richness: 4.5 species. Soil chemistry characteristics: mean soil pH 7.29; %N 0.012; %C 0.232	<i>Leymus mollis</i> spp. <i>mollis</i> , <i>Lathyrus japonicus</i> , <i>Vicia gigantea</i> , <i>Rubus spectabilis</i> , <i>Fragaria chiloensis</i> , <i>Epilobium ciliatum</i> , <i>Eurhynchium oreganum</i> .
Association 3: <i>Festuca rubra</i> – <i>Fragaria chiloensis</i> Herbaceous Vegetation	Late-successional meadow community with organic-rich substrates; species-rich and productive; tall grasses and forbs; shrubs occasional; includes wet dune slacks in depressional areas. Vegetation characteristics: mean percent cover 96.3%; mean percent bryophyte and lichen cover 17.5%; mean species richness: 9.3 species. Soil chemistry characteristics: mean soil pH 6.10; %N 0.043; %C 0.566	<i>Festuca rubra</i> , <i>Fragaria chiloensis</i> , <i>Achillea millefolium</i> , <i>Poa pratensis</i> , <i>Dactylis glomerata</i> *, <i>Equisetum arvense</i> , <i>Juncus breweri</i> , <i>Plantago lanceolata</i> *, <i>Aster</i> species, <i>Taraxacum officinalis</i> *, <i>Hypochaeris radicata</i> *, <i>Rhizidadelphus triquetrus</i> , <i>Holcus lanatus</i> *.
Association 4: <i>Ammophila arenaria</i> Herbaceous Vegetation	Dry, open meadow dominated by <i>Ammophila arenaria</i> . Includes foredune ridge and stabilized dune areas. Shrub cover generally absent. Bryophytes and lichens common. Vegetation characteristics: mean percent cover 61.6%; mean percent bryophyte and lichen cover 21.1%; mean species richness: 9.0 species. Soil chemistry characteristics: mean soil pH 6.46; %N 0.018; %C 0.266	<i>Ammophila arenaria</i> *, <i>Aira praecox</i> *, <i>Leymus mollis</i> spp. <i>mollis</i> , <i>Hypochaeris radicata</i> *, <i>Lathyrus japonicus</i> , <i>Fragaria chiloensis</i> , <i>Cladonia</i> species, <i>Ceratodon purpurea</i> , <i>Ammophila brevifolulata</i> *, <i>Peltigera</i> species.
Association 5: <i>Arctostaphylos uva-ursi</i> Dwarf Shrubland Vegetation	Distinct matt of <i>Arctostaphylos uva-ursi</i> along margin of dunes and between the upper beach and conifer forest. Relatively species-rich bryophyte and lichen layer. Vegetation characteristics: mean percent cover 103.7%; mean percent bryophyte and lichen cover 25.5%; Mean species richness: 8.1 species. Soil chemistry characteristics: mean soil pH 5.92; %N 0.011; %C 0.252	<i>Arctostaphylos uva-ursi</i> , <i>Ammophila arenaria</i> *, <i>Gaultheria shallon</i> , <i>Hypochaeris radicata</i> *, <i>Eurhynchium oreganum</i> , <i>Aira praecox</i> *, <i>Leptogium corniculatum</i> , <i>Cladonia</i> species, <i>Peltigera</i> species.
Association 6: <i>Eurhynchium oreganum</i> / <i>Gaultheria shallon</i> Shrubland Vegetation	Late-successional phase which includes shrub and tree seedling dominated fringe along forest edge. Transitional from <i>Arctostaphylos uva-ursi</i> Dwarf Shrubland Vegetation. Vegetation characteristics: mean percent cover 105.4%; mean percent bryophyte and lichen cover 38.3%; mean species richness: 11.2 species. Soil chemistry characteristics: mean soil pH 5.88; %N 0.023; %C 0.489	<i>Eurhynchium oreganum</i> , <i>Gaultheria shallon</i> , <i>Picea sitchensis</i> , <i>Vaccinium ovatum</i> , <i>Ammophila arenaria</i> *, <i>Aira praecox</i> *, <i>Tsuga heterophylla</i> , <i>Leymus mollis</i> spp. <i>mollis</i> , <i>Hypochaeris radicata</i> *, <i>Peltigera</i> species.
Association 7: <i>Poa macrantha</i> Sparse Vegetation	Regionally rare but locally abundant plant association; generally species-poor with very sparse plant cover (<5%); actively moving sand surface in some areas. Vegetation characteristics: mean percent cover 3.4%; mean percent bryophyte and lichen cover 0.1%; mean species richness: 3.5 species. Soil chemistry characteristics: mean soil pH 6.31; %N 0.004; %C 0.057	<i>Poa macrantha</i> , <i>Polygonum paronychia</i> , <i>Abronia latifolia</i> , <i>Glehnia leiocarpa</i> , <i>Carex macrocephala</i> , <i>Convolvulus soldanella</i> , <i>Poa confinis</i> , <i>Tanacetum bipinnatum</i> .

¹ Species richness values are mean number of species per 4 m² plot.

² Characteristic species are ranked according to their frequency (% of plots in which they were present) in the association.

* denotes exotic species.

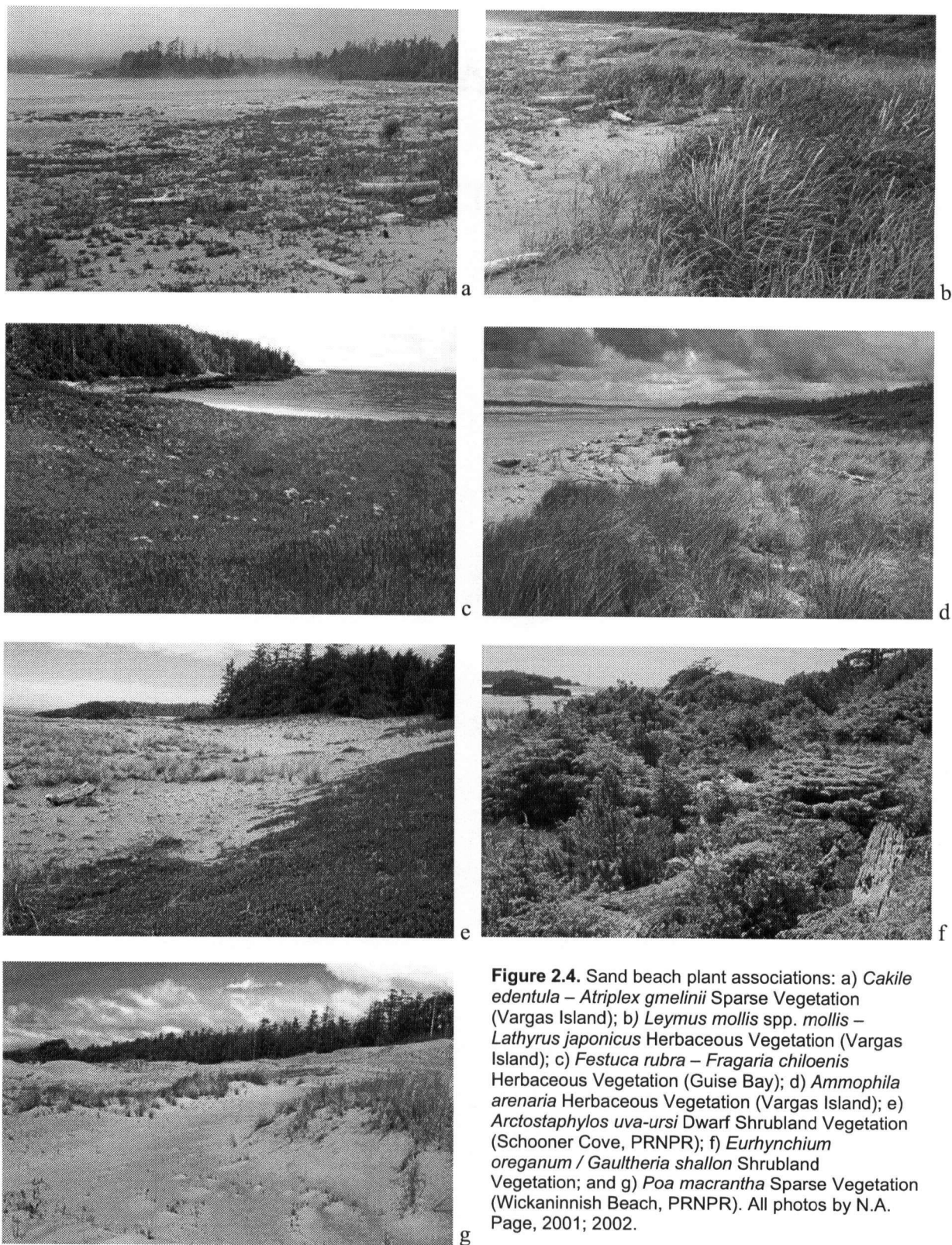


Figure 2.4. Sand beach plant associations: a) *Cakile edentula* – *Atriplex gmelinii* Sparse Vegetation (Vargas Island); b) *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* Herbaceous Vegetation (Vargas Island); c) *Festuca rubra* – *Fragaria chiloensis* Herbaceous Vegetation (Guise Bay); d) *Ammophila arenaria* Herbaceous Vegetation (Vargas Island); e) *Arctostaphylos uva-ursi* Dwarf Shrubland Vegetation (Schooner Cove, PRNPR); f) *Eurhynchium oregonum* / *Gaultheria shallon* Shrubland Vegetation; and g) *Poa macrantha* Sparse Vegetation (Wickaninnish Beach, PRNPR). All photos by N.A. Page, 2001; 2002.

Table 2.3. Synoptic table of diagnostic species for sand beach plant associations on the west coast of Vancouver Island. Only species with presence class III or greater (present in >40% of plots) in at least one association are included.

Association No.		1	2	3	4	5	6	7
Number of Relevés (612 total)		192	87	51	103	36	40	103
	Diag. Value ¹	Presence class ² and mean species significance ³						
Association 1: <i>Cakile edentula</i> – <i>Atriplex gmelinii</i> Sparse Vegetation								
<i>Cakile edentula</i>	d, c	V 2	I +	I +	I +		I +	II +
<i>Atriplex gmelinii</i>	ic	II 1						
Association 2: <i>Leymus mollis</i> spp. <i>mollis</i> – <i>Lathyrus japonicus</i> Herbaceous Vegetation								
<i>Leymus mollis</i> spp. <i>mollis</i>	d,c	I +	V 4	III 3	II 2	I 1	II 2	I +
<i>Lathyrus japonicus</i>	d	I +	III 4	I 1	II 2	I +	II 2	I +
Association 3: <i>Festuca rubra</i> – <i>Fragaria chiloensis</i> Herbaceous Vegetation								
<i>Festuca rubra</i>	dd	I +	I +	IV 5		I +	I +	
<i>Fragaria chiloensis</i>	d		I 2	IV 4	II 1	II +	II 2	
<i>Juncus breweri</i>	d	I +	I +	III 2	I +		I +	
<i>Achillea millefolium</i>	d	I +	I +	III 1	I +	I +	I +	I +
Association 4: <i>Ammophila arenaria</i> Herbaceous Vegetation								
<i>Ammophila arenaria</i>	d, cd	I +	I 2	I +	V 6	III 3	III 3	I +
Association 5: <i>Arctostaphylos uva-ursi</i> Dwarf Shrubland Vegetation								
<i>Arctostaphylos uva-ursi</i>	d, cd				I +	V 8	II 1	I 2
Association 6: <i>Eurhynchium oreganum</i> / <i>Gaultheria shallon</i> Shrubland Vegetation								
<i>Eurhynchium oreganum</i>	dd,cd	I +	I 3	I 3	II 2	II 4	V 5	
<i>Gaultheria shallon</i>	dd		I 2	I +	I 1	II 3	IV 5	
<i>Picea sitchensis</i>	d		I +	I +	I +	I +	III 4	
<i>Vaccinium ovatum</i>	d				I +	II 1	III 3	
Association 7: <i>Poa macrantha</i> Sparse Vegetation								
<i>Poa macrantha</i>	d, c	I +	I +	I +	I 1	II 1	I +	V 2
<i>Glehnia littoralis</i> ssp. <i>leiocarpa</i>	d		I +	I +	I +	I +		III +
<i>Polygonum paronychia</i>	d			I +		I +		III +
Other species								
<i>Aira praecox</i>	-			I +	III 1	II +	II 1	I +

Notes:

¹ Diagnostic values: d = differential (presence class III or greater and more than two presence classes higher than other taxa), dd = dominant differential, cd = constant dominant, c = constant, ic = companion species) (see Pojar et al. (1987) for definitions).

² Presence class as percent frequency in association: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%.

³ Species significance class as percent cover range: 0.1 = 0.1-0.3%, 1 = 0.4-1%, 2 = 1.1-2.1%, 3 = 2.2-5%, 4 = 5.1-10%; 5 = 10.1-20%, 6 = 20.1-33%, 7 = 33.1-50%, 8 = 50.1-70%, 9 = 70.1-100%.

Table 2.4. Summary of the distribution of plots, plant associations, and total species by sampling site. Total plots and percentage of plots by plant association, and number of sites in which each plant association was found is also included.

Site Name	Plant Association ¹							Total Plots	Total No. Species ²
	1	2	3	4	5	6	7		
Cape Scott	1	2	17				26	46	59
San Josef Bay	6	5	4					15	35
Raft Cove	7	4	1					12	20
Grant Bay	9	1	10					20	35
Whitesand Cove	10				3	2	17	32	29
Vargas North	7	1		14	4	12		38	46
Vargas Dune	4	1		13	5	5		28	41
Ahous Bay North	11	3		4	7	2		27	54
Ahous Bay South	12	4		4		2		22	56
Clayoquot Island	22	5	5	35		1		68	73
Radar Beach	15	1		2	2	6	8	34	44
Schooner Cove	15			11	1	1	3	31	59
Wickaninnish Beach	14	9	4	19	10	4	29	89	54
Florencia Bay	15	10	2			2		29	40
Keeha Bay	3	7			3	1	13	27	39
Pachena Bay	33	3	3				1	40	29
Cheewhat Beach	2	4	1	1	1	2	5	16	40
Port Renfrew	6	27	4					37	34
Total Plots	192	87	51	103	36	40	103	612	154
Percentage of Plots	31.4%	14.2%	8.3%	16.9%	5.8%	6.5%	16.9%		
Number of Sites	18	16	10	9	9	12	8		

¹ Plant associations: 1) *Cakile edentula* – *Atriplex gmelinii* Sparse Vegetation; 2) *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* Herbaceous Vegetation; 3) *Festuca rubra* – *Fragaria chiloensis* Herbaceous Vegetation; 4) *Ammophila arenaria* Herbaceous Vegetation; 5) *Arctostaphylos uva-ursi* Dwarf Shrubland Vegetation; 6) *Eurhynchium oreganum* / *Gaultheria shallon* Shrubland Vegetation; 7) *Poa macrantha* Sparse Vegetation.

² Total No. Species is the number of plant species (native and exotic) that were recorded in plots in each site.

The first nonmetric multidimensional scaling (NMS) analysis which included all 612 plots showed distinct groupings for some of the plant associations, and a high degree of overlap in others (Figure 2.5). In particular, there was a relatively clear separation of the lower beach (*Cakile edentula* – *Atriplex gmelinii*) and dune (*Poa macrantha*) associations from the five associations with denser plant cover. Two factors likely contributed to the overlap between five of the plant associations in the three-dimensional solution. The large number of plots in combination with the random sampling method resulted in inclusion of a greater number of transitional plots with shared species. As well, these five associations share some broad ecological similarities including higher species richness compared to dune and lower beach associations, and bryophyte or lichen cover indicative of successional maturity.

The second NMS analysis showed the relationships of the associations based on spatial and environmental gradients. Four variables – pH, specific conductivity, distance, and bryophyte / lichen cover, provided the greatest explanation of floristic variation. Associations are separated on a

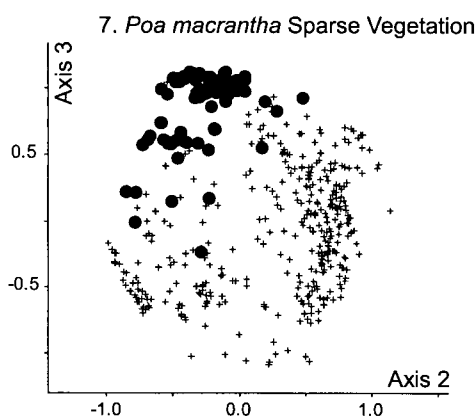
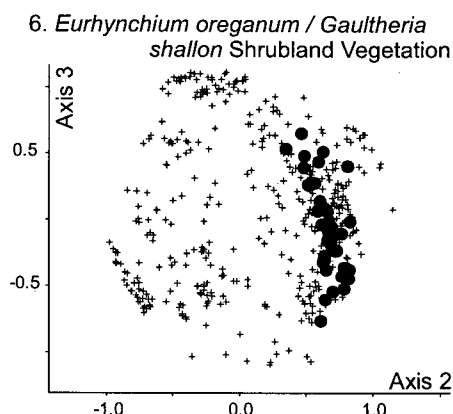
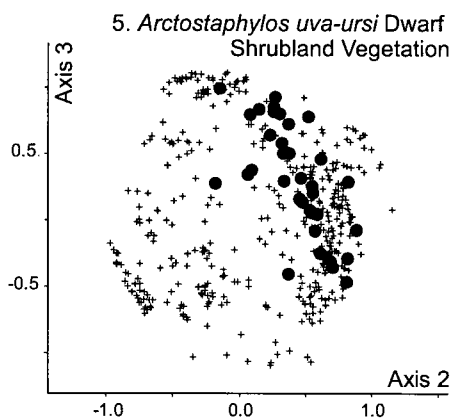
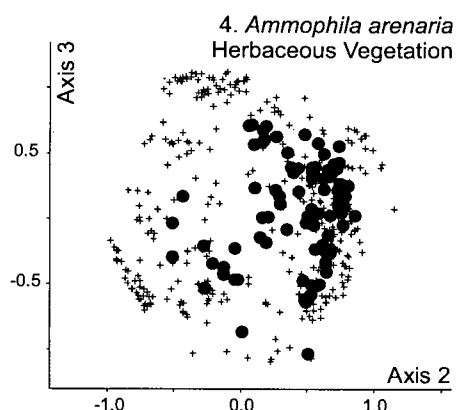
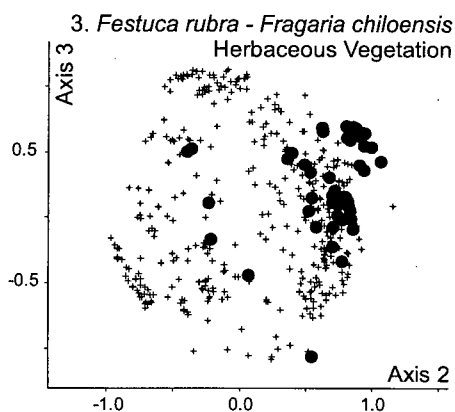
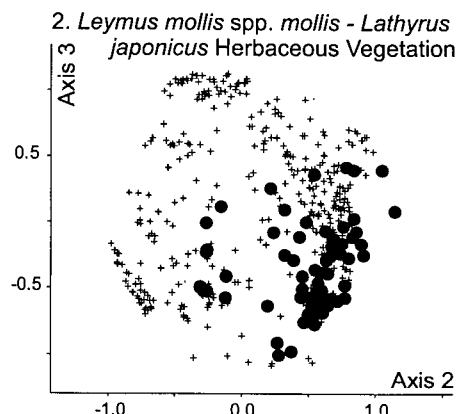
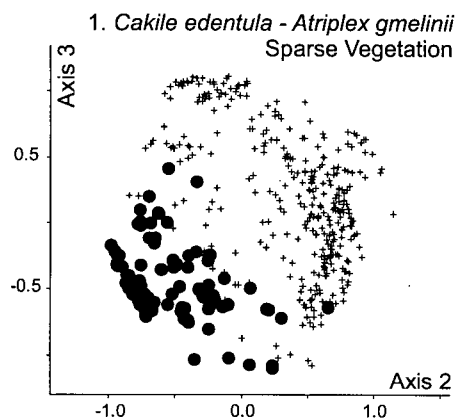


Figure 2.5. Relationships of 612 sand beach plots by plant association using nonmetric multidimensional scaling. The stress of the solution was 20.15 and the instability was 0.039. The cumulative explanation of variance provided by the three axes was $r^2 = 0.62$ (Axis 1, $r^2=0.12$; Axis 2, $r^2=0.19$, Axis 3, $r^2=0.31$). The high degree of overlap between plant associations 2 through 6 is less pronounced using three-dimensional rotation. Associations 1 and 7 are more floristically distinct and do not overlap with the other associations.

distance gradient from the shoreline to the forest that it accompanied by declining pH and specific conductivity. The *Poa macrantha* association was generally the farthest inland with less bryophyte and lichen development than the upper beach associations.

Both NMS solutions had relatively high stress (20.15 for the 612 plot ordination; 18.14 for the 257 plot ordination) which indicated the difference between the final solution and the original data was relatively large. McCune and Grace (2002) cautioned against reliance on detailed interpretation when stress was greater than 20. The inclusion of a large number of plots likely inflated the stress. However, the interpretability of the ordination solution was not compromised by the relatively high stress of the final solution.

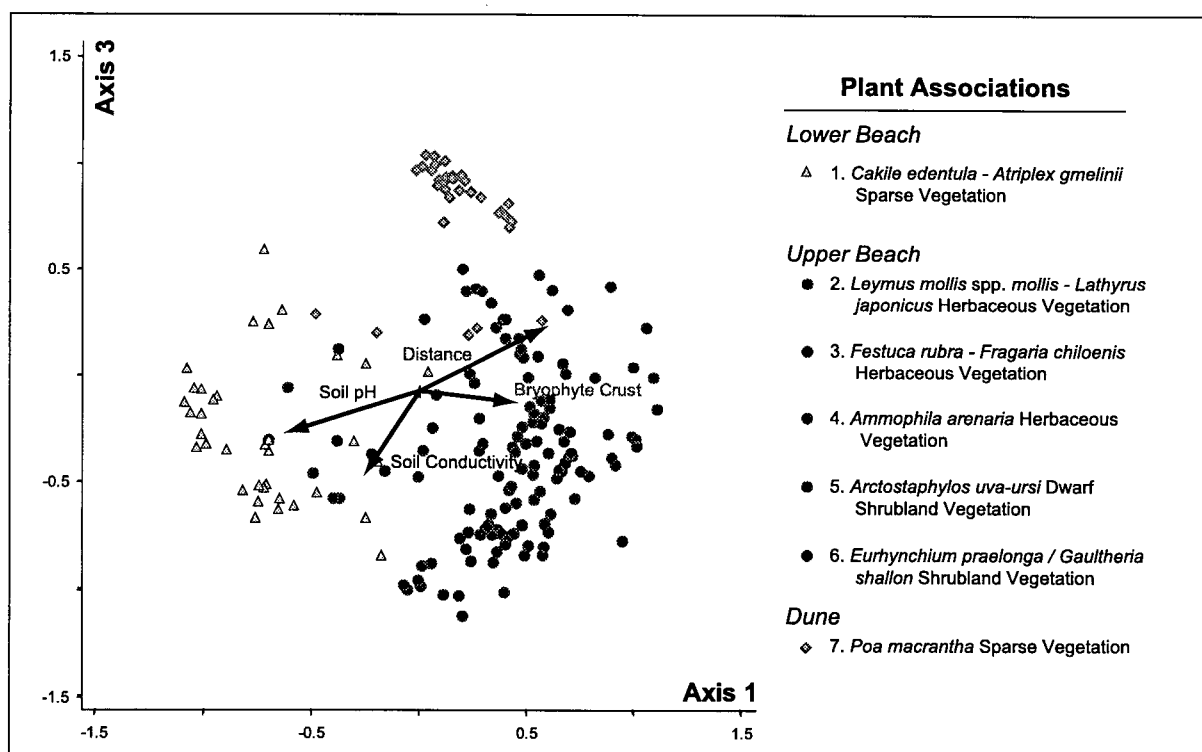


Figure 2.6. Relationships of 257 sand beach plots by physiographic zone (lower beach, upper beach, and dune) along spatial and environmental gradients using nonmetric multidimensional scaling. The stress of the solution was 18.14 and the instability was 0.034. The cumulative explanation of variance provided by the three axes was $r^2 = 0.70$ (Axis 1, $r^2=0.23$; Axis 2, $r^2=0.18$, Axis 3, $r^2=0.29$).

Spatial, vegetation, and soil chemistry characteristics varied substantially between the seven plant associations (Figures 2.7 and 2.8). Mean distance and mean elevation increased inland; the *Cakile edentula* – *Atriplex gmelinii* association was closest to the shore and lowest elevationally while the

Poa macrantha association was furthest inland and second highest elevationally. The other five plant associations varied incrementally along the spatial gradient.

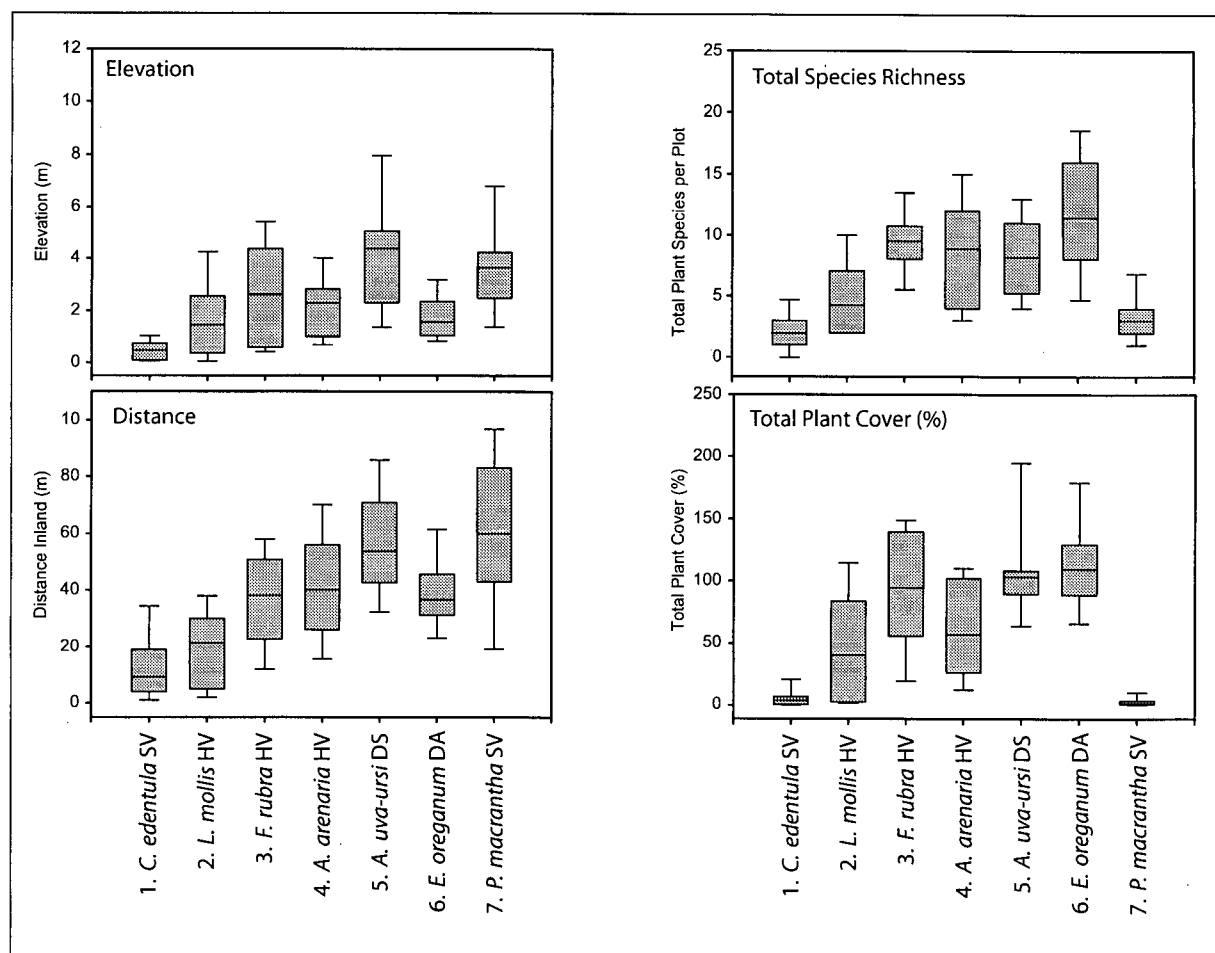


Figure 2.7. Environmental and plant community characteristics (elevation, distance, total species richness, and total plant cover) of seven beach plant associations on the west coast of Vancouver Island. Box plots present mean and quantile values (10%, 25%, 75%, 90%). Full plant association names are: 1) *Cakile edentula* – *Atriplex gmelinii* Sparse Vegetation; 2) *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* Herbaceous Vegetation; 3) *Festuca rubra* – *Fragaria chiloensis* Herbaceous Vegetation; 4) *Ammophila arenaria* Herbaceous Vegetation; 5) *Arctostaphylos uva-ursi* Dwarf Shrubland Vegetation; 6) *Eurhynchium oreganum* / *Gaultheria shallon* Shrubland Vegetation Association; and, 7) *Poa macrantha* Sparse Vegetation.

Species richness per plot and total plant cover followed a similar pattern (Figure 2.7). Both the *Cakile edentula* – *Atriplex gmelinii* and *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* associations had low species richness (<5 species per plot) and low total plant cover (<50% cover). Mean species richness increased to greater than seven per plot and plant cover increased to 70 to 120% in the *Festuca rubra*

– *Fragaria chiloensis*, *Ammophila arenaria*, *Arctostaphylos uva-ursi*, and *Eurhynchium oreganum* / *Gaultheria shallon* associations. The pattern of increasing richness and plant cover away from the shoreline was disrupted by species-poor, sparsely vegetated dunes; plots in the *Poa macrantha* association generally had less than four species per plot and less than 10% plant cover.

Soil chemistry is influenced by the proximity to the shoreline and pH and specific conductivity are elevated in both the *Cakile edentula* – *Atriplex gmelinii* and *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* associations (Figure 2.8). With increasing distance inland, pH and specific conductivity in

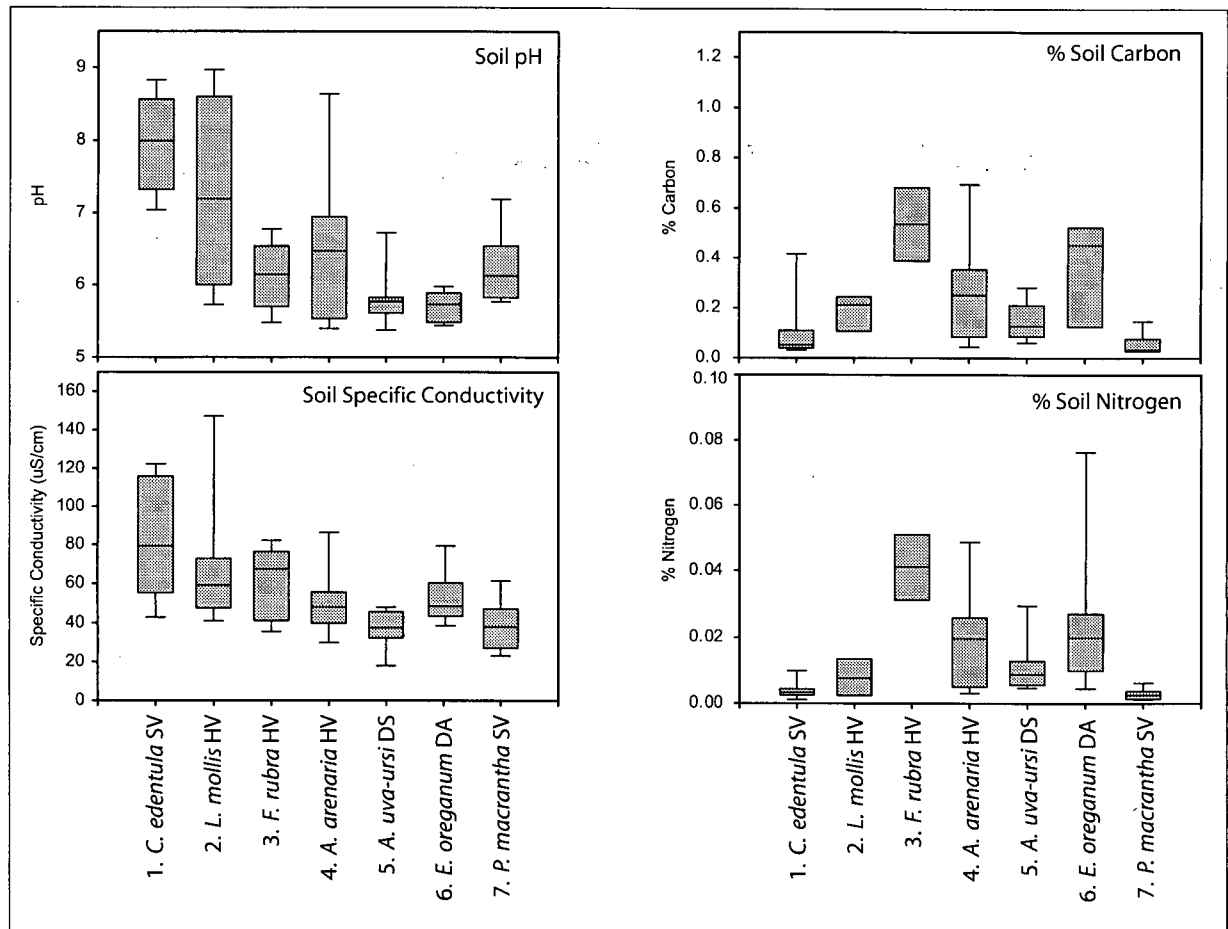


Figure 2.8. Soil chemistry characteristics (pH, specific conductivity, total carbon, and total nitrogen) of seven beach plant associations on the west coast of Vancouver Island. Box plots present mean and quantiles values (10%, 25%, 75%, 90%). Full plant association names are: 1) *Cakile edentula* - *Atriplex gmelinii* Sparse Vegetation; 2) *Leymus mollis* spp. *mollis* - *Lathyrus japonicus* Herbaceous Vegetation; 3) *Festuca rubra* - *Fragaria chiloensis* Herbaceous Vegetation; 4) *Ammophila arenaria* Herbaceous Vegetation; 5) *Arctostaphylos uva-ursi* Dwarf Shrubland Vegetation; 6) *Eurhynchium oreganum* / *Gaultheria shallon* Shrubland Vegetation Association; and, 7) *Poa macrantha* Sparse Vegetation.

the remaining five associations declined. This is likely caused by reduced ocean spray and precipitation-induced soil leaching. Total soil carbon and total soil nitrogen show a unimodal pattern similar to species richness and plant cover; they are generally low in *Cakile edentula* – *Atriplex gmelinii* and *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* associations, higher through *Festuca rubra* – *Fragaria chiloensis*, *Ammophila arenaria*, *Arctostaphylos uva-ursi*, and *Eurhynchium oreganum* / *Gaultheria shallon* associations and then low for the *Poa macrantha* association (Figure 2.8). Both nitrogen and carbon were substantially higher in the *Festuca rubra* – *Fragaria chiloensis* association.

DISCUSSION

The classification, description, and ordination results presented in this chapter provide a general structure for understanding plant community development in beaches of the west coast of Vancouver Island. The results indicate that sand beaches support plant associations that have varying floristic and environmental distinctiveness; associations with a high degree of overlap in the ordination indicate shared species which likely reflects closer spatial or successional relationships. Environmental characteristics showed similar patterns. This is not unexpected based on the distinct spatial zonation of some beach plant associations in the study area, and the successional gradation of others.

Plant associations of sand beaches on the west coast of Vancouver Island can be separated into three broad groups that reflect their spatial position and the characteristic environment in which they are found: lower beach, upper beach, and dune. These groups are reflected in the NMS ordination results and analytical summaries of environmental characteristics. The lower beach association (*Cakile edentula* – *Atriplex gmelinii* association) is comprised primarily of annual species that use rapid, single season growth and high seed production as a life-history adaptation to frequent disturbance and environmental stress (Zhang and Maun, 1992). Adaptations to environmental stress were not a focus of this study but likely include mechanisms for tolerating high salinity, alkalinity, and low nutrient availability (Gagne and Houle, 2001). Dunes are also floristically and environmentally unique and support a distinctive association (*Poa macrantha* association) that has relatively few species with sparse cover. Many of the species in the association have high fidelity to dune environments because of unique adaptations to the harsh environmental conditions (i.e., low soil nutrients, low moisture). The other five associations encompass more floristically diverse plots that develop in the more stable and fertile environment of the upper beach. Generally, these associations

occur between the lower beach and dunes. The NMS results indicate the five upper beach associations are less floristically distinctive (e.g., share more species). All have some bryophyte development and most have shrub or dense perennial grass development. All are more developed successional, although the two shrubland associations (*Arctostaphylos uva-ursi* and *Eurhynchium oreganum* / *Gaultheria shallon* association) are the closest successional to forest. Cordes (1972) examined the development of Sitka spruce-dominated coastal forest and Singleton (1978) studied soil chronosequences in coastal areas on the west coast of Vancouver Island. Both studies found that dunes or herbaceous meadows are eventually replaced by Sitka spruce forest over time.

Many of the plant associations described in this study are synonymous with associations described by previous researchers. I compared my results to the findings of Kuramoto (1965), Wiedemann (1984), and Christy *et al.* (1998) to create a current and standardized nomenclature for beach plant associations on the outer BC coast. As noted previously, Kuramoto's research focused on plant associations in Wickaninnish Beach, while Wiedemann (1984), and Christy *et al.* (1998) studied the diverse vegetation of the Oregon Coast. Kuramoto's classification was not published and the associations he described are not commonly used despite the thoroughness of his study. Since 1965, several scientific names have changed and it is now less common to use Braun-Blanquet naming methods.

Kuramoto's *Cakiletum edentulae* is analogous with the *Cakile edentula* – *Atriplex gmelinii* association described in this study. *Atriplex gmelinii* is still uncommon in Wickaninnish Beach, although it is more common regionally. Neither Wiedemann (1984) nor Christy *et al.* (1998) recognized a *Cakile edentula*-dominated lower beach association in the Oregon coast.

The *Elymetum vancouverensis* recognized by Kuramoto (1965) is very similar to the *Leymus mollis* spp. *mollis* – *Lathyrus japonicus* association in terms of composition and spatial location (e.g., upper beach). The taxon "*Elymus vancouverensis*" is a misidentification and the new association name clarifies this confusion (*Elymus vancouverensis*, or more correctly, *Leymus* x *vancouverensis*, is considered a hybrid between *L. mollis* ssp. *mollis* and *L. triticoides* (see Douglas *et al.* (2001)) and is rare in beaches in the study area). Christy *et al.* (1998) identified a synonymous association (*Leymus mollis* spp. *mollis* association) that was dominated by *L. mollis* spp. *mollis*, *L. japonicus*, *Juncus leseurii*, and *Achillea millefolium*). They noted the association has declined throughout its range because of *A. arenaria* invasion. Wiedemann (1984) recognized an *Elymus mollis* – *Abronia latifolia* association which is similar, but floristically distinct, to the dominant native foredune association on

the west coast of Vancouver Island (note the name *Elymus mollis* has been superseded by the name *Leymus mollis* spp. *mollis*). He also stated that it was a rare association that forms low hummocks as an initial stage of foredune development.

A subassociation dominated by *Ammophila arenaria* was described by Kuramoto (1965) as part of the *Elymeton vancouverensis*, and he stated that: "the limited extent of the variant precluded the establishment of a sufficient number of plots". *A. arenaria* now dominates widespread areas of many sand beaches throughout the Pacific Coast (Wiedemann and Pickart, 1996; Seabloom and Wiedemann, 1994) and a new association (*Ammophila arenaria* association) was described to encompass this development in the study area. Both Wiedemann (1984) and Christy *et al.* (1998) described synonymous *A. arenaria*-dominated associations.

Two associations dominated by *Arctostaphylos uva-ursi* were described by Kuramoto (1965). They differed in bryophyte and shrub composition (*Arctostaphyleto* – *Eurhynchietum oregani* with *Picea sitchensis*, *Gaultheria shallon* and higher cover of *Eurhynchium oreganum* and *Leptogium corniculatum* (*palmatum*), and *Arctostaphyleto* – *Rhacomitrietum canascentis* with *Rhacomitrium canescens* and higher cover of *Peltigera* species). With the inclusion of plots from a broader region in my study, these associations were encompassed by the new *Arctostaphylos uva-ursi* association. They may be recognized as subassociations. Wiedemann (1984) described a synonymous association (*Arctostaphylos uva-ursi* / *Rhacomitrium canescens* association) that he recognized as a successional community that eventually develops into conifer forest. He noted it was rare because of off-road vehicle disturbance. Christy *et al.* (1998) described only one association with a substantial *A. uva-ursi* component: *Pinus contorta* var. *contorta* / *Arctostaphylos uva-ursi* association. It is structurally similar, but floristically distinct, from the association described from the west coast of Vancouver Island.

The dune association described in this study (*Poa macrantha* association) and Kuramoto's *Poetum macranthae* are identical. Wiedemann (1984) and Christy *et al.* (1998) also described a dune association dominated by *P. macrantha*. Wiedemann described it as the *Poa macrantha* – *Lathyrus littoralis* association which is structurally very similar but floristically distinct because of the presence of *Lathyrus littoralis* (*L. littoralis* is rare in dunes and beaches of the west coast of Vancouver Island; I recorded it only once in dunes at Wickanninish Beach). It is perhaps better described as a subassociation. Christy *et al.* (1998) described it simply as *Poa macrantha* association (note: Kagan

et al., (2001) modified the name using a synonym for *P. macrantha* to *Poa douglasii* ssp. *macrantha*).

The *Eurhynchium oreganum* / *Gaultheria shallon* association described in this study, Kuramoto's (1965) *Piceo – Gaultherieto – Maianthemetum dilatati*, Wiedemann's (1984) *Gaultheria shallon – Vaccinium ovatum* association, and Christy *et al.*'s (1998) *Gaultheria shallon – Vaccinium ovatum / Pteridium aquilinum* association are synonymous and the different names reflect the interpretation of minor successional differences. This association is the most successional developed of the beach plant associations recognized in this study.

Kuramoto (1965) recognized a bryophyte-rich association (*Aireto – Ceratodontetum purpurei*) that developed on the dune margin behind the foredune ridge in Wickaninnish Beach. This is likely a distinct unit but it is not widespread regionally. It is not recognized as a separate association in this classification and may be better described as a subassociation of the *Ammophila arenaria* association. It was not recognized by Wiedemann (1984) or Christy *et al.* (1998).

Neither Kuramoto (1965) or Wiedemann (1984) described an association that is synonymous with the *Festuca rubra – Fragaria chiloensis* association described in this study. Wickaninnish Beach does not support any wet herbaceous vegetation areas which precluded the description of a *F. rubra*-dominated association in Kuramoto's (1965) classification. Wiedemann (1984) described a physiognomically-similar association (*Festuca rubra – Lupinus littoralis* association) that he found as the typical meadow community on the Oregon Coast. Christy *et al.* (1998) also identified several *Festuca rubra*-dominated plant associations in the Oregon Dunes area including the *Festuca rubra – Pteridium aquilinum* and *Festuca rubra – Juncus lesueurii* associations. The *Festuca rubra – Juncus lesueurii* association is the closest floristically to the association described from the west coast of Vancouver Island (note *J. lesueurii* is now recognized as *Juncus breweri*). Additional sampling may clarify the distinctiveness or similarity of these associations. Both are species-rich meadow communities on moist older dunes.

Several points are important for contextualizing rarity of beach plant associations on the west side of Vancouver Island. First, because of the rarity of sand-dominated shorelines, all beach plant associations are considered regionally rare. The total area of all plant associations assessed in this study was 104 hectares and encompasses the majority of large beach vegetation areas on the west

coast of Vancouver Island. Because of these factors, the conservation significance of all beach plant associations is likely higher than currently indicated by provincial conservation databases.

Second, the comparative assessment of rarity indicated that several plant associations are more uncommon either because of limited regional representation or low abundance than others. Three associations have higher conservation value because of regional rarity and this should be reflected in their inclusion and ranking in provincial conservation databases. However, because the region was not assessed uniformly, caution should be used in interpreting the absolute numbers in Table 4.

The rarest association by site presence is the *Poa macrantha* association. It is found at eight sites, although where it occurs it is locally abundant (16.9% of plots and prevalent at Wickaninnish Beach, Whitesand Cove, Cape Scott, and Keeha Bay). Sparsely vegetated open dunes with this association also support a group of distinctive plant species (e.g., *Poa macrantha*, *Glehnia littoralis* spp. *leiocarpa*, *Abronia latifolia*, *Polygonum paronychia*, *Convolvulus soldanella*) with adaptations to dune environments. The conservation significance of these species is currently being evaluated by the B.C. Conservation Data Centre. The *Arctostaphylos uva-ursi* association is also uncommon regionally (9 sites) but is of conservation concern because of its low abundance (5.8% of plots). This association typically occurs along the margin between dunes and forest which limits its development. It contains few plant species that can be considered of regional conservation significance, although more detailed work on its bryophyte and lichen community is needed. The *Festuca rubra* – *Fragaria chiloensis* association is also considered regionally rare (10 sites; 8.3% of plots) and is only abundant in two of the northern sites (Cape Scott and Grant Bay). The association contains several species that are of provincial conservation significance (e.g., *Carex pansa*). The *Gaultheria shallon* / *Eurhynchium oreganum* association is not considered regionally rare despite its relatively low abundance in terms of percentage of plots (6.5% of plots). It is considered a successional community through which open dunes develop into closed forest. Neither the *Cakile edentula* – *Atriplex gmelinii* and *Ammophila arenaria* associations are regionally rare and it is also noteworthy that both are dominated by exotic plant species.

In summary, the classification presented here provides a useful structure for understanding plant community development in sand beaches on the west coast of Vancouver Island. The results, I hope, will be used as a basis for better conservation planning of plant associations in sand beaches, and also serve as background information for more detailed analyses of the role of environmental factors in influencing patterns of native and exotic plant species in the following chapters.

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CHAPTER 3

SPATIAL PATTERNS OF NATIVE AND EXOTIC PLANT RICHNESS IN SAND BEACHES

INTRODUCTION

As the intensity and effect of exotic species invasions on natural ecosystems has increased, understanding ecological processes and factors that influence patterns of invasion has become an important practical and theoretical question for ecology (Lonsdale, 1999; Levine, 2000; Shea and Chesson, 2002; Stohlgren, 2002). Plant community studies have found that exotic plant species are proportionately more common in fertile, disturbed habitats such as riparian zones, wetlands, and grasslands (e.g., Rejmanek, 1989; Deferrari and Naiman, 1994; Planty-Tabacchi *et al.*, 1996; Stohlgren *et al.*, 1998, 1999; Sobrino *et al.*, 2002). An important aspect of this invasion pattern is that these habitats also support the highest diversity of native species (Stohlgren *et al.*, 1999; Lonsdale, 1999; Levine, 2000). This suggests that the intrinsic susceptibility of plant communities to invasion is influenced by environmental factors or processes that also increase native species richness. This pattern is a major conservation concern because it indicates that sites with the highest biological diversity ("hotspots of plant diversity": Stohlgren *et al.*, 1999) are also at greatest risk from exotic species invasion.

Variation in resource availability may be an important explanation for some spatial patterns of plant community invasion (Hobbs and Huenneke, 1992; Davis *et al.*, 2000; Wardle, 2001; Wilson and Tilman, 2002). Where physical resources (light, nutrients, and water) are sparse (e.g., deserts, mires) or tightly controlled by the existing plant community (e.g., forests), invasibility¹ is generally low. In contrast, where resources are available to new species for establishment and growth, invasibility is generally high. This is an intuitively attractive explanation because it corresponds with general observations on ecosystem processes that structure riparian zones, grasslands, and other invulnerable communities. The importance of resource availability in promoting invasibility is summarized as the *theory of fluctuating resource availability* by Davis *et al.* (2000). They highlighted three key points: 1) a variety of mechanisms can increase resource availability (e.g., addition of new resources, loss of resource control by the existing community by natural or anthropogenic disturbance, etc.); 2) resource availability varies temporally and spatially within communities; and, 3) the structure and

¹ *Invasibility* is the likelihood that an exotic species will become established in a community (Williamson, 1999; Davis *et al.*, 2000).

composition of the existing community is an important influence on resource availability. This last point is important because it highlights the potential role of species richness and species identity in imparting invasion resistance or susceptibility to plant or other communities (Crawley *et al.*, 1999).

Resource availability may also be important for understanding two spatially-dependent relationships between species richness and invasibility. At a local scale (e.g., 1 m²), ecological theory and experimental studies suggest that species rich plant communities are resistant to invasion from new species (Elton, 1958; Tilman, 1997, 1999; Naeem *et al.*, 2000; Prieur-Richard *et al.*, 2000; Kennedy *et al.*, 2002). High species richness is hypothesized to limit resource availability by efficiently partitioning the resource pool among species with different requirements (Trenbath, 1974; Tilman, 1999). However, the effect of species richness in imparting invasion resistance (i.e., *diversity resistance hypothesis*; Kennedy *et al.*, 2002) is disputed. Wardle (2001) reviewed six recent studies that concluded increased species richness reduced invasibility. In each, he found that sampling effects, particularly the higher probability that competitive species will be included in treatments with the highest species richness, may account for the observed invasion resistance provided by high species richness.

In contrast to experimental studies, observational studies have found exotic species richness is associated with high native plant species richness at the community or regional scale (Lonsdale, 1999; Stohlgren *et al.*, 1999; 2001; Levine, 2000). At broader spatial scales, the physical complexity of natural communities (e.g., environmental heterogeneity, edge effects, disturbance history) appears to obscure the invasion resistance provided by high species richness (Levine and D'Antonio, 1999; Stohlgren *et al.*, 1999; Levine, 2000; Shea and Chesson, 2002). The results from observational studies also suggest that the combination of ecological processes and factors that maintain high native species richness in plant communities also increase invasibility.

To better understand spatial patterns of exotic plant invasion, I compared community scale spatial patterns of exotic and native plant species richness within sand beach plant communities of the Pacific Coast. Two inter-related questions are the focus of this chapter: 1) are the spatial patterns of native and exotic plant species richness along environmental gradients similar?; 2) which environmental factors are associated with patterns of native and exotic species richness within beach plant communities? Spatially compressed environmental gradients and a high number of exotic species make beach plant communities useful model ecosystems for studying spatial patterns of

exotic species invasion within communities. As described in Chapter 2 (*Description and Classification of Plant Associations of Sand Beaches on the West Coast of Vancouver Island*), plant community development varies zonally from shoreline to forest edge in sand beaches.

METHODS

Plant Species Richness and Plant Cover

Native and exotic plant species richness and abundance were measured on linear transects within eleven sand beaches on the west coast of Vancouver Island, British Columbia, between Cape Scott (50°46'N; 128°24'W) and Port Renfrew (48°34'N; 124°24'W). Transects were from a subset² of eighteen beaches that were sampled to evaluate regional patterns of exotic plant species invasion. More information on the study area and beach plant communities is presented in Chapter 2.

Transects were established perpendicular to the shoreline and 4 m² plots were placed along the transect using a stratified random sampling design. The average sampling intensity was 1 plot per 10 m of transect length. I used a subset of the total group of transects for analyses in this chapter; only transects between 75 and 100 m long were used because they provided the greatest expression of plant community development (e.g., lower beach, upper beach, dune) and environmental variation. A total of 256 plots from twenty-six transects were used.

A list of vascular plant, bryophyte, and lichen species was compiled for each plot and percent cover was estimated for each species. Species richness was measured as the number of vascular and non-vascular plant species per plot. For analysis, species richness was divided into three components: *total species richness* included all plant species in each plot; *native species richness* included the number of native plant species (vascular and nonvascular) in each plot; and, *exotic species richness* included the number of exotic plant species in each plot. As a result of taxonomic uncertainties or lack of adequate voucher specimens for identification, *Cladonia* species were placed into one of three morphologically defined groups, and *Peltigera* species were grouped at the generic level. All specimens were deposited at the University of British Columbia herbarium.

Determination of status as either native or exotic was accomplished by consulting published sources including Douglas *et al.* (1998-2002); Hitchcock and Cronquist (1973); Calder and Taylor (1968);

² Transects from Cape Scott, Whitesand Cove, Vargas Island North, Vargas Island Dune, Ahous Bay North, Clayoquot Island, Radar Beach, Schooner Cove, Wickaninnish Beach, Keeha Bay, Port Renfrew were used for analysis (see Figure 2.1 for locations).

and Barbour and Rodman (1970). Exotic species were defined as plants accidentally or purposefully introduced outside the geographic range in which they evolved as a result of human activity (modified from Richardson *et al.*, 2000).

Environmental Variables

Distance - I measured the location of each plot from the seaward extent of terrestrial vegetation using a 50 m tape.

Total Plant Cover – Total plant cover was calculated as a synthetic variable by summing percentage cover values for each species in the plot. Plant cover can be greater than 100% because of the overlap of foliage between different species or vegetation layers.

Soil Chemistry – I collected one 200 ml sample of shallow surface soil (5–10 cm below the surface) from each plot. Samples were kept in polyethylene bags and air dried at approximately 20°C for one month prior to a storage period of 7 to 10 months. Samples were screened through a 2 mm sieve and large inorganic or organic material was discarded before analysis. Samples were selected for soil chemistry analysis from the total set of samples using a stratified random design. Samples were grouped into 10 m distance bands and approximately equal numbers of samples were selected at random from each group.

For 195 samples, pH and specific conductivity were measured in the aqueous phase of a mixture of 20 g soil and 40 ml distilled water. Samples were prepared in disposable paper cups, stirred intermittently for 45 minutes and analyzed. pH was measured using an Orion Model 420A pH meter. Specific conductivity was measured using a Fisher Scientific Digital Conductivity Meter with automatic temperature compensation (to 25°C).

For 95 samples, 2 g of soil was analyzed for percent total carbon and percent total nitrogen using a Leco CN-2000 induction furnace. For an additional 20 samples, total carbon was measured using loss-on-ignition (12 hrs at 450°C in a muffle furnace) and total nitrogen was measured using Kjeldahl digestion methods respectively. Equipment problems prevented the analyses being completed using the induction furnace.

Seedling Experiment

To test of the effect of soil conditions on plant establishment, I conducted a laboratory experiment of seedling germination and growth. The hypothesis was that seedling germination and growth would follow similar patterns to the plant species richness and plant cover along the spatial gradient. 100 ml of screened sand from 92 plots from twelve transects were placed in rectangular 4 by 6 cm plastic pots. Transects were selected qualitatively. In each pot, six spinach seeds (*Spinacia oleracea* L. cv Olympia F1 from West Coast Seeds (2002)) were planted at a depth of 5 mm and covered with sand. The pots were watered with distilled water and kept together in a warm room for 48 hours. All pots were then transferred outside to an unheated, covered area with indirect sunlight for 33 days (April 9 to May 14, 2002). Each pot was watered once or twice per day with distilled water. To minimize variation in light levels or other external factors, pots were frequently rearranged.

Thirty-five days after sowing, seedlings were carefully removed from each pot and washed free of sand. The number of germinated seedlings and the number of healthy seedlings (e.g., firm, green, unwrinkled leaves with no discoloration) were recorded for each pot. The seedlings from each pot were then combined and divided into root and shoot tissue. Tissue samples were initially air dried at room temperature and then placed in an oven at 40°C for 4 hours before weighing. Final measurements for each pot were number of germinated seedlings, number of healthy seedlings, total shoot weight, total root weight, total seedling weight, and ratio of total shoot weight to total root weight.

Statistical and Comparative Analyses

Analysis focused on comparing the similarity of regression relationships between native species richness and exotic species richness, and environmental variables. I also used regression analyses to examine trends in response variables from the seedling experiment (percent seedling germination, percent healthy seedlings, total seedling weight, and root to shoot ratio) from soil samples along the spatial gradient. I used the statistical analysis programs JMPN (Version 3.2.6) complemented with graphical presentation in Sigmaplot (Windows Version 8.0) for analysis and data presentation. Tests of spatial autocorrelation were undertaken in PASSAGE (Rosenberg, 2003).

Exploratory Data Analysis – Prior to regression analyses, I used a bivariate scatterplot matrix to examine correlations between variables. The scatterplots were used to form general hypotheses about which environmental factors may influence patterns of species richness and invasibility. The

bivariate scatterplots also permitted the visual identification of outliers. Four plots were removed prior to further analysis because of bivariate outliers.

Zonal patterns of plant community development suggested that spatial autocorrelation was an important statistical issue to address for this study. Spatial autocorrelation is the non-independence of samples because of their similarity in space, and it is both an interesting aspect of spatially-structured data and a difficult problem to resolve statistically (Sokal and Ogden, 1978; Legendre, 1993; Thomson *et al.*, 1996; Dale and Fortin, 2002). Spatial autocorrelation compromises tests of statistical significance by inflating the effective sample size used in determining degrees of freedom. I used correlograms of Moran's *I* statistic to evaluate the presence and scale of spatial autocorrelation.

Regression Analyses – I fit linear and nonlinear ordinary least squares (OLS) regression models to test the relationship of native and exotic species richness to environmental variables. Second-order polynomial models were only shown if both the overall model and all exponential terms in the regression equation were significant. I used an analysis method developed by Clifford *et al.*, (1989) (CHR analysis) to correct sample sizes based on spatial autocorrelation. Significance values depicted in the results are corrected values based on the reduced sample size.

Nonparametric regression was undertaken using the smoothing spline function in JMPN. Smoothing splines divide the independent variable into segments and fit a curve to the local variation in the dependent variable using polynomial regression. At each segment boundary, it uses a smoothing function to join the adjacent segments. The number of segments influences the fit and smoothness of the spline line. I assessed each fit iteratively to find a fit that balanced variance explanation and smoothness. For each paired graph (e.g., native and exotic species richness versus soil pH), the same smoothing function was used to increase comparability.

Nonparametric regression models are effective in identifying complex relationships that are common in ecology (Palmer, 1994). Parametric regression relies on the assumption that the dependent variable follows predictable changes throughout the range of the independent variable. The parametric model is constrained by the entire set of observations and is influenced by extreme datapoints (Eubank, 1988). Inspection of the bivariate scatterplots indicated that patterns of species richness or environmental variables were likely to be complex and asymmetric; linear relationships may characterize parts of the gradient while quadratic or higher polynomial models may better describe other parts of the gradient. Nonparametric regression does not rely on conformity to underlying

statistical distributions (e.g., normality) and therefore was useful in detecting trends where parametric regression relationships were not appropriate.

Ordination – I also used nonmetric multidimensional scaling to synthesize trends in native and exotic species richness, and relate them to a limited group of abiotic or biotic environmental variables. I used the same group of plots used for the ordination in Chapter 2, but excluded six plots in which no plant species were recorded. A total of 251 plots were used. I followed the same general procedures as described in Chapter 2, although the final solution was 2-dimensional. Only total nitrogen, pH, distance inland, and total plant cover were included as environmental variables. Each was \log_{10} -transformed.

RESULTS

Bivariate scatterplots showed intercorrelations between many of the untransformed variables (Figure 3.1). Most of the variables showed some relationship to distance inland (see last column of scatterplots in Figure 3.1). Only two correlation coefficients were greater than 0.75 (total carbon versus total nitrogen, $r=0.88$; total nitrogen versus total cover, $r=0.80$), which indicates linear relationships tended to be weak. The majority of data distributions suggested nonlinear responses. Most had high variance at one end of the data range which is common in ecology (Thomson *et al.*, 1996). Some relationships (e.g., native and exotic species richness versus total plant cover) appeared to be weakly unimodal. The four outliers are not shown because many were outside of the data range depicted in the scatterplots.

Correlograms of Moran's I values showed that spatial autocorrelation was present in all variables, with the autocorrelation changing from positive to negative at approximately 25 m (Figure 3.2).

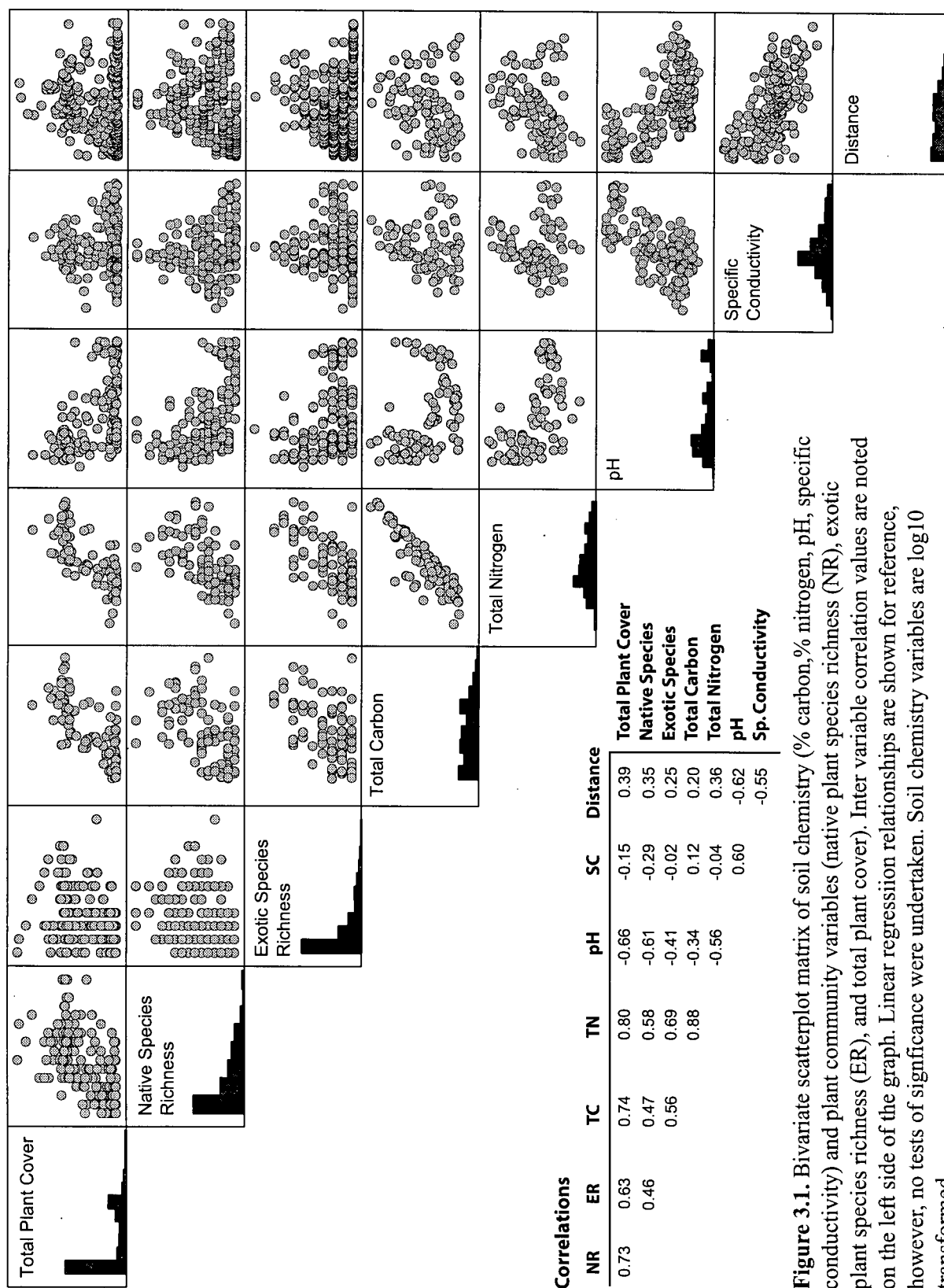


Figure 3.1. Bivariate scatterplot matrix of soil chemistry (% carbon, % nitrogen, pH, specific conductivity) and plant community variables (native plant species richness (NR), exotic plant species richness (ER), and total plant cover). Inter variable correlation values are noted on the left side of the graph. Linear regression relationships are shown for reference, however, no tests of significance were undertaken. Soil chemistry variables are log10 transformed.

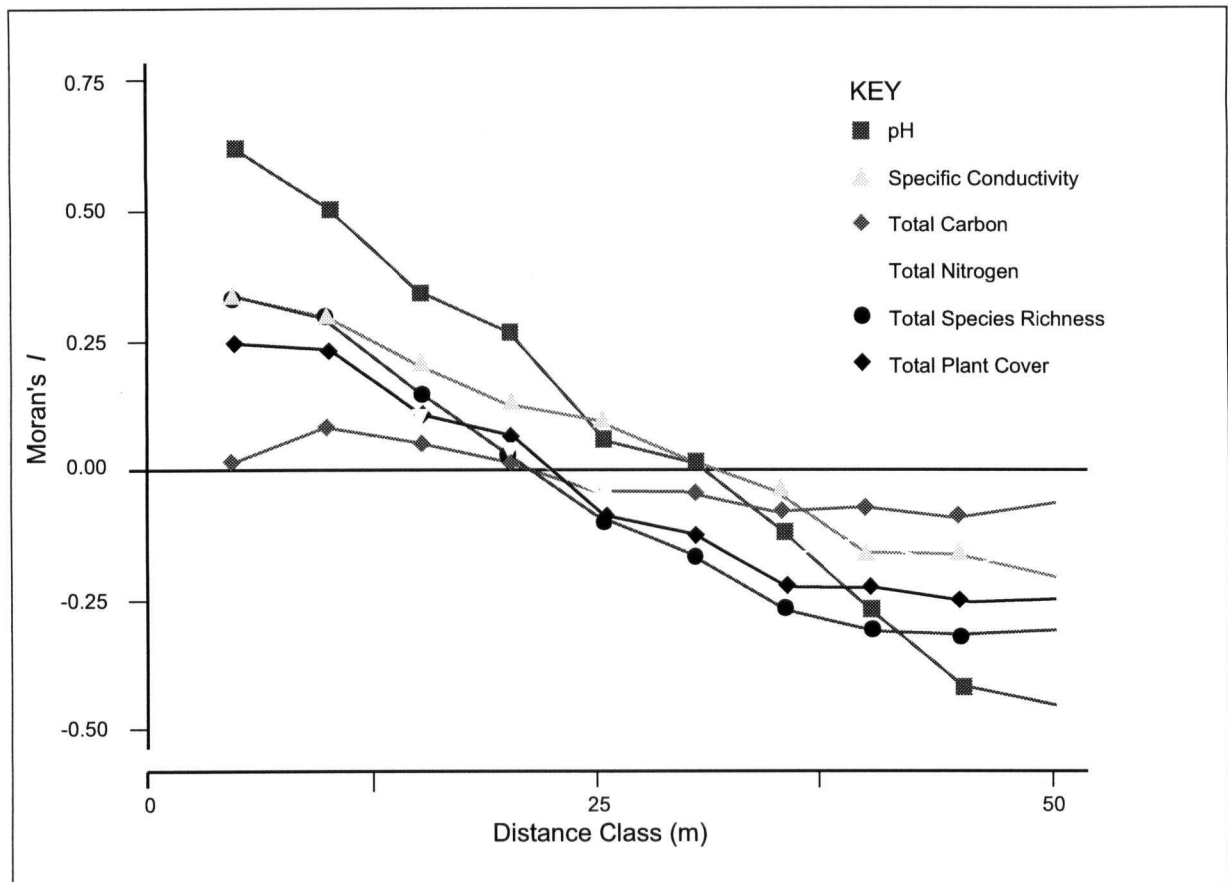


Figure 3.2. Correlograms of Moran's I values for key environmental and plant community variables in sand beaches. Positive values from 0 to approximately 25 m indicate positive spatial autocorrelation. Negative values indicate negative autocorrelation. Five meter distance classes were used.

Spatial Trends in Soil Chemistry – Two general spatial patterns were observed in soil chemistry and general plant community variables (see Figure 3.3). pH declined rapidly from greater than 8.0 near the shore to less than 6.0 near the mid-point of the distance gradient, although the relationship was not statistically significant because of high spatial autocorrelation. Comparative regression indicated that there was little change in pH between the mid-point of the spatial gradient and the open dunes further inland. pH declines as calcium carbonate derived from sea water is leached by soil weathering and are replaced by hydrogen and aluminum ions (Therington, 1990). It stabilizes near 5.5 because of the buffering capacity of aluminum ions. Jordanes (1990) found pH ranged between 4.3 and 4.8 in forest soils along the coastal fringe in the same study area, which likely indicates the pH end-point for soil development on beach sands.

Specific conductivity followed a similar pattern as pH; it reached a maximum of approximately 170 uS/cm near the shoreline and declined to less than 50 uS/cm in the dunes near the forest edge. This relationship was also not statistically significant. Other studies have shown that ion enrichment from ocean spray, principally from sodium and chloride ions, declines and precipitation-induced leaching increases inland from the shoreline (Cordes, 1972; Gerlach *et al.*, 1994; Wilson and Sykes, 1999; Gagne and Houle, 2002).

Both percent total soil carbon and percent total soil nitrogen showed a significant unimodal relationship with distance; maximum values were distributed approximately midway along the distance gradient with nutrient-poor soils characterizing the lower beach and dunes. Similarly, mean values of total plant species richness and total plant cover showed a significant unimodal relationship with distance.

Species Richness and Total Plant Cover – Native and exotic species richness were positively and significantly related; plots with the highest number of native plant species generally had the highest number of exotic plant species (Figure 3.4). The parametric linear and nonparametric regression showed the same relationship. However, the overall strength of the relationship was low ($r^2=0.13$ for both) and exotic species richness was highest (>8 exotic species per plot) in plots with moderate richness (3–9 species) of native plants.

Nonlinear regression indicated a weak unimodal relationship between components of species richness and total plant cover (Figure 3.4). Total species richness initially increased as total plant cover increased, but declined as plant cover increased beyond 100%. This suggests that competitive exclusion reduces plant diversity in plots with the highest plant cover. This result should be interpreted with caution because of the weakness of the relationship and the potential leverage of a small number of plots with high plant cover. Differences in the relationships between native and exotic species richness and total plant cover were more difficult to interpret. While both relationships were significantly unimodal, native species richness declined proportionately less in plots with high plant cover.

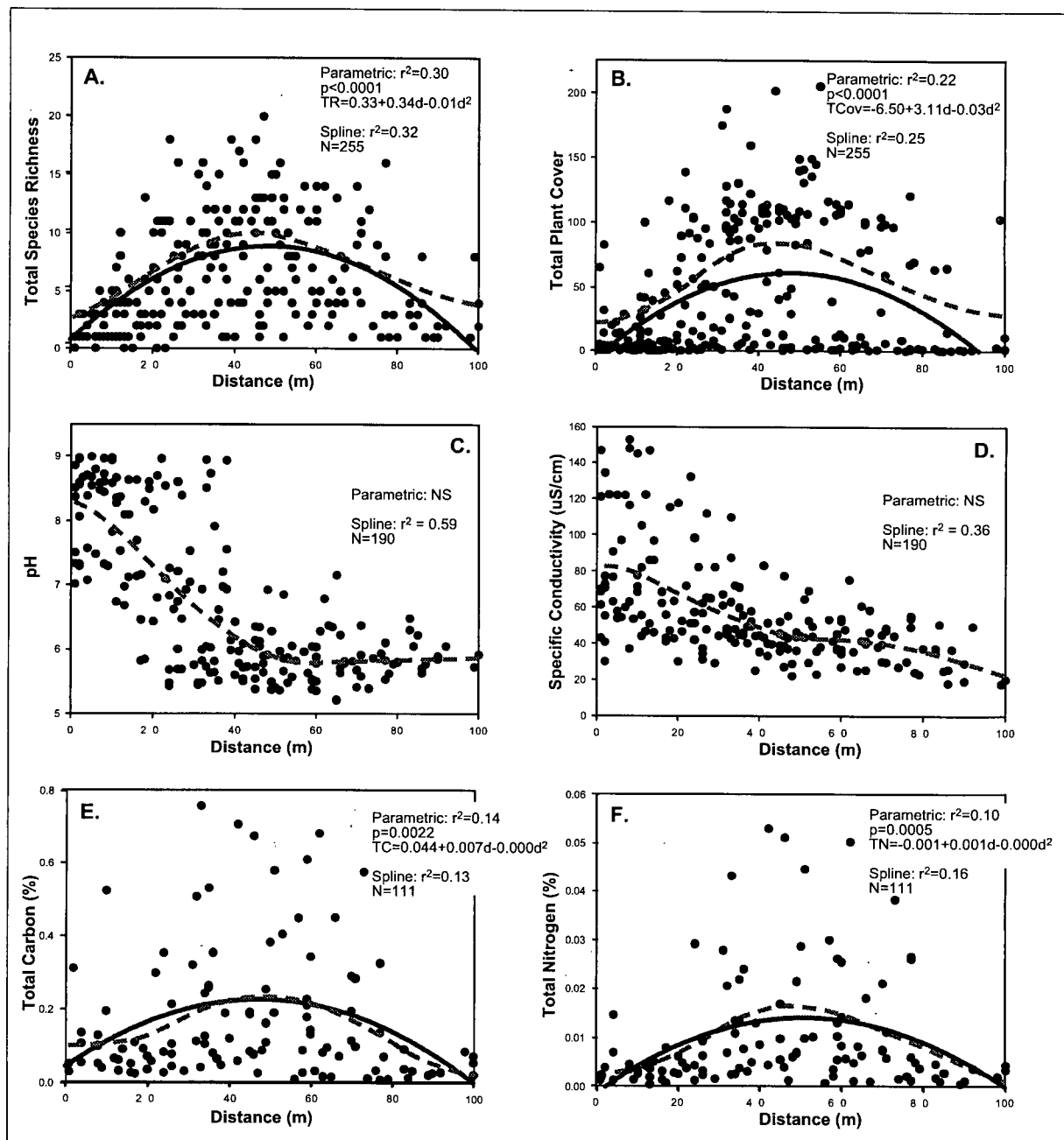


Figure 3.3. Parametric and nonparametric regression relationships for spatial patterns of total plant species richness (A), total plant cover (B), soil pH (C), specific conductivity (D), total carbon (E), and total nitrogen (F) from the shoreline (0 m) to the forest edge (100 m). Parametric relationships are shown with solid lines. The significance value, coefficient of determination (r^2), and regression equation are provided for each model. Nonparametric smoothing splines are shown with a dashed line. Coefficient of determination (r^2) and sample size (N) are depicted for each relationship.

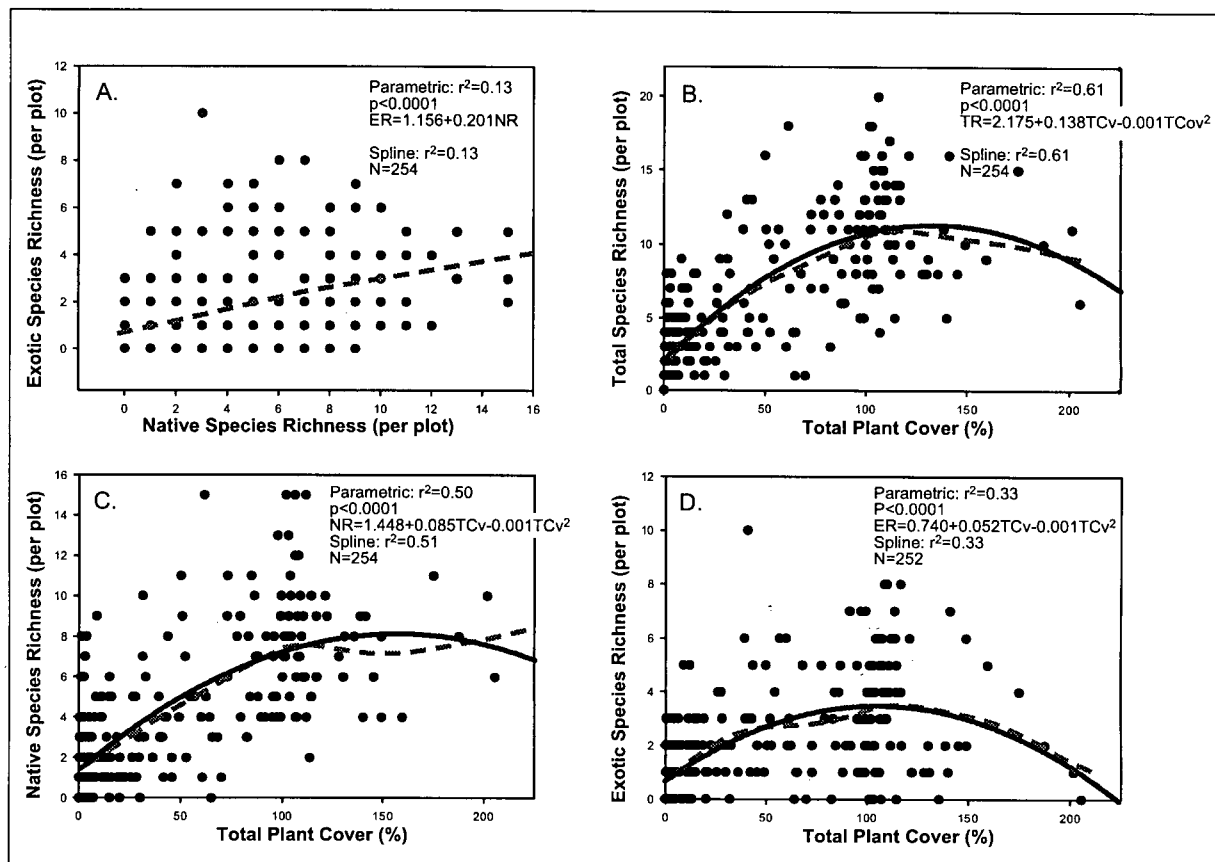


Figure 3.4. Parametric and nonparametric regression relationships between native and exotic plant species richness per plot (A), and components of plant species richness per plot in relation to total plant cover in sand beach plots: B) total species richness; C) native species richness; and D) exotic species richness. Parametric and nonparametric regression relationships are shown using the same format as Figure 3.3.

Native and Exotic Plant Species Richness along Soil Chemistry Gradients – Native and exotic species richness declined with increasing pH (Figure 3.5). This reflects the high pH of the lower beach and the lack of substantial change in soil pH inland from the mid-point of the distance gradient (e.g., species poor dune communities have similar pH to species rich beach ridge communities). Native and exotic species richness had a significant unimodal relationship with specific conductivity (Figure 3.5).

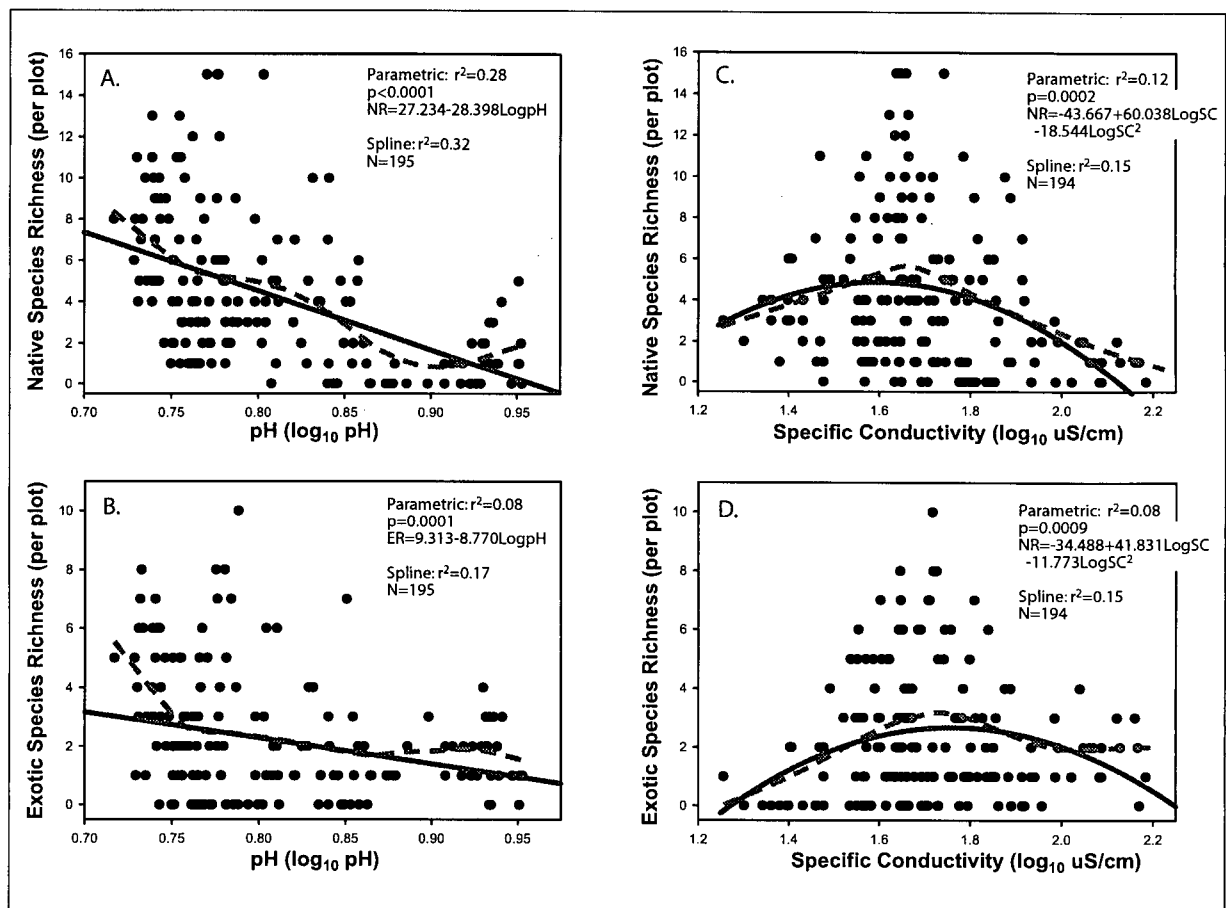


Figure 3.5. Native and exotic plant species richness along soil pH (A and B) and specific conductivity (C and D) gradients using parametric and nonparametric regression relationships. Soil chemistry variables were \log_{10} transformed prior to regression. Parametric and nonparametric regression relationships are shown using the same format as Figure 3.3.

Relationships between native and exotic species richness and total nitrogen and total carbon were similar (Figure 3.6). All components of plant species richness had a significant linear relationship with total carbon and total nitrogen. However, nonparametric regression indicated that species richness reached a maximum at moderate concentrations of total carbon or nitrogen and then declined at the highest concentrations. Similar to relationships between species richness and plant cover, relatively few plots with high total carbon and total nitrogen have a strong influence on this relationship.

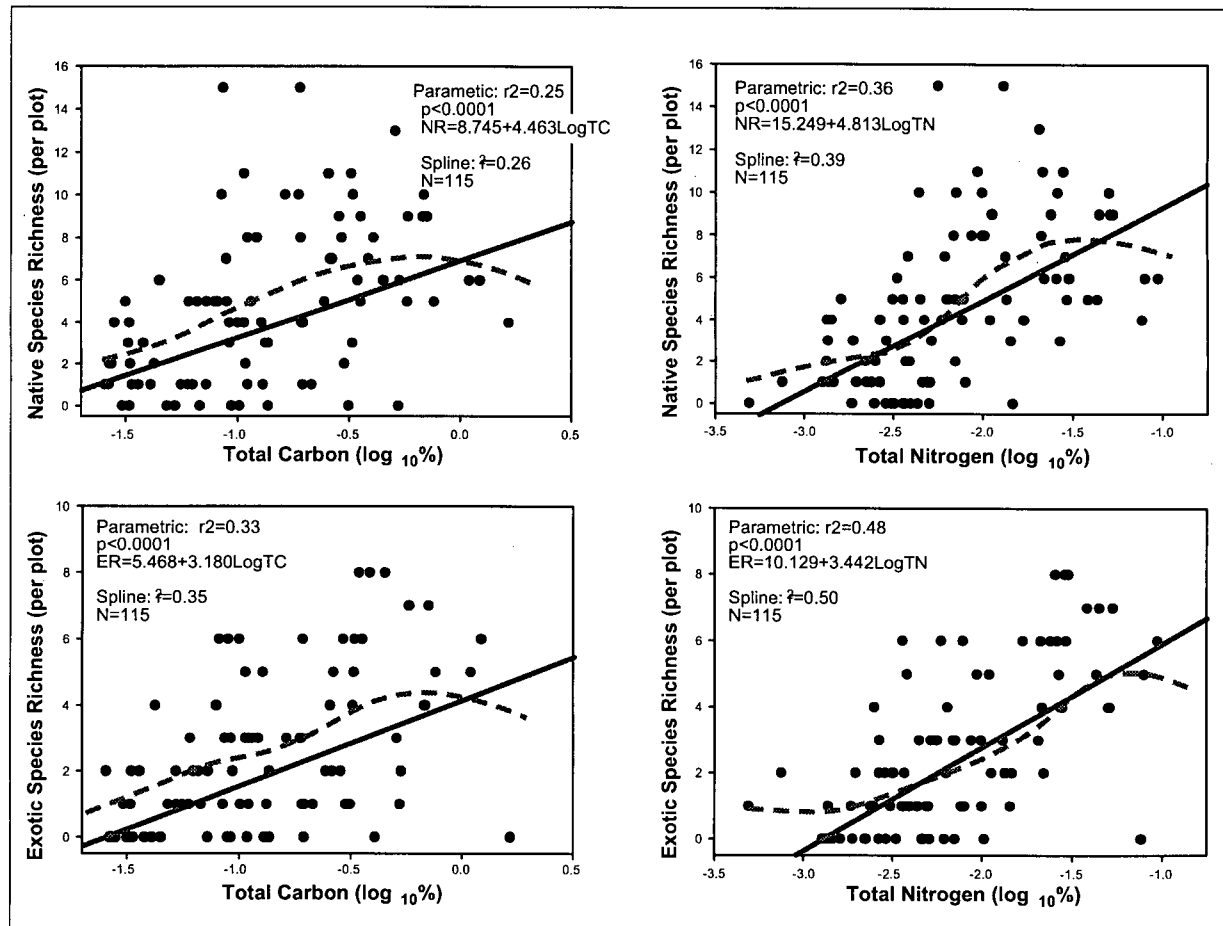


Figure 3.6. Native and exotic plant species richness along total carbon (A and B) and total nitrogen (C and D) gradients using parametric and nonparametric regression. Soil chemistry variables were \log_{10} transformed prior to regression. Parametric and nonparametric regression relationships are shown using the same format as Figure 3.3.

Seedling Establishment and Growth – None of the parametric regression relationships showed statistically significant spatial trends in seedling establishment or growth. However, nonparametric regression indicated that germination success, seedling health and total seedling weight declined with increasing distance from the shoreline (Figure 3.7).

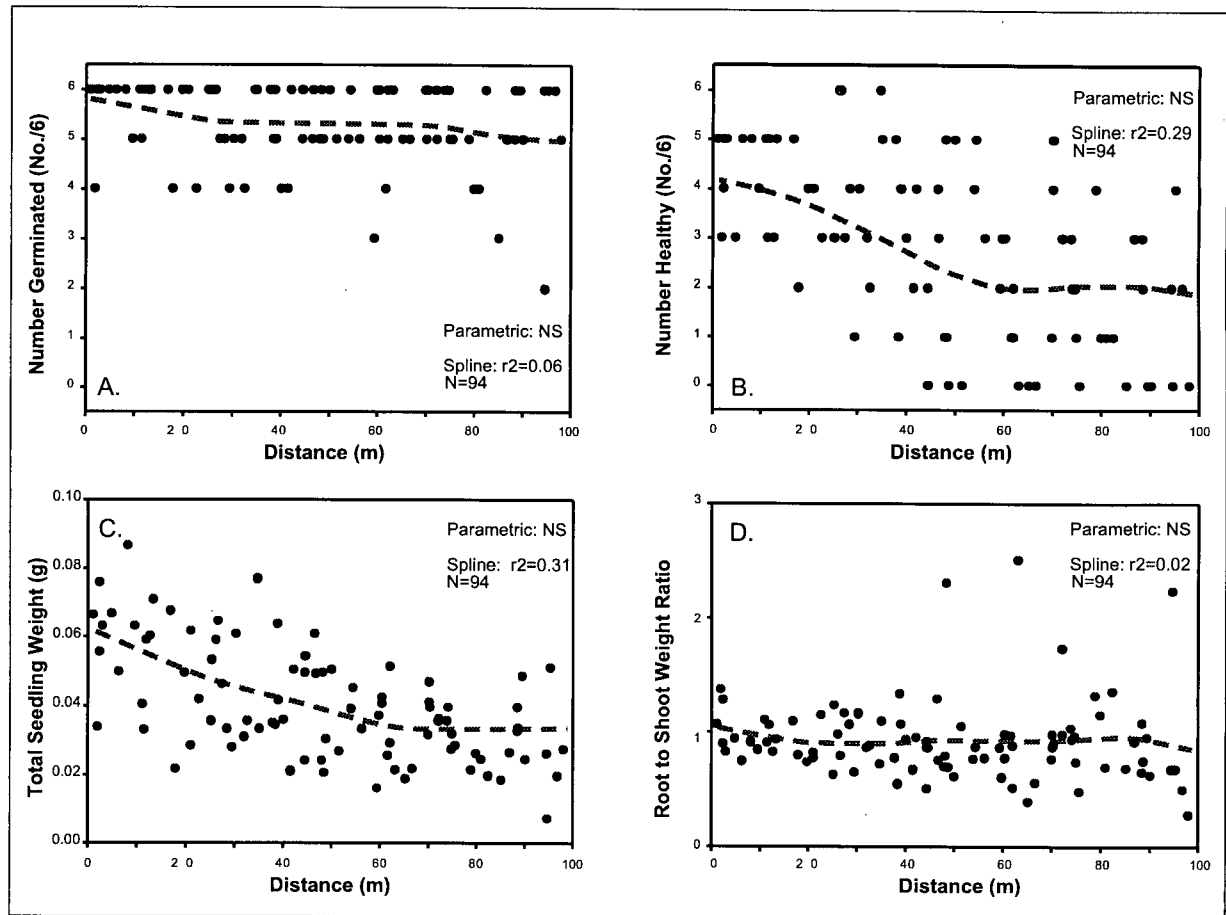


Figure 3.7. Nonparametric regression relationships of spinach germination and growth in soil collected on a spatial gradient from the shoreline to the forest edge. Six seeds were planted in each plot. The following variables were measured after 35 days: A) germinated seedlings (no. of out 6); B) healthy seedlings (no. out of 6); C) total seedling weight; and D) root weight to shoot weight ratio. Coefficient of determination (r^2) and sample size (N) is shown for each relationship. None of the parametric regression models were statistically significant.

Ordination – The results of the constrained nonmetric multidimensional scaling are presented in Figure 3.8. Plots with the highest native and exotic species richness share similar locations in ordination space. Multiple regression of the four environmental variables indicated that total plant cover and distance inland had the strongest relationships with species richness.

While the ordination results indicate plots with high exotic plant species richness are similar to plots with native plant species richness, there are also noticeable differences. In particular, plots with the highest number of exotic species often had moderate number of native species. As well, these plots generally had lower total plant cover and were slightly closer to the shore than plots with the highest number of native plant species.

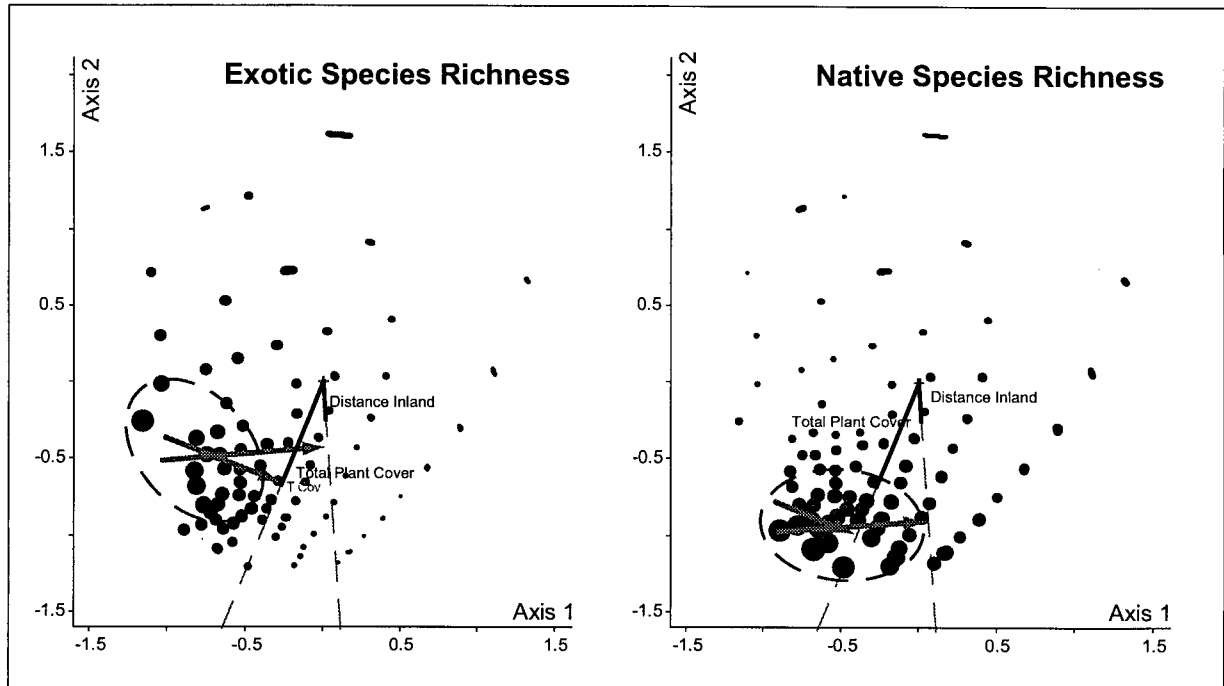


Figure 3.8. Nonmetric multidimensional scaling ordination of 251 sand beach plots by native and exotic plant species richness. The size of the dots indicates the relative richness of exotic and native plant species (note, the maximum number of native species in a plots was 15; the maximum number of exotic species was 10). Ellipses were drawn around the plots with the highest native and exotic species richness. Differences in the location of ellipses in relation to the solid lines indicating total plant cover and distance inland variables are shown with arrows. The stress of the 2-dimensional ordination solution was 17.71 and the instability was 0.059. The cumulative explanation of variance provided by the two axes was $r^2 = 0.82$ (Axis 1, $r^2=0.16$; Axis 2, $r^2=0.67$).

DISCUSSION

Native and exotic plant species richness covaried on a spatial gradient in sand beaches I studied; both were low near the shore, increased rapidly to a maximum approximately 50 m inland, and then declined in the dunes behind. The results support the generalization that increased invasibility from exotic species is associated with sites of high species richness within plant communities (Robinson *et al.*, 1995; Planty-Tabacchi *et al.*, 1996; Lonsdale, 1999; Stohlgren *et al.*, 1999; Levine, 2000). However, my results suggests the relationship between native and exotic species richness is more variable than some studies have found. Although the relationship between exotic and native plant species richness

was positive and linear, I found that exotic species richness reached a maximum in plots with moderate native plant species richness (see Figure 3.4 and 3.8). Relationships between plant species richness and total plant cover also indicated that exotic species are more affected by competition than native species (e.g., stronger decline in exotic species at highest plant cover values). In combination, these results suggest that native and exotic plants respond similarly to abiotic environmental factors, but competition from the existing plant community may exert a disproportionately strong force on invading species.

Despite the clear similarity between the spatial patterns of exotic and native plant species richness in beach plant communities, unravelling the ecological factors that control this pattern is difficult. My results suggest that soil fertility is the primary factor influencing the richness of both native and exotic plant species in beach plant communities. Native and exotic plant species richness was highest in plots where total nitrogen and total carbon were high and pH was moderate, which was generally near the midway between the shoreline and the forest. Species richness apparently declines in plots further inland because of nutrient and organic matter leaching, while the lower beach is species poor because of the combination of physical disturbance and stress caused by wave and tide disturbance, ocean spray, low nutrient availability, and high pH. Based on my results, high species richness and heightened invasibility are components of the same general pattern controlled by soil fertility. Nitrogen, in particular, is an important limiting nutrient in coastal ecosystems (Vitousek *et al.*, 1997) and my results indicate it is an important control over vegetation development in beaches. Stohlgren *et al.* (1999) also found plots with the highest total soil nitrogen and total soil carbon in grasslands in the US Midwest were associated with the highest richness of exotic plants. Similarly, Kolb *et al.*, (2002) found invasibility in coastal meadows was associated with sites of high soil nitrogen left by dying *Lupinus arboreus* shrubs.

It is less clear if disturbance plays a strong or weak role in increasing invasibility in beach plant communities. As noted previously, disturbance may increase the availability of resources for invading species and reduce competition from existing species for those same resources. The lack of strong unimodal relationships between total foliar cover and total species richness, and between total carbon and total nitrogen and species richness, suggests that competitive exclusion (e.g., the loss of competitively “weak” species in the most productive plots) is generally uncommon in the beach plant communities I studied. Two causes may account for this result. First, disruption of competitive interactions by frequent marine-related disturbance may prevent highly competitive communities from developing. However, the lack of direct estimates of disturbance frequency and intensity

prevents any detailed analysis of its role making soil resources available to invading species. Indirect evidence including the development of the foredune ridge from the trapping of windblown sand and the deposition of wood debris in the upper beach suggests that disturbance is frequent in beaches on the west coast of Vancouver Island. Even short term increases in resource availability from disturbance may increase invasibility (Davis and Pelsor, 2001). Second, low soil fertility of sand beaches compared to other herbaceous plant communities (Gerlach *et al.*, 1994; Cain *et al.*, 1999) may also reduce the rate at which competitive interactions between species return following disturbance (see Huston, 1979; 1994). Here again, the lack of temporal data on plant community change prevents more detailed analysis. Disturbance may also be important for dispersing seeds and root fragments of invading species to new sites. Similarly, it may be important for enriching nutrients in beach soils through the transport of marine-derived organic debris (e.g., wood, algae, etc.) (Christy *et al.*, 2001).

Separating the spatial gradient into three zones is useful for interpreting and explaining patterns of plant species richness and invasibility in beach plant communities (see Figure 3.9). In the lower beach (Zone A), plant species richness and invasibility are low because of the combined effects of frequent disturbance from waves and tides and high physical stress from soil salinity, alkalinity, and low nutrient availability (Ranwell, 1972; Barbour and De Jong, 1977; Hesp, 1989; Gagne and Houle, 2002). Species richness and invasibility increase as these effects diminish with increasing distance inland. The effects of marine processes (e.g., waves, tides, ocean spray) on plant establishment and growth are most intense within a narrow band near the shoreline and decline rapidly inland (Houle, 1997; Wilson and Sykes, 1999; Verhoeven, 2002). Why spinach seedlings grew best in soils from the lower beach is unknown. The seedling test results should be treated with caution both because of the lack of statistical significance and the potential effect of reduced salinity, increased nitrogen availability from microbial action, or other soil changes caused by pot culture in the seedling experiment (see Kachi and Hirose, 1983).

Native and exotic plant species richness, and plant cover, reached a unimodal peak in the second zone (Zone B; upper beach). This generally corresponds to the development of a foredune ridge, as well as the peak in soil fertility indicated by the highest amount of total carbon and total nitrogen. The unimodal peak in soil carbon and nitrogen on the beach ridge is likely caused by the conversion and internal cycling of inorganic soil nutrients into organic constituents by plant growth and decomposition (Tamm, 1991; Gerlach *et al.*, 1994). The internal feedback between biotic and abiotic processes appear to lead to nutrient enrichment, and ultimately, increased species richness. Other

factors, such as the role of mycorrhizal fungi in releasing nutrients that are associated with sand grains, may also be important in increasing the rate of nutrient enrichment in this zone (Jehne and Thompson, 1981; Cain *et al.*, 1999). Similarly, the increase in organic matter in the beach ridge may improve water holding capacity compared to the lower beach or dunes.

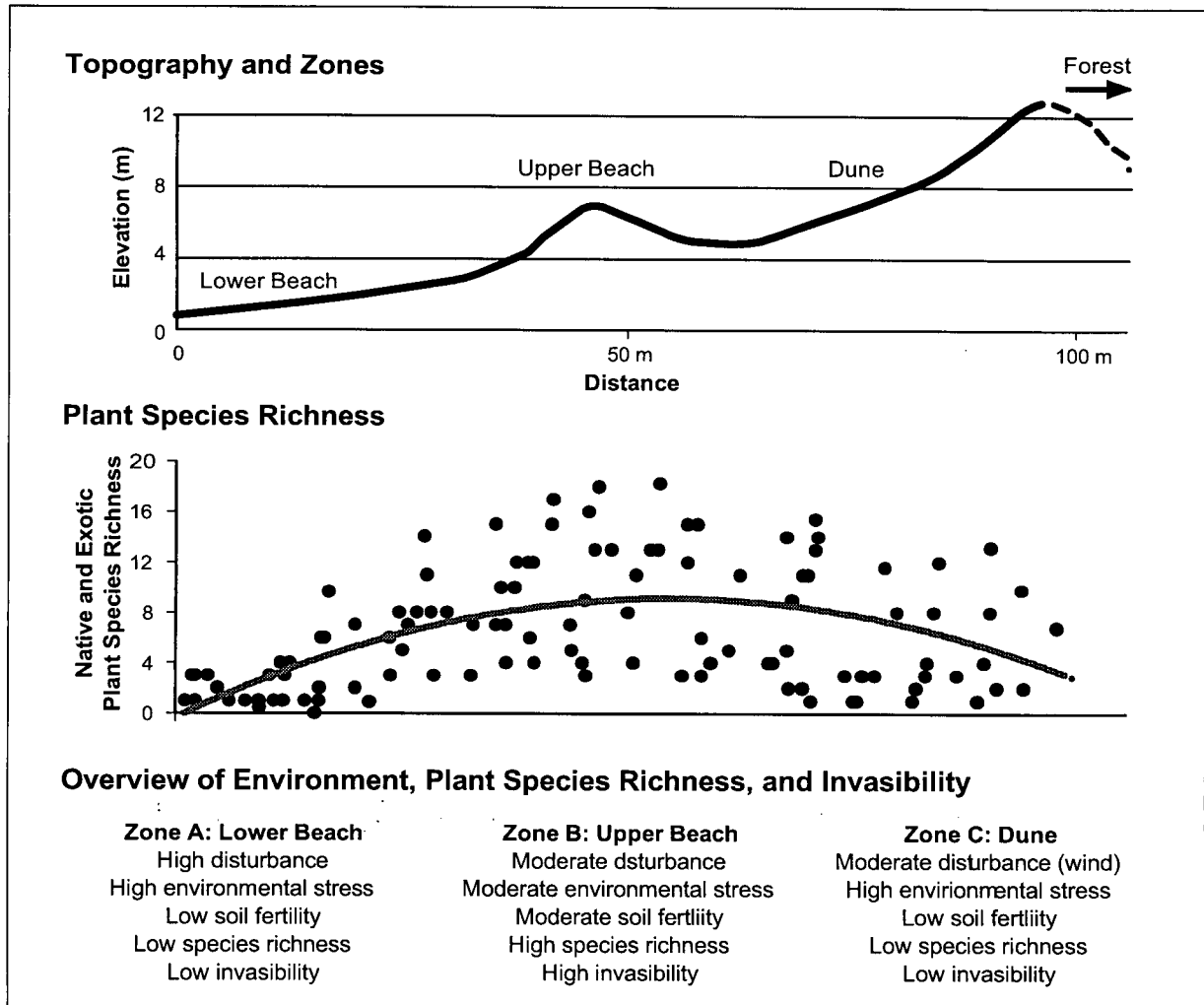


Figure 3.9. Schematic of topography, environmental conditions, and plant species richness in lower beach, upper beach, and dune zones in sand beaches.

The last third of the spatial gradient (Zone C; dune) is more difficult to interpret ecologically. Plant species richness and plant cover clearly declined landward of the upper beach. However, it is unclear if low species richness and low total foliar cover in this zone is caused primarily by nutrient decline, related soil fertility changes accompanying soil development, or other factors such as wind

disturbance or low soil moisture. Nutrients in sandy soils are impoverished by long-term soil development processes (Salisbury, 1925; Walker *et al.*, 1981; Sevink, 1991; Verhoeven, 2002). Over time, calcium carbonate, nitrate, and organic constituents are lost from surface horizons because of precipitation-induced soil weathering and leaching (Salisbury, 1925; Walker *et al.*, 1981; Kellman and Roulet, 1990). Walker *et al.* (1981) referred to this as “nutrient leakage” and documented phosphorous and calcium enrichment of lower soil horizons in Australian dune soils as surface concentrations declined. The high annual precipitation on western Vancouver Island (>2500 mm/annually) likely accelerates leaching.

The seedling test results indicated that soil chemistry factors limit plant establishment and growth in open dunes; seedlings grown in soil from dune plots generally grew poorly despite adequate moisture and stable conditions under controlled conditions. Interestingly, soil analysis found that the pH of soils of the species-poor open dunes is not more acidic than soils of the more species-rich upper beach. Several other points support the hypothesis that low nutrient availability reduces species richness in the open dunes. Nutrient enrichment in western Europe from atmospheric nitrogen deposition causes the development of grass-dominated meadows in areas that were previously sparsely vegetated open dunes (Gerlach, 1993; Veer, 1997). Similarly, dunes of the Pacific Coast are rapidly affected by *Cytisus scoparius* and *Lupinus arboreus* which use nitrogen-fixation to overcome nutrient limitations of dune soils (Christy *et al.*, 2001). Kachi and Hirose (1983) also found that nitrogen was the most important nutrient controlling plant development in beaches.

Management Implications

As both this chapter and Chapter 2 have shown, beaches support distinctive plant communities that are adapted to unique environmental conditions that occur along a narrow spatial gradient along marine shorelines. Not coincidentally, beaches support plant communities and species that are regionally rare. Protecting beach plant communities will require that information on ecological processes is incorporated into management decisions. Three general results from this chapter may be useful for guiding management.

First, exotic plant species are common in beaches and most are found on the beach ridge which also supports the highest diversity of native species. While this study has emphasized importance of environmental factors in controlling the location of invasion in beach plant communities, the influx of new species from marine-, wind- and anthropogenic transport is also likely important in controlling the overall pool of exotic species.

Second, results from this study suggest that only at the highest levels of total plant cover does plant species richness decline. This indicates that although exotic species can reduce the richness of native species in some plant communities, it is uncommon in sparsely vegetated beach plant communities. However, lack of strong competition in beach plant communities may make them susceptible to exotic species invasion because resources are frequently available to new species.

Third, while sand beaches can be considered infertile environments, native and exotic plant species richness is associated with sites with the highest soil carbon and nitrogen. Anthropogenic inputs of nutrient resources such as atmospheric nutrient deposition or the introduction of nitrogen-fixing exotic species such as *Cytisus scoparius* and *Lupinus arboreus* could cause systemic changes in diversity patterns in beach plant communities. Atmospheric nitrogen deposition is a critical problem in some dune systems in western Europe (Gerlach, 1993; Veer, 1997), although there is no indication that it is a problem on the west side of Vancouver Island. Dunes may be particularly susceptible to changes in soil nutrients. Dune plant species have unique adaptations to the ecologically stressful conditions in the open dunes and more conservation efforts should focus on maintaining unique nutrient poor, open sand conditions.

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CHAPTER 4

DO NATIVE AND EXOTIC PLANTS HAVE DIFFERENT DISTRIBUTION-ABUNDANCE RELATIONSHIPS IN REGIONAL PATCH NETWORKS?

INTRODUCTION

Exotic species invasion is a process of spatial expansion that occurs at both local and regional scales (Forcella, 1985; Higgins and Richardson, 1996; Hastings, 1996; Shigesada and Kawasaki, 1997; With, 2002). While most current research in invasion ecology emphasizes processes and patterns occurring at small spatial scales (e.g., Tilman, 1997; Stohlgren *et al.*, 1999; Levine, 2000; Naeem *et al.*, 2000; Kolb *et al.*, 2002; and see Chapter 3), regional scale analyses may be useful for uncovering generalizations about invasion dynamics, identifying potentially damaging exotic species early in the invasion process, and developing monitoring strategies. Regional-scale patterns may also be valuable as a link between practical aspects of exotic species invasion and ecological theory (Gaston, 1999).

The ecological effect of an exotic species is related to three factors¹: regional distribution, local abundance, and species-specific impact (Parker *et al.*, 1999; Williamson, 2000). Species that are regionally common and locally abundant are generally more ecologically damaging than species that are regionally rare and locally sparse. This relationship assumes that abundant species have a proportionately larger effect on ecosystem structure and processes through their monopolization of physical resources or energy (Peters, 1983; Brown and Maurer, 1986; Brown, 1995). A fundamental aspect of this relationship is that a species' regional distribution and its local population size are not independent; as local abundance increases it is generally accompanied by an increase in the number of sites in which the species is found within a region (Hanski, 1982; Brown, 1984; Hanski and Gyllenberg, 1997; Maurer, 1990; Gaston, 1996). The relationship between regional distribution and local abundance is generally positive and linear, and it has been observed in a broad range of studies on such disparate taxa as intestinal parasites in waterfowl, grassland plants in prairies, bryophytes on downed logs, beetles in dung, fish in rivers, and moths on islands (see summary in Gaston (1996), and Scheiner and Rey-Benayas (1997) for plants). Indeed, it has been argued that the positive distribution-abundance relationship is one of the few statistical generalizations on which ecology can be based (Hanski, 1982; Shrader-Frechette and McCoy, 1993; Brown, 1995; Gaston *et al.*, 2000).

¹ This was summarized as the equation $I = R \cdot A \cdot E$ where I is impact, R is regional distribution, A is local abundance, and E is per-biomass or per individual effect (Parker *et al.*, 1999). It has been called the Lonsdale equation (Williamson, 2000).

To examine regional-scale patterns of exotic species invasion, I tested for differences in distribution–abundance relationships for native and exotic plant species from eight regional networks of patchy plant communities in North America. I asked two questions: 1) Are there differences in the distribution–abundance relationship between native and exotic plants in regional patch networks?; 2) Do patch occupancy patterns differ between native and exotic plant species within regional patch networks? I hypothesized that exotic species would be more common and more regionally abundant than native species. This was based on the idea, which underlies much invasion ecology research, that the competitive and dispersal abilities of many exotic species allow them to rapidly establish, both locally and regionally, in new environments (Baker 1965; Crawley, 1986; Noble 1989; Cadotte and Lovett-Doust, 2001; Blossey and Notzold, 1995; Rejmanek and Richardson, 1996; Wolfe, 2002; Mitchell and Power, 2003). For both questions, I tested the null hypothesis that exotic and native had equal distribution–abundance and patch occupancy relationships ($H_0: u_o = u_i$).

METHODS

Data from eight regional networks of herbaceous terrestrial and wetland plant communities in North America were used for analysis. All eight plant communities were considered spatially patchy and consisted of between twelve and twenty-two patches within a region. Datasets were selected based on comparability of sampling methods across the region, richness of exotic plants, and data accessibility. Summary information on sampling methods is provided with references to additional published or unpublished information on sampling design and plant community structure and composition. The regional patch networks varied greatly in size. For analysis and presentation, they are arranged by size, from largest to smallest, of the maximum size of the region sampled (i.e., greatest distance between patches). For each dataset exotic and native species were distinguished based on information provided in the original study descriptions or by consulting regional floras. Some species were grouped because of taxonomic uncertainty and are treated in the analyses as a single taxon. Cryptogenic species (i.e., species with both morphologically indistinguishable native and exotic taxa such as *Prunella vulgaris* and *Achillea millefolium* (Carlton, 1996)) or species whose origin was unclear were removed from analysis.

Summary of Datasets

North Pacific Beaches – I used vegetation data from eighteen sand beach communities on the west coast of Vancouver Island, British Columbia that were collected to examine local and regional patterns of exotic species invasion. Composition and plant cover estimates were obtained from 850

randomly sited 4 m² plots in 2001. Plots were located on transects perpendicular to the shoreline and extended from the shoreline to the forest edge. More detail on sampling methods, sites, and plant community structure is found in Chapter 2 (*Description and Classification of Plant Associations in Sand Beaches of the West Coast of Vancouver Island*).

Georgia Basin Estuaries – Estuarine marsh vegetation was sampled at seventeen river deltas in the Georgia Basin region of British Columbia and Washington State in 1985 (see Hutchinson, 1988). Plant species composition and plant cover was recorded in 2 m² plots randomly located along transects arranged perpendicular to the shoreline. The number of plots per site was proportional to the transect length and a total of 905 plots were sampled. Sampling methods and information on plant communities composition is found in Hutchinson (1988).

Alberta Fescue Grasslands – Plant communities in eleven remnant, uncultivated fescue grasslands in the Aspen Parkland region of south central Alberta were sampled by K. Vujnovic to evaluate patterns of species composition in 1996 (Vujnovic and Wein, 1997). Species composition and percent foliar cover of vascular plants and bryophytes was estimated in approximately 40 randomly selected 1 m² plots in each grassland patch. More information on sampling methods and plant community composition is found in Vujnovic *et al.*, 2000, 2002.

Wisconsin Oak Savanna – Species rich grasslands in twelve remnant oak savannas in southern Wisconsin were sampled by Leach and Givnish (1999) to examine gradients in plant community composition, structure, and diversity. Patch area varied from 1 to 6 hectares. Data consisted of species composition and plant cover estimates in 722 1 m² plots. The number of plots varied between 50 and 100 per patch. A summary of sampling methods and other information on plant community structure is found in Leach and Givnish (1999).

Puget Sound Freshwater Wetlands – Plant communities were sampled at nineteen freshwater wetlands in the Puget Sound region of Washington State as part of a study of effects of urbanization on wetland ecology (see Cooke and Azous, 1997). Plant community composition and foliar cover were estimated in permanent 19.5 m² circular plots adjacent to linear transects. Transects were established across the hydrologic gradient of each wetland and typically encompassed a margin of forested hydrophytic vegetation with emergent shrub and marsh communities near the centre of the wetland. Only data from 1995 were used for this analysis. More information is found in Azous and Horner (2000).

Vancouver Island Grasslands – Twelve small grasslands (0.5 to 2 ha) in the Georgia Basin region of British Columbia were sampled by H. Roemer between 1995 and 2000 using subjectively distributed 2 m² plots. The number of plots ranged from four to thirteen per patch. Grasslands were selected based on their native plant diversity and it is important to note that they do not include communities that have been extensively modified by exotic species. Data consisted of composition and foliar cover estimates. The data are unpublished.

Columbia Plateau Vernal Pools – Plant communities in twenty vernal pools in the Columbia Plateau region of Washington State were sampled in 1997. Vernal pools are seasonal wetlands with winter inundation and summer desiccation. Vegetation data consisted of estimates of composition and foliar cover in four distinct zonal plant communities in each pool. Plot size was highly variable. Unpublished data were provided by C. Randall.

Kansas Tallgrass Prairie – Tallgrass prairie plant communities have been sampled annually at Konza Prairie Research Natural Area in northeastern Kansas as part of ecological monitoring research (LTER site). Plant community data were collected in small watersheds using twenty permanent plots (10 m²) on transects in upland soils. Composition data from twenty-two watersheds from 2000 were used for analysis. Plant communities in the Konza Prairie have been used extensively to examine distribution–abundance patterns and background information on sampling methods and other aspects of this research is available in Gotelli and Simberloff (1987), Collins and Glenn (1990; 1991), Smith and Knapp (2001), and Collins *et al.* (2002).

Regional Distribution: Patches and Patch Occupancy

Patch occupancy is a measure of regional distribution for species in patchy habitats. Patch occupancy is the number of patches or sites in which a species is present relative to the total number of patches in the network. It can be expressed as an absolute number of patches occupied by a species or, as I have used for this study, as the proportion (or percentage) of the total number of patches in a region in which a species is found. Compared to other measures of regional distribution that have been used in macroecology (e.g., range size), patch occupancy has the advantage of providing a discrete measure of the relative number of rare and common species in a region (He and Gaston, 2000; Maurer, 1990). Because many species are distributed in patchy habitats, patch occupancy is also a

useful dimension for modelling metapopulation or other dynamic population structures (Hanski, 1994; Hanski, 1998; Wu and Levin, 1997).

I defined a *patch* as a single, spatially discrete and contiguous area of similar vegetation, and a *patch network* as a group of similar patches within a broad region. Patches are analogous to islands and patch networks to archipelagos (Figure 4.1). The area between patches is called the *matrix*. While the matrix may share some of the characteristics and species with the patch, differences in species composition are generally distinct. Most of the plant community datasets described in the preceding section are either herbaceous-dominated communities surrounded by a matrix of forest, or wetlands in a matrix of terrestrial communities. The Konza prairie data are different in that the patches are watersheds, whose boundaries are defined topographically rather than by plant community differences (Collins and Glenn, 1990).

The analysis of patch occupancy patterns has resulted in the development of terms for different distribution classes (see Olff and Bakker, 1998). I use the terms *satellite* and *core* to denote species in the left and right patch occupancy classes. Species found in less than 10% of patches in a patch network were considered *satellite species*, while *core species* were found in greater than 90% of patches. These terms and definitions were proposed by Hanski (1982) and have become commonly used in macroecological studies (see Olff and Bakker, 1998). I refer to the pattern of increased occupancy in both core and satellite classes as *core-satellite modality*.

Local Abundance

The local abundance of a species is the average population size in the patches in which it is present (Hanski *et al.*, 1993; Blackburn and Gaston, 1998). It can be measured directly as the number of individuals in the local population, or indirectly using indicators such as the area it occupies in a patch. I used the mean frequency that a species was counted in plots as an estimate of local abundance. Mean plot frequency was determined as the number of plots in which a species was found in each patch divided by the number of patches in which the species was present in at least one plot (see Figure 4.1 for hypothetical example). This definition of local abundance avoids the problem of artificially inflating regional rarity by including unoccupied patches in the calculations (Wright, 1991). Percentage frequency was \log_{10} transformed for analysis.

I recognize the weakness inherent in the using data collected in different types and numbers of

communities, using different sampling methods (particularly different plot sizes), and during different time periods. To improve comparability between the datasets, I used frequency as both a measure of local abundance (i.e., frequency at which species were encountered in plots). This removes the observer bias introduced by different methods of plant cover estimation in the different datasets. As well, plant cover has been found to be a poor measure of local abundance in previous distribution–abundance research on plant communities (Hanski *et al.*, 1993). This is likely caused by clonal growth of some plant species which increases their disproportional contribution to cover estimates without increasing the number of individuals. There is a large variation in size of individuals in plants that is unrelated to the abundance in terms of number of individuals.

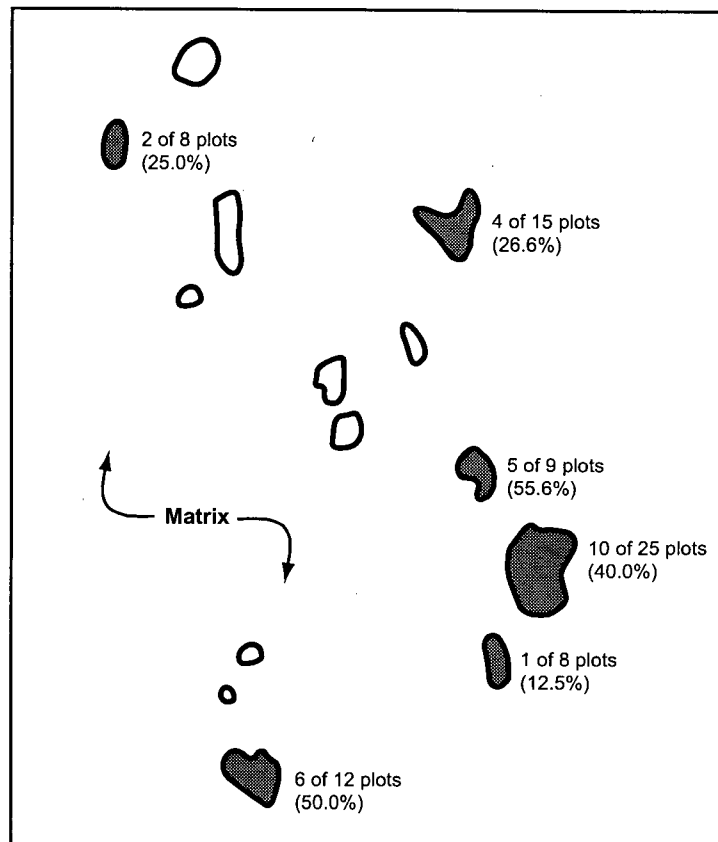


Figure 4.1. Hypothetical regional patch network of a patchy plant community. Species A is found in 6 out of 14 patches in the network (denoted in grey tone). The average local abundance is the mean number of plots (in percent) in which the species was found over the six patches. The patch occupancy for Species A is 0.43 and the mean local abundance is 35.0%.

Statistical Analyses

Ordinary least squares linear regression was used to determine the significance of the relationship between regional distribution (i.e., proportion of patches occupied) and local abundance (i.e., \log_{10} of mean percentage frequency of species occurrence in patches occupied) for all species, and for native and exotic species groups. The coincidence of regression relationships (i.e., same slope and intercept) for native and exotic species groups was tested using a partial F-test (Kleinbaum *et al.*, 1988). The F-test is considered robust in cases of non-normality and heterogeneous variance. Both are inherent

properties of distribution-abundance relationships (i.e., more species at lower occupancy classes) (Blackburn and Gaston, 1998; Williamson and Gaston, 1999).

Differences in patch occupancy patterns for native and exotic species were tested using a Chi-squared test. The null hypothesis was that patch occupancy is the same between native and exotic species. This is analogous to the Chi-square test to evaluate independence of two discrete distributions. The Chi-squared test is considered robust in cases where the high frequency of small cell values in many of the frequency classes (Upton, 1982; D'Agostini *et al.*, 1988). For all analyses, patch occupancy classes were amalgamated into five classes: species occupying between 0 and 0.2 of patches, 0.2 to 0.4, ..., etc, to increase predicted cell values (Zar, 1984).

All statistical tests were undertaken in S-Plus 6.0 for Windows and graphing was done using Sigmaplot 5.0. I used $P < 0.05$ as the significance level for all tests.

RESULTS

Total plant species richness and the number and percentage of exotic species was extremely variable in patch networks (Table 4.1). The number of patches sampled, the total number of plots, and the maximum distance between patches (an indicator of the spatial extent of the region) is also provided in Table 4.1. The maximum total plant species richness was 471 species in the Wisconsin oak savanna patch network while Georgia Basin estuaries had only 83 plant species. Wisconsin oak savannas also had the most exotic species (60 species), although the highest proportion of exotic species was 28% on North Pacific beaches. Kansas tall grass prairies had substantially fewer exotic species both in absolute terms (7 species) and by percentage contribution to total species richness (5%).

Table 4.1. Summary information on plant community patch networks including total number of patches, total number of plots, maximum distance between the patches in the network, number of native plant species, number of exotic plant species, and total number of plant species.

Plant Community	No. of Patches	No. of Plots	Max. Distance ¹	Native Species	Exotic Species	Total Species
North Pacific Beaches	18	855	400 km	118 (72%)	45 (28%)	163
Georgia Basin Estuaries	17	901	375 km	64 (77%)	19 (23%)	83
Alberta Grasslands	11	490	220 km	175 (85%)	30 (15%)	205
Wisconsin Oak Savanna	12	722	175 km	411 (87%)	60 (13%)	471
Puget Sound Wetlands	19	150	60 km	130 (82%)	28 (18%)	158
Vancouver Is. Grasslands	12	84	60 km	134 (77%)	39 (23%)	173
Columbia Vernal Pools	20	80	8 km	146 (89%)	18 (11%)	164
Kansas Tallgrass Prairie	22	440	4 km	146 (95%)	7 (5%)	153

¹ The maximum distance between patches in the network as an indicator of the spatial extent of the region sampled. Mean values were difficult to calculate because of the lack of spatial coordinates from some datasets.

The size of the regional patch networks were also variable. Based on the maximum distance between patches, they ranged from a maximum of 4 km apart for the Kansas tallgrass prairie dataset to 400 km apart for beaches from the North Pacific coast.

All components of species richness (total, native, and exotic) showed significant positive linear relationships between regional distribution and local abundance (Figure 4.2 and Table 4.2). The variance explained by the linear models for all species (native and exotic species combined) was moderate (r^2 range: 0.17–0.68; mean: 0.39) which is characteristic of distribution–abundance relationships. Gaston (1996) found that the median variance explained in eighty-nine distribution–abundance relationships was 20 to 30%. Co-efficients of determination were slightly higher for native species (r^2 range: 0.15–0.69; mean: 0.41) than for exotic species (r^2 range: 0.25–0.69; mean: 0.36).

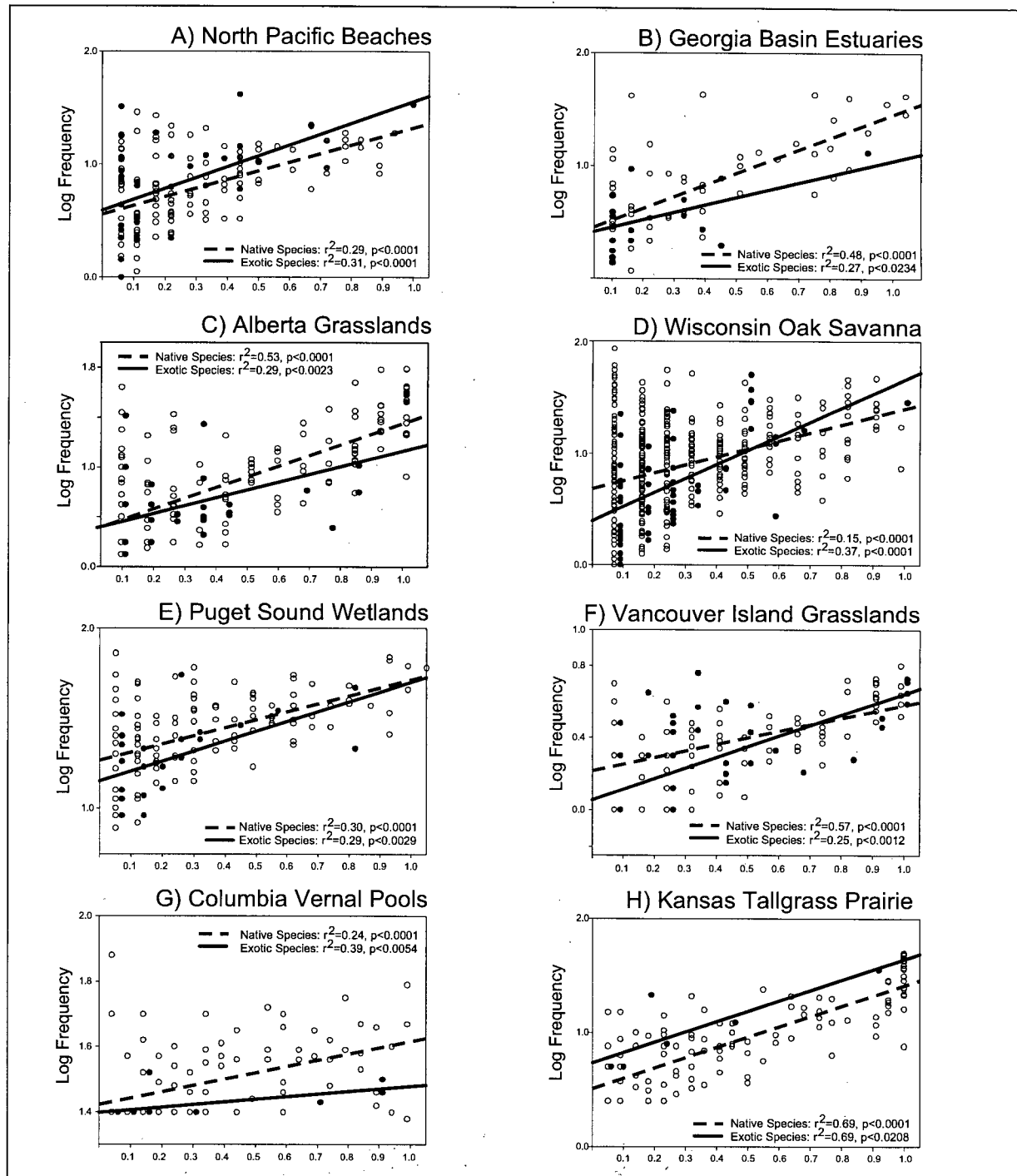


Figure 4.2. Linear regression relationships for regional distribution-local abundance relationships for exotic and native plant species in regional patch networks. Abundance is measured as log₁₀ transformed mean frequency. Regional distribution is measured as proportional patch occupancy. Exotic species are shown with solid tone circles and solid lines; native species are shown with open circles and dashed lines. The significance and r² values of each line are noted.

Table 4.2. Regression coefficients and significance levels for linear relationships between local abundance and regional distribution for total species richness, native species richness, and exotic species richness in plant community patch networks.

Plant Community	Species Component	N	r^2	b_0	b_1	Significance of Model
North Pacific Beaches	Total	163	0.28	0.574 ^A	0.793 ^A	<0.0001
	Native	118	0.29	0.559 ^A	0.767 ^A	<0.0001
	Exotic	45	0.31	0.594 ^A	0.963 ^A	<0.0001
Georgia Basin Estuaries	Total	83	0.47	0.438 ^A	1.018 ^A	<0.0001
	Native	64	0.48	0.459 ^A	1.035 ^A	<0.0001
	Exotic	19	0.27	0.420 ^A	0.654 ^D	0.0234
Alberta Grasslands	Total	205	0.50	0.500 ^A	0.864 ^A	<0.0001
	Native	175	0.53	0.502 ^A	0.885 ^A	<0.0001
	Exotic	30	0.29	0.513 ^A	0.649 ^C	0.0023
Wisconsin Oak Savanna	Total	471	0.17	0.639 ^A	0.785 ^A	<0.0001
	Native	411	0.15	0.672 ^A	0.722 ^A	<0.0001
	Exotic	60	0.37	0.408 ^A	1.264 ^A	<0.0001
Puget Sound Wetlands	Total	158	0.32	1.237 ^A	0.480 ^A	<0.0001
	Native	130	0.30	1.261 ^A	0.447 ^A	<0.0001
	Exotic	28	0.29	1.156 ^A	0.549 ^A	<0.0001
Vancouver Is. Grasslands	Total	167	0.49	0.084 ^B	0.544 ^A	<0.0001
	Native	128	0.57	0.049 ^D	0.589 ^A	<0.0001
	Exotic	39	0.25	0.219 ^B	0.367 ^C	0.0012
Columbia Vernal Pools	Total	164	0.24	1.419 ^A	0.183 ^A	<0.0001
	Native	146	0.24	1.421 ^A	0.192 ^A	<0.0001
	Exotic	18	0.39	1.400 ^A	0.079 ^C	0.0054
Kansas Tall Grass Prairie	Total	151	0.68	0.523 ^A	0.895 ^A	<0.0001
	Native	144	0.69	0.508 ^A	0.906 ^A	<0.0001
	Exotic	7	0.69	0.740 ^C	0.911 ^D	0.0208

A. $p < 0.0001$; B. $p < 0.001$; C. $p < 0.01$; D. $p < 0.05$; E. not significant

Tests of coincidence between the distribution–abundance relationship for native and exotic components of species richness were more variable (Table 4.3). Four datasets (North Pacific Beaches, Georgia Basin Estuaries, Alberta Grasslands, Puget Sound Wetlands) showed statistically significant coincidence of regression relationships, while other remaining datasets (Wisconsin Oak Savanna, Vancouver Island Grasslands, Columbia Vernal Pools, Kansas Tall Grass Prairie) rejected coincidence. However, there was no general pattern of test rejection (e.g., regression lines with different intercepts, higher or lower slopes).

Table 4.3. Results of F-tests of the coincidence of regression relationships of distribution–abundance relationships for native and exotic species components. Coincidence was rejected if the p-values was less than 0.05. Rejection of the hypothesis is indicated with underlined values.

Plant Community	k, DF	SS _{reduced}	SS _{combined}	MS _{combined}	F-value	P
North Pacific Beaches	2, 158	5.93	6.21	0.09	1.47	0.2340
Georgia Basin Estuaries	2, 78	6.58	6.87	0.09	1.65	0.1987
Alberta Grasslands	2, 200	16.32	16.57	0.079	1.58	0.2085
Wisconsin Oak Savanna	2, 466	13.98	15.52	0.14	5.40	<u>0.0048</u>
Puget Sound Wetlands	2, 153	2.53	2.70	0.03	2.38	0.0959
Vancouver Is. Grasslands	2, 162	4.61	4.94	0.03	6.01	<u>0.0031</u>
Columbia Vernal Pools	2, 159	0.43	0.48	0.01	3.27	<u>0.0405</u>
Kansas Tall Grass Prairie	2, 146	15.29	15.65	0.05	3.90	<u>0.0223</u>

None of the contingency table tests between patch occupancy distributions rejected the null hypothesis that exotic and native species have the same statistical distribution (Figure 4.3 and Table 4.4). Another way of interpreting this is that exotic and native species are not independent in their distribution in regional patch networks.

Table 4.4. Chi-squared test results for differences in patch occupancy distributions between native (N) and exotic (E) in regional patch networks.

Plant Community		Patch Occupancy Class					χ ²	P ¹
Native (N) or Exotic (E)		0.0-0.2	0.2-0.4	0.4-0.6	0.6-0.8	0.8-1.0		
North Pacific Beaches	N	56	30	16	9	6	3.782	0.4363
	E	29	7	6	3	1		
Georgia Basin Estuaries	N	33	13	5	7	6	3.407	0.4922
	E	13	3	2	0	1		
Alberta Grasslands	N	81	22	24	10	39	4.112	0.3911
	E	13	8	3	2	5		
Wisconsin Oak Savanna	N	228	79	64	20	20	3.105	0.5403
	E	33	14	11	1	1		
Puget Sound Wetlands	N	64	24	17	14	11	5.265	0.2612
	E	19	5	2	0	2		
Vancouver Is Grasslands	N	56	24	15	14	19	5.992	0.1997
	E	11	11	8	2	7		
Columbia Vernal Pools	N	80	30	12	13	11	5.331	0.2550
	E	14	1	0	1	2		
Kansas Tall Grass Prairie	N	60	22	17	12	33	1.220	0.8748
	E	4	1	1	0	1		

¹ Four degrees of freedom for all tests.

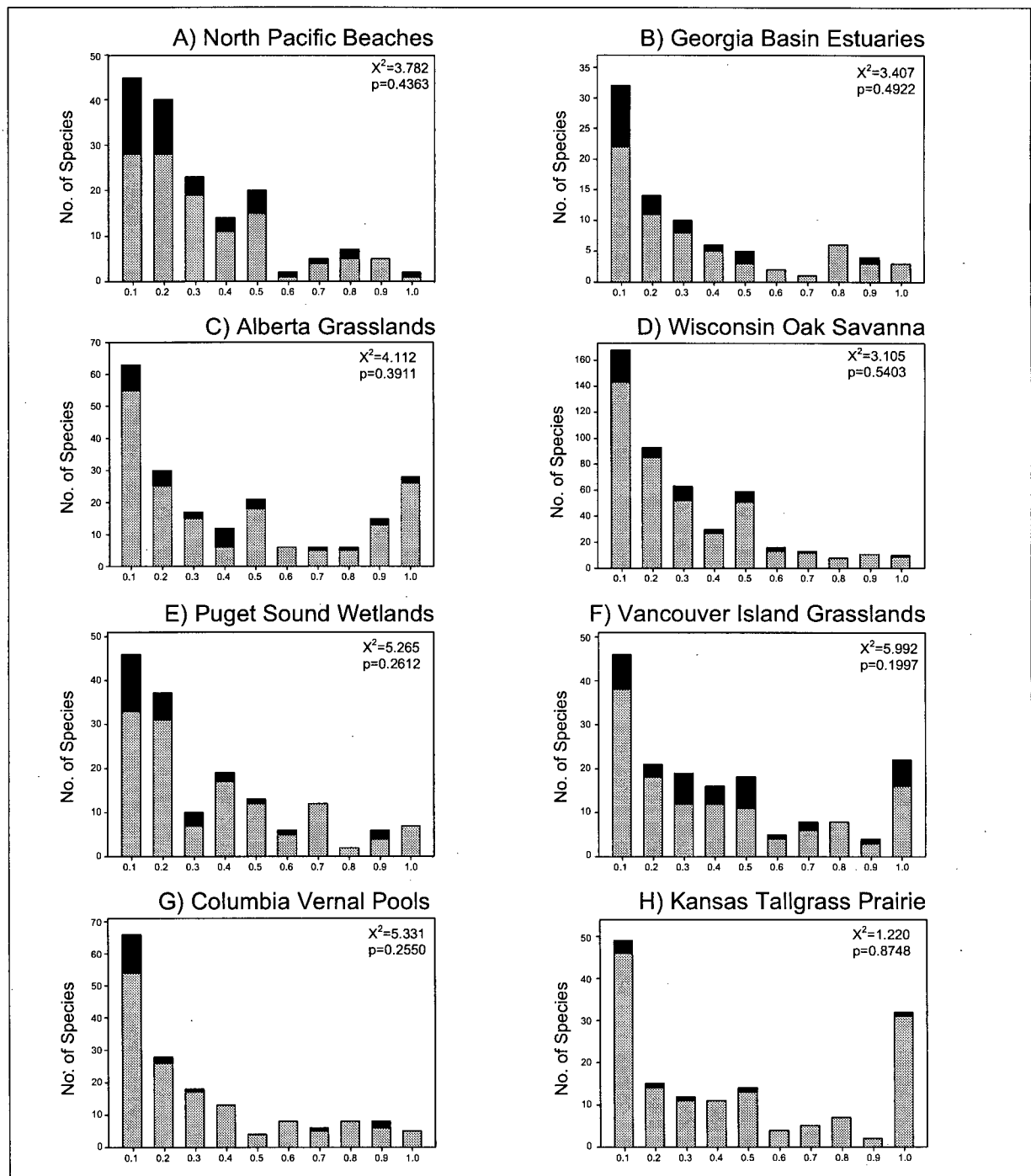


Figure 4.3. Patch occupancy relationships for exotic and native plant species in regional patch networks. Patch occupancy is expressed as the proportion of occupied patches in the region. Exotic species are shown in solid tone and native species are shown in grey tone. No significant differences between native and exotic distributions were detected using Chi-square test on amalgamated patch occupancy classes (0-0.2, 0.2-0.4, etc.). Chi-square values are shown.

DISCUSSION

The null hypothesis that exotic and native plant species have statistically equal patch occupancy and distribution–abundance relationships was not rejected. Native and exotic plant species have similar, or statistically equal, regional distribution–local abundance relationships in regional patch networks. For four plant communities where partial F-tests indicated the distribution–abundance relationship was not statistically coincident, the causes of rejection varied, and no general pattern was apparent. There are few studies to which these results can be compared. Holt and Gaston (2003) recently found that mean abundance and the number of sites occupied was not significantly different between native and exotic bird species in Britain.

The proportions of native and exotic species in patch occupancy classes were statistically equal in all regional patch networks. Most native and exotic species were rare and locally sparse in regional patch networks, and, antithetically, few species were regionally common and locally abundant. This pattern suggests that patch occupancy patterns are not constrained by population dynamics. If population dynamics were a strong force in structuring distribution patterns in regional patch networks, exotic species would be expected to be disproportionately less common than native species. Exotic species have small population sizes when they initially establish which should limit their ability to colonize new patches. While core-satellite modality patterns were not formally tested in this study, visual assessments of patch occupancy patterns do not support the hypothesis that regional commonness is reinforced through population dynamics in patch networks (e.g., *rescue effect*: Gotelli (1991)). In contrast to what metapopulation theory would predict, exotic species which are new to the region with few, small populations initially, have similar distribution–abundance patterns as native species.

Spatial scale is important for understanding regional distribution–abundance relationships and most studies of regional patterns assume that patches within a region are environmentally similar (Hanski, 1982; Brown, 1984; Maurer, 1990). However, this is a difficult assumption to test. Some studies have used very small spatial scales to minimize environmental differences (e.g., they predict that sites closer together are more likely to be environmentally similar and are more likely to exchange individuals than larger regions). In particular, the spatial extent of the regional patch networks may influence the prevalence of core-satellite modality by reducing or preventing the movement of individuals between patches or decreasing the environmental comparability of patches (Tokeshi, 1992; Scheiner and Rey-Benayas, 1997; van Rensburg *et al.*, 2000). The data in this study indicate that the incidence of core-satellite modality decreases with the size of the region sampled. Of three

datasets that appear to have a peak of species richness at both core and satellite modes, two were sampled from patch networks that were relatively small (4 km was the largest distance between patches in the Konza dataset and 60 km was the largest distance between patches in the Vancouver Island grasslands dataset). The Alberta grasslands dataset was the only patch network from a large region (220 km maximum distance) that appeared to have core-satellite modality. Van Rensburg *et al.* (2000) also found that the frequency of bimodal patterns decreased with increasing spatial extent.

Collectively, the results indicate that the distribution and abundance of native and exotic plant species are not independent in regional patch networks. Exotic plant species do not distinguish themselves from native species in terms of abundance, commonness, or other regional patterns. Indeed, the broadest conclusion from this study is that exotic species appear to share the breadth of life history strategies and competitive abilities that characterize the assemblage of native species in a region. Nature, it would seem, does not make distinctions between exotic and native species. Exotic species reinforce rather than degrade established distribution–abundance and patch occupancy patterns in plant communities. It is important to point out that these conclusions rely on the assumption that exotic species have not already changed the local abundance or regional distribution of native species in the communities studied. This assumption is impossible to test without temporal data.

Management Implications

One of the most useful aspects of this study is that it has clearly established a link between regional distribution and local abundance of exotic plant species. Based on this relationship, high local abundance is an indicator of regional invasion potential, and similarly, widespread regional distribution is an indicator of potential local abundance. This finding is similar to recent studies that have established the converse relationship between local population decline and range contraction (Conrad *et al.*, 2001; Rodriguez, 2002), and the predictive ability of distribution data in assessing local population size in plants (He and Gaston, 2000). It also compliments the correlation between final range size and the rate of spread in exotic plants (Forcella, 1985).

Two monitoring strategies for exotic species may be devised based on the results of this study. First, incidents of high local abundance are cause for concern because exotic species that form large populations at the initial sites in which they establish are of generally higher risk for regional invasion than species with low or diffuse initial populations. Early warning systems that target infestations of exotic species when they are confined locally may be particularly effective in slowing

or preventing invasion (Moody and Mack, 1988; Westbrooks, 2001; see Wadsworth *et al.*, 2000 for converse view). This monitoring and assessment strategy is often done intuitively for exotic species but the distribution–abundance relationship provides a stronger ecological basis for its application.

Regional monitoring networks or simple distribution mapping may also be useful for flagging species with potentially high ecosystem effects without detailed monitoring of specific communities.

However, the effectiveness of regional monitoring strategies deteriorates when problematic invasive species are identified too late in the invasion process to be useful for management and control.

Regional monitoring is effective in identifying rapidly spreading exotic species.

A monitoring strategy that combines both local and regional monitoring may be particularly effective in identifying invasive exotic species before they become widespread in a region. Local abundance of native and exotic species should be monitored in a variety of similar sites in a region over time to provide specific information on the relative distribution and abundance of native and exotic species, as well as providing information on the rate of exotic species invasion and native species decline.

This monitoring strategy requires the use of fixed plots in 10 to 15 comparable sites within a region. Assessment should be undertaken annually at the same time of year and with well-defined sampling methods for percent cover estimates or presence-absence counts.

Based on the generalisation that the impact is proportional to regional distribution and local abundance (Parker *et al.*, 1999), the results of my study quantitatively show that within the total group of exotic species introduced into a region, there is a small subset of species that are both widespread and abundant. Figure 4.4 subdivides the exotic species based on their position in four zones in the distribution–abundance relationship: 1) rare, sparse species with low invasion potential; 2) common, sparse species with low ecological impact; 3) rare, abundant species with increased risk of invasion; and, 4) common, abundant species with high ecological impact. The final two groups of species could be amalgamated as *invasive or potentially invasive exotic species*, while the former two groups could be called *innocuous exotic species*. Two points are important in using this classification. First, the thresholds between groups are arbitrary and exotic species occur on a gradient of distribution and abundance. Second, exotic species are expected to change their position over time as their regional distribution, local abundance, or both, change. Temporal monitoring, as discussed above, will be critical for the identification of species with the highest invasion potential.

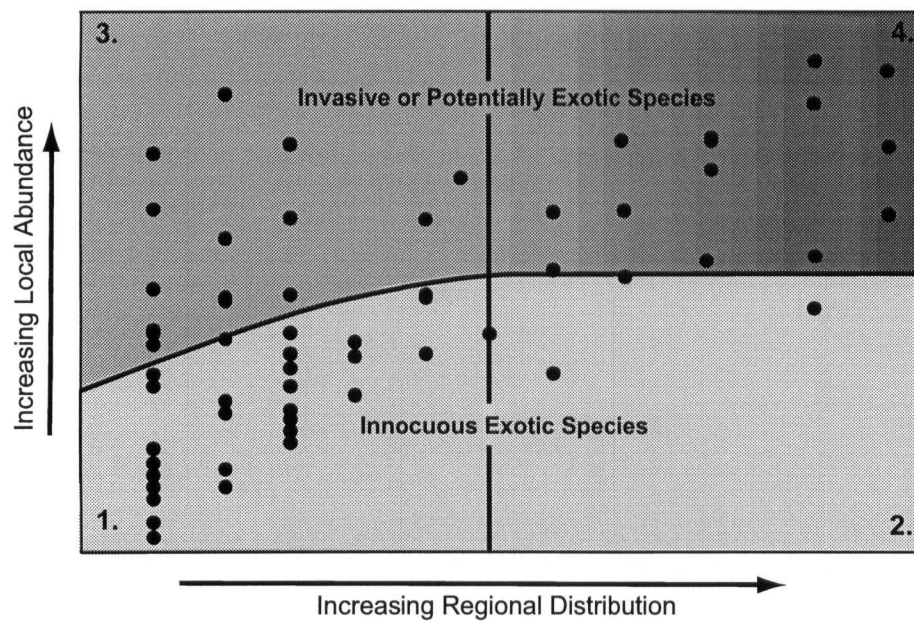


Figure 4.4. Schematic representation of four general patterns of exotic species invasion based on their distribution–abundance relationship: 1) rare, sparse species with low invasion potential; 2) common, sparse species with low ecological impact; 3) rare, abundant species with increased risk of invasion; and, 4) common, abundant species with high ecological impact.

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