Invertebrate communities and drivers of their composition on gravel beaches in New Zealand

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Published online: 17 December 2012

Abstract: Gravel beaches are discrete, irregularly separated habitats along New Zealand's coasts. They are one of a diverse range of small, disparate, naturally rare ecosystems that tend to occur in extreme environments, and provide critical habitat for threatened, rare and endemic species. New Zealand's gravel beaches are threatened by urbanisation, weeds, adjacent agriculture, introduced animals and predicted sea-level rise. We studied 51 gravel beaches distributed along the New Zealand coastline to provide primary information on invertebrate composition, habitat patterns and threatened species, and how these relate to national (climate), landscape (surrounding habitat type and human influences), and site-level (geomorphology, vegetation) factors. Invertebrate abundance was mostly driven by beach-scale factors with little influence of the surrounding landscape. However, urbanisation and the presence of exotic plants were significant drivers of invertebrate community composition. A number of observations of interest (i.e. rare species, new localities, habitat specialists, threatened species and exotic species with incursion risk) were also recovered from gravel beaches. Our results demonstrate that vegetation surveys are not necessarily adequate indicators of other biotic components of gravel beach ecosystems and suggest that further ecological assessments of gravel beaches are warranted.

Keywords: community composition; conservation; landscape context; rare ecosystem; shingle beach; spatial scale; substrate texture; surface-down invertebrates

Introduction

Worldwide and in New Zealand, gravel beaches (those that are predominantly covered by particles larger than sand but smaller than boulders; also called 'shingle beaches') are a less common coastal feature than sandy beaches. In New Zealand, they are relatively limited in natural extent and are classified as nationally rare (Williams et al. 2007). These beaches occur as discrete patches of habitat resulting from rivers delivering excess quantities of gravel to the coast, or through the erosion of nearby coastal cliffs. The combination of coarse substrate (mostly sand, water-smoothed gravel and cobbles), high disturbance (gravel mobility and redeposition) and salinity, and extremes in temperature and moisture, creates a harsh habitat that supports a unique flora and fauna (Randall 1992; Davy et al. 2001; Packham & Spiers 2001; Shardlow 2001; Vestergaard 2001; Wiser et al. 2010). Drivers of plant composition on gravel beaches are complex and include site- (e.g. substrate texture), landscape- (e.g. proximity to different land cover types) and national-scale (e.g. climate) factors (Wiser et al. 2010). There is an increasing awareness of threats to gravel beach habitats, which include impacts of human activities and introduced alien species. Globally, the plant communities of gravel beaches are beginning to be more comprehensively understood; the invertebrate fauna, however, remains poorly studied (Shardlow 2001) and is undocumented in New Zealand. We have no knowledge of the invertebrate species present on New Zealand gravel beaches, the drivers of their composition, or threats to their persistence. Without this basic understanding it is impossible to set conservation priorities and objectives adequately, or improve the management of gravel beaches to benefit invertebrate communities.

New Zealand's gravel beaches, like many coastal ecosystems, are becoming increasingly threatened by human activities (e.g. coastal development, 4WD vehicles), invasion by exotic plants (including herbs, grasses and shrubs) and animals (e.g. rabbits), and sea-level rise resulting from global warming. The surface conditions presented by gravel beaches likely select for a unique invertebrate fauna and specialist species with adaptations for tolerating environmental extremes in temperature, moisture and salinity (Morris & Parsons 1993; Shardlow 2001). The physical structure of gravel beaches, however, is spatially variable with respect to the relative abundance of fine (≤ 10 mm) and coarse (> 10 mm) substrates (see Fuller 1987), and thus offers invertebrates a latticework of subterranean microhabitats and a sheltered, more uniform microclimate than on the surface. Resident and transient thermophilic species that otherwise would only occur at lower latitudes may gain refuge in this habitat (Shardlow 2001).

Without knowledge of the invertebrate communities of New Zealand gravel beaches we are left with, at best, the assumption that the local plant communities can serve as a surrogate for invertebrate composition. While there is evidence that this assumption holds for predominantly above-ground invertebrates in grasslands (Quinn & Walgenbach 1990; Morris 2000; Foord et al. 2003; Schaffers et al. 2008), heath and heather moorland (Sanderson et al. 1995; De Bruyn et al. 2001; Hartley et al. 2003; Schaffers et al. 2008), and alluvial forests (Antvogel & Bonn 2001), it is poorly supported for invertebrates living in surface substrates or below ground (Osler et al. 2006; St.

John et al. 2006b; Wardle & Chase 2006) and untested for gravel beaches. Furthermore, rare ecosystems and ecotones, including gravel beaches, may contribute disproportionately to regional or national species pools (Shardlow 2001; Collier & Smith 2006), so their importance to biodiversity conservation cannot be assumed to be a function of the area they occupy on a landscape.

This paper provides the first overview of invertebrates on New Zealand gravel beaches. We asked two questions: which invertebrate groups are present on New Zealand gravel beaches and in what abundance, and what are the drivers of invertebrate composition on New Zealand gravel beaches? Specifically, we determine (1) the predictors of invertebrate community composition on New Zealand gravel beaches, (2) whether these predictors are the same as those for plant communities, and (3) whether or not gravel beach invertebrate communities are independent of, or co-dependent on, plant communities.

Materials and methods

Data collection

For the purpose of this study, gravel beaches were defined as those occurring inland from the foreshore (i.e. above the high-tide mark) with a substrate comprising a mixture of sand, water-smoothed gravel and cobbles, at least 50% of the top 10 cm of substrate being gravel (> 2 mm in diameter) but not boulders (> 256 mm in diameter). To identify sites, the present study relied on a geomorphological inventory of New Zealand gravel beaches (Gibb 1978), occurrences of herbarium specimens collected from coastal habitats that included the terms 'shingle' or 'gravel' in habitat descriptions, previous knowledge, local experts, and field reconnaissance to determine appropriate beaches for surveying. Sampled beaches were primarily located on open shores.

At each gravel beach locality, we randomly located small plots (1-m^2 quadrats) along transects running perpendicular to the shoreline, with the constraint that no plots were contiguous and transects were at least 10 m apart. This resulted in plot numbers along each transect ranging from 1 to 10. We recorded the names of all vascular plant species present and visually estimated the percentage of ground cover (e.g. vegetation, bare ground, litter, coarse woody debris (CWD), bryophytes, lichens, bedrock, and flotsam) to the nearest 5%, aspect, slope, depth (cm) to underlying substrate particles < 2 mm in diameter, and substrate particle sizes for each quadrat as detailed in Wiser et al. (2010). These measurements were averaged to provide a 'beach-scale' value.

Climate-related national-scale predictors of invertebrate community composition on gravel beaches were investigated (e.g. mean annual temperature following Leathwick et al. (2003)) as described in Wiser et al. (2010). Additionally, we visually categorised the land adjacent to and within 100 m of each beach according to the proportions of each cover class (e.g. urban, bare ground, pastoral, indigenous forest) as defined by the New Zealand Land Cover Database (LCDB2, see http://www.mfe.govt.nz/issues/land/land-cover-dbase/classes.html). We determined proximity to human dwellings (as an indicator of potential for disturbance) using aerial photographs and satellite imagery.

We restricted our quantitative sampling of invertebrates to the surface litter (defined as loose dead vegetative material) and subsurface gravel habitats (collectively referred to as 'surface-down' hereafter) from 51 gravel beaches around the North Island and South Island that were surveyed by Wiser et al. (2010) (Fig. 1, Appendix 1). An additional 10 gravel beaches included in that study were not sampled because of a lack of litter or finer gravels (< 2 mm fraction). At each gravel beach, samples of litter were taken by hand or by raking with a hand trowel across each quadrat in which litter was present. Using a hand trowel, gravel was extracted to the depth of fines or to a depth of 15 cm in deeper gravels. Surface-down samples were stored in cotton sacks, processed by Tullgren extraction within 10 days (Edwards 1991; Sakchoowong et al. 2007), and extracted into 95% ethanol. Because of our limits in budget, time and taxonomy (see McGeogh 1998), we assigned groups of invertebrates to orders or classes within terrestrial Bilateria (predominantly Arthropoda) according to the Tree of Life web project (http://tolweb.org/Bilateria/2459). This level of taxonomic identification, while alleviating previously recognised constraints (Balmford 1996b), was deemed suitable to resolve the research questions proposed in this study. All sorted material, including rare and unusual specimens, was deposited in the New Zealand Arthropod Collection.

Data analysis

All statistics and figures were generated using R v. 2.11.1 (R Development Core Team 2010). We used regression tree analysis (function *rpart* of package *mvpart*, trees V-fold cross-validated and pruned to 1 SE) to individually relate the abundance of the seven most common, or commonly studied, arthropods that we had collected (Acari, Collembola,

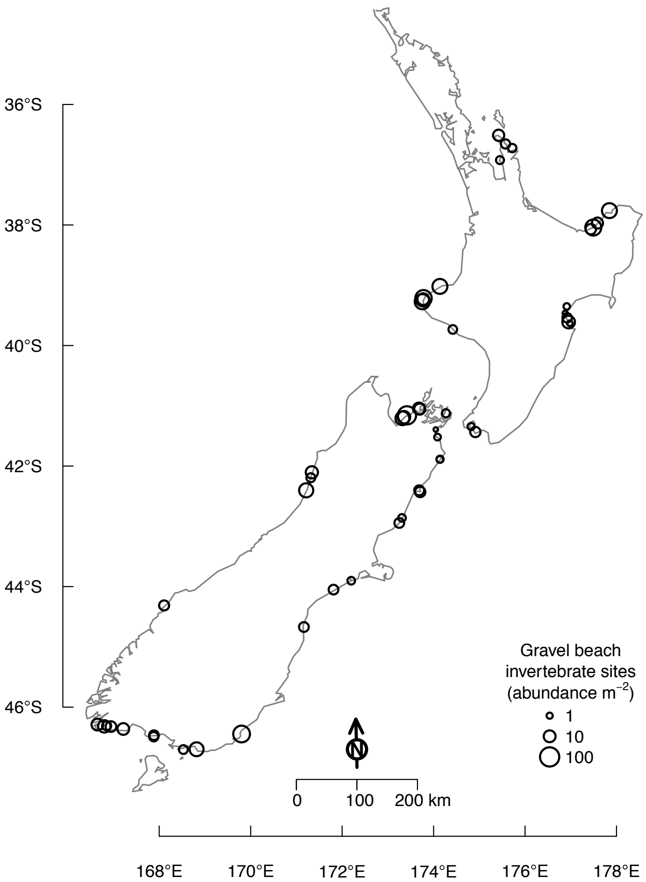

Figure 1. Distribution of the 51 sites (indicated as circles) where gravel beaches were sampled in New Zealand. Diameters of the circles are relative to invertebrate abundance (m^{-2}) on a $\log_{10}$ scale.

Table 1. All gravel beach site characteristics measured at beach, landscape and national scales used for analysis and generation of figures in R v. 2.11.1 (R Development Core Team 2010).

Beach scale	Landscape scale	National scale
Maximum canopy height	Distance to nearest building	Annual rainfall
Mean particle size	Percentage of surrounding land cover type classed as:	Mean annual vapour pressure deficit
Percent plant cover	Urban	Spring (October) vapour pressure deficit
Percent exotic plant cover	Exotic forest	Mean minimum temperature of the coldest month
Percent organic layer	Grassland	Maximum annual temperature of the warmest month (February)
Percent organic layer [litter + humus] cover	Wetland	Mean annual temperature[1]
Percent CWD cover	Water	
Percent sand in fines	Native woody vegetation (forest + shrubland)	
Percent lichen cover	Sand	
Plant species richness		
Variation (coefficient) of particle size		
Volume of stones		

CWD is coarse woody debris. [1]Mean of the 12 monthly averages for daily values.

Hymenoptera, Diptera, Coleoptera, Araneae and Lepidoptera) to site characteristics. Site characteristics were measured at beach, landscape, and national scales (Table 1). Division by the measured beach characteristic with the highest complexity score (i.e. most predictive) was used to relativise the importance of each predictor variable prior to plotting as a bar chart for each arthropod group. Regression tree analysis allowed us to overcome the likelihood of collinearity among predictor variables and the lack of a priori information about the type of response (unimodal, linear, non-linear) to the predictors.

In order to understand environmental or habitat factors differentiating invertebrate community composition, we then plotted gravel beaches as non-metric multidimensional scaling (NMDS) points in surface-down invertebrate space (using Bray-Curtis dissimilarities; function *metaMDS* of package *vegan*). Observations of scree-plots and stress were used to determine the optimal number of axes (k) each with 20 random starts and 1000 permutations of the data, prior to choosing the final NMDS solution. We tested the fit of our measured beach characteristics as predictors of invertebrate community composition by overlaying them on the final NMDS ordination and rejected all that were non-significant ($\mu = 0.05$), using 1000 Monte Carlo permutations of the data (function *envfit* of package *vegan*). Using data from Wiser et al. (2010) we conducted a similar NMDS ordination with the plant community and overlaid the same beach characteristics to determine whether the invertebrate and plant communities were related to the same variables. Finally, we tested whether the invertebrate community was related to the vegetation type by conducting a Mantel test using Bray-Curtis distances (function *vegdist* of package *vegan*), Pearson correlations, and 1000 permutations of the data to determine significance (function *mantel* of package *vegan*).

Rare taxonomic groups (abundance less than three individuals collected across the entire study) were removed and data were then converted to proportions by site, and arcsin-square-root-transformed. Beach characteristics were relativised to each of their maximum values then arcsin-square-root-transformed.

Results

Gravel beach invertebrate abundance and community composition

A total of 11 149 invertebrates from 24 taxonomic groups were recovered from the 51 gravel beaches sampled (Appendix 1) throughout New Zealand. The abundance of surface-down invertebrates varied considerably between gravel beaches, ranging from less than one to as many as 70 m^{-2} with a mean of 10 m^{-2} (±2 SE) (Fig. 1). Acari and Collembola were by far the most abundant invertebrates; combined they made up 63 ± 3% of the total invertebrate fauna across all beaches (Fig. 2). A number of invertebrates of special interest (i.e. rare species, new localities, habitat specialists, threatened species, or exotic species with incursion risk) were also recovered from gravel beaches (Appendix 2).

Specific taxonomic groups varied greatly with respect to which factors were most important for their abundance (Fig. 3). Overall, beach-scale factors were the most important for all groups of biota, whereas landscape context appeared to be of relatively low importance. Generally, arthropod abundance varied according to substrate factors including average particle size of the coarse substrate fraction (i.e. gravel and cobble), sand volume, and the presence of dead organic cover (litter, humus and CWD). Of the landscape-scale factors, distance to human dwellings was negatively related to Coleoptera abundance, whereas Lepidoptera decreased in abundance with increasing proportions of the surrounding area being forest. National-scale patterns of temperature and moisture were not strong predictors of invertebrate abundance, except for Diptera, which displayed a unimodal, or optimal, response to rainfall, and the Hymenoptera, which were negatively related to spring vapour pressure deficit. Variables that did not significantly influence groups of gravel beach invertebrates were percent plant cover, percent exotic plant cover, percent of surrounding land cover type classified as exotic forest, water, urban, grassland or wetland; and all temperature measures (mean minimum of the coldest month, maximum annual temperature of the warmest month, and mean annual temperature).

Non-metric multidimensional scaling ordination of invertebrate community composition on the gravel beaches produced a stable, low-stress (9.9) solution with $k = 4$ axes. We arbitrarily plotted the first two axes in Fig. 4; however,

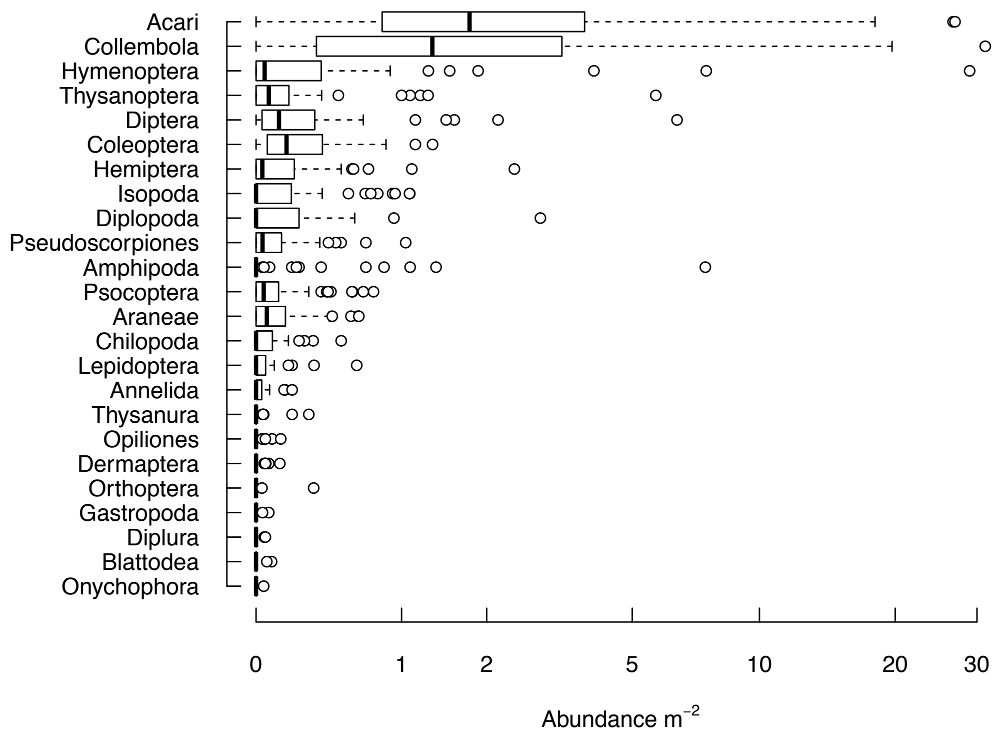

Figure 2. Abundance (m^{-2}) boxplot of major taxa of surface-down invertebrates from 51 gravel beaches across New Zealand. Note abundance values (n) are back-transformed from log10 (n + 1).

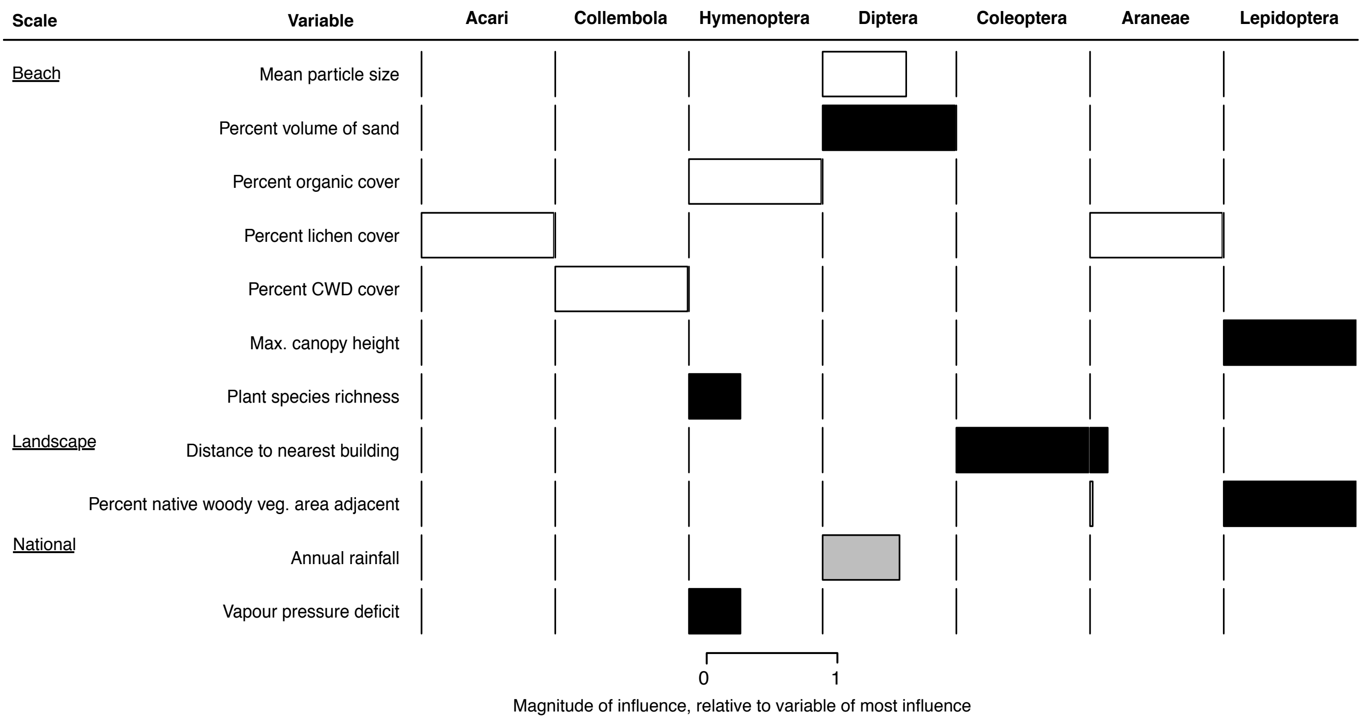

Figure 3. Summary of regression tree analysis of the relationships between seven invertebrate groups of interest and gravel beach characteristics at beach, landscape and national scales. Bar length indicates magnitude of influence (i.e. complexity factor) for each variable relative to the most influential variable for each invertebrate group. White bars show positive relationships; black bars negative ones; except for Diptera, which were unimodally related to annual rainfall and are shown in grey.

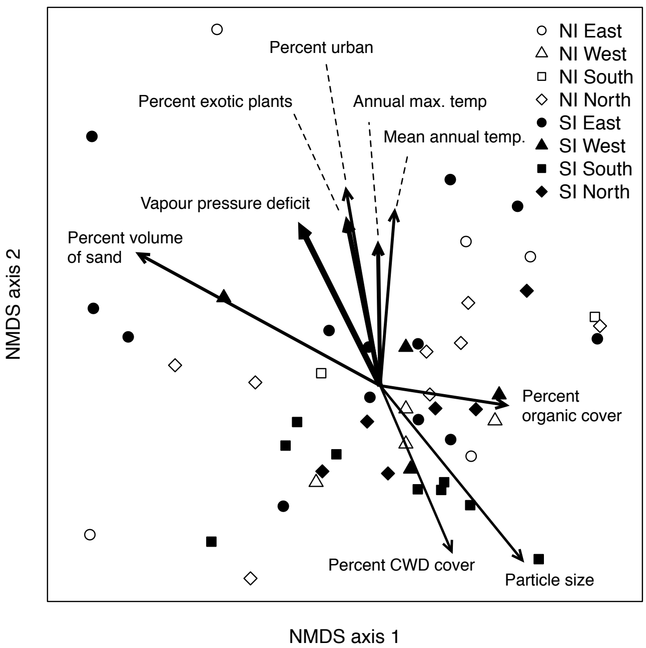

Figure 4. Non-metric multidimensional scaling (NMDS) ordination plot of New Zealand gravel beaches in surface-down invertebrate space. The first two axes are shown from a four-axes solution. Symbols indicate the geographic localities of individual beaches (NI = North Island, SI = South Island). Arrows indicate beach characteristics in relation to the structure of the ordination space. Widths of arrows are proportional to total r^2 for that particular vector in all four dimensions.

interpretation of the results was based on all possible axis combinations. There was little indication that invertebrate community composition on gravel beaches was related to geographic location (i.e. occurrence on the North or South Island or the side of the islands where the beach occurred). In decreasing order, the beach characteristics most highly related to the composition of the invertebrate community (in all four dimensions of the NMDS ordination) were annual and spring vapour pressure deficit (r^2 = 0.49, P < 0.001), the percentage of plant species present that were exotic (r^2 = 0.40, P < 0.001), maximum annual temperature (r^2 = 0.33, P = 0.002), proportion of sand in the substrate (r^2 = 0.27 , P = 0.007), percentage of organic ground cover (litter + humus; r^2 = 0.25, P = 0.007), percentage of surrounding landscape that is urbanised (r^2 = 0.25, P = 0.009), mean annual temperature (r^2 = 0.24, P = 0.009), mean particle size on the beach (r^2 = 0.21, P = 0.027), and percentage of CWD ground cover (r^2 = 0.20, P = 0.029). Moreover, there was no evidence that composition of the invertebrate group-level and plant species-level communities on gravel beaches were interdependent (Mantel test r = 0.08, P = 0.12).

Discussion

Invertebrates on New Zealand gravel beaches

Globally gravel beaches have been studied far less than sandy beaches (Packham et al. 2001) and the understanding of invertebrates on gravel beaches is very poor. Our survey of invertebrate assemblages associated with 51 gravel beaches is the first of its kind in New Zealand. It revealed an impressive diversity of invertebrates spanning 24 taxonomic groups in the phyla Annelida, Arthropoda, Mollusca and Onychophora across the majority of beaches surveyed. The greatest abundances were among the microarthropods, particularly Acari and Collembola, as is evident in a number of studies of surface and below-ground habitats (Adis 1988; Stanton 1988; St. John et al. 2012) making them ideal focal groups in ecological, environmental and biodiversity research (Koehler et al. 1995; Gonzalez et al. 1998; Rusek 1998; Demšar et al. 2006). Macroarthropods present included several primarily decomposer groups (e.g. Isopoda, Diplopoda and Amphipoda). The breadth of life-history strategies (including a full range in parity, voltinism, r- and K-strategists) and feeding habits (including saprovores, fungivores, herbivores, predators and parasitoids) represented by the invertebrates we recovered suggests considerable heterogeneity in gravel beach microhabitats among beaches at a national scale.

Drivers of invertebrate abundance on New Zealand gravel beaches

The patterns in abundance of specific groups of gravel beach invertebrates suggest that where site conditions were suitable (beach scale), and climate allowed (national scale), arthropods colonised gravel beaches with little influence from their immediate surroundings (landscape scale) (Fig. 3). The minimal influence of adjacent vegetation contrasts strongly with the influences on plant composition on gravel beaches (Wiser et al. 2010). Exceptions included Coleoptera, which were more abundant where human dwellings were closer to gravel beaches, and Lepidoptera, which were negatively related to the area of surrounding forest vegetation (Fig. 3). The latter likely reflects a reduction of grass-root-feeding moth species where trees are dominant. This latter speculation is supported by the negative relationship between Lepidoptera and canopy height on the beaches (i.e. taller-stature canopies likely reflect woody plant dominance over herbs and graminoids). The relationship between the proximity of human dwellings to beaches and the abundance of Coleoptera is more difficult to explain without specific data on life histories of the beetles involved, but regardless, is indicative of human influence on the invertebrate fauna of gravel beaches.

The abundance of Acari (mites), Collembola (spring tails), Hymenoptera (e.g. ants, wasps), Diptera (flies) and Araneae (spiders) generally reflected the physical structure or disturbance (i.e. lichen cover) of gravel beach surface substrates (e.g. the size of particles or the volume of sand, organic cover, CWD), and fits well with expectations that the quantity and heterogeneity of microhabitats is a driver of surface-down invertebrate abundance and richness (Anderson 1978; Hansen 2000; St. John et al. 2006a). Notable variables that did not influence abundance of gravel beach invertebrates included plant species richness (except for Hymenoptera) and percent area of gravel beach vegetation. This suggests that, at least in terms of abundance, the nature of the plant community was not a good predictor of invertebrates on these beaches.

This landscape-independent pattern for invertebrates fits with expectations that inhabitants of these rare habitats are likely to be specialists, good dispersers and not simply opportunists or transient populations being supported by dissimilar nearby ecosystems (Morris & Parsons 1993; Shardlow 2001). We do not have the data, however, to conclude whether this holds for gravel beach invertebrates at the species level. It is possible that species composition of the observed groups of invertebrates may be related to landscape influences even if abundances of the coarser-level groupings were not. However, we know that once disturbed or extirpated, some groups of gravel arthropods, particularly oribatid mites, can take decades or longer to recover (St. John et al. 2002). It was notable, then, that mites and spiders were positively related to lichen cover on gravel beaches. Lichens, in addition to providing habitat and food for some species of mites (Seyd & Seaward 1984; Barlow & Ferry 1989), are negatively impacted by disturbance. Thus, the positive relationship with lichen cover suggests that mites and spiders do not fare well on disturbed gravel beaches, and that human activity there may have a negative impact on invertebrates, with potentially long-term consequences.

Drivers of invertebrate composition on New Zealand gravel beaches

In contrast to invertebrate abundance, we found that the proportion of exotic species in the plant community was a strong predictor of invertebrate community composition on gravel beaches (Fig. 4), suggesting that the higher the ratio of exotic plants to native species, the greater the invertebrate diversity. We are unable to determine from our study what effects exotic plants are having at the species level, or on native invertebrate species, specifically. We can assume – since there was no relationship between exotic plants and the abundance of gravel beach invertebrates – that exotic plants are not having an additive effect, but rather reconfiguring the invertebrate communities. This strong effect at a high level of taxonomic resolution raises serious concerns for conservation and indicates that species-level investigations of these habitats are warranted given the rarity of gravel beaches and the likelihood of endemic specialist species inhabiting them.

Both the plant (Wiser et al. 2010) and invertebrate communities were influenced by climatic factors (e.g. vapour pressure deficit and mean annual temperature), supporting theories that plant and animal communities vary independently but predictably with global-scale climatic indicators (Currie 1991). In contrast to the plant community, however, invertebrate communities were less influenced by landscape settings as only the percentage of surrounding urban area was significantly related to invertebrate community composition. Interestingly, we found no support for congruence between the plant and invertebrate communities (Mantel test) despite finding several shared, strong predictors of their composition (e.g. vapour pressure deficit and mean annual temperature, percent exotic plant species, volume of sand). This lack of congruence fits with Currie's (1991) observation that despite plants and animals responding in a similar manner along a gradient of environmental energy, the relationship between the taxonomic richness of both groups is poor. Our results could also reflect incongruence in taxonomic resolution between the invertebrate and plant data, the latter having been identified to species. Higher level taxonomic groupings can provide sufficient resolution to support broader questions and processes in community ecology (this study; Hodkinson et al. 2002). However, the loss of resolution resulting from the use of taxonomically coarse data (Balmford et al. 1996a, b) is a limiting factor in elucidating more specific questions not asked in this study and which can only be answered with genus- and/or species-level identifications of functional or focal groups (e.g. lichenicolous mites – Barlow & Ferry 1989; predatory ground beetles – Gardner 1991).

Conclusions

Our preliminary investigation of New Zealand gravel beaches has revealed distinctive invertebrate communities whose composition varied independently of vegetation, and included endemic species of conservation interest, and exotic species representing biosecurity threats. Invertebrate assemblages varied independently of vegetation type, but both responded to similar macro-scale climatic drivers. There was ample evidence to suggest that invertebrate abundance and composition on gravel beaches was influenced by human activity, proximity to urbanisation and exotic plant species, but was minimally influenced by landscape context. Our study provides a platform from which to employ species-level investigations to explore in more detail the links between invertebrate species and human-induced pressures such as use of beaches, urbanisation of the surrounding landscape, and spread of exotic plant species.

Acknowledgments

This research was funded by the New Zealand Foundation for Research, Science and Technology (Contract C09X0503). Jeremy Foley, Helen and Richard Parsons, Brian Cooper, Simon Lulworth and Walter Wilson kindly provided access to private property. We thank the following colleagues who contributed to key aspects of this project: Chris Winks, Grace Hall and Stephen Thorpe for processing and identification of invertebrate samples; Robert Hoare, John Dugdale, Darren Ward, John Early, Don Chandler and Dianne Gleeson for identification of notable invertebrate finds; Rowan Buxton, Beverly Clarkson, Mark Smale, Peter Williams, Sarah Richardson and Carol West for help in providing samples; Brian Rance, Owen Spearpoint, Meredith McKay, Chris Morse, Zoe Ellett, Garry Watson, Helen Jonas and Renske Terhurne for help in the field. We also thank Bill Lee, Michael Winterbourn and two anonymous reviewers for their useful comments and input into the latter stages of this manuscript.

References

Adis J 1988. On the abundance and density of terrestrial arthropods in central Amazonian dryland forests. Journal of Tropical Ecology 4: 19–24.

Ahn K-J 2004. *Moorea zealandica*, new genus and species from New Zealand with a discussion of its phylogenetic relationships (Coleoptera: Staphylinidae: Aleocharinae. New Zealand Journal of Zoology 31: 255–261.

Anderson JM 1978. Inter- and intra-habitat relationships between woodland *Cryptostigmata* species diversity and the diversity of soil and litter microhabitats. Oecologia 32: 341–348.

Antvogel H, Bonn A 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography 24: 470–482.

Balmford A, Green MJB, Murray MG 1996a. Using higher-taxon richness as a surrogate for species richness: I. Regional tests. Proceedings of the Royal Society of London B 263: 1267–1274.

Balmford A, Jayasuriya AHM, Green MJB 1996b. Using higher-taxon richness as a surrogate for species richness: II. Local applications. Proceedings of the Royal Society of London B 263: 1571–1575.

Barlow SL, Ferry BW 1989. Population dynamics of lichenicolous mites at Dungeness. Botanical Journal of the Linnean Society 101: 111–124.

Collier KJ, Smith BJ 2006. Distinctive invertebrate assemblages in rockface seepages enhance lotic biodiversity in northern New Zealand. Biodiversity and Conservation 15: 3591–3616.

Crosby TK, Dugdale JS, Watt JC 1998. Area codes for recording specimen localities in the New Zealand subregion. New Zealand Journal of Zoology 25: 175–183.

Currie DJ 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137: 27–49.

Davy AJ, Willis AJ, Beerling DJ 2001. The plant environment: aspects of the ecophysiology of shingle species. In: Packham JR, Randall JM, Barnes RSK, Neal A eds Ecology and geomorphology of coastal shingle. Otley, West Yorkshire, Westbury. Pp. 191–201.

De Bruyn L, Thys S, Scheirs J, Verhagen R 2001. Effects of vegetation and soil on species diversity of soil dwelling Diptera in a heathland ecosystem. Journal of Insect Conservation 5: 87–97.

Demšar D, Džeroski S, Larsen T, Struyf J, Axelsen J, Bruus Pedersen M, Henning Krogh P 2006. Using multi-objective classification to model communities of soil microarthropods. Ecological Modelling 191:131–143.

Dugdale JS 2001. Cloudy Bay coastal habitats: entomological values of the foreshore and associated inland habitats. Occasional Publication 49. Nelson, Department of Conservation Nelson/Marlborough Conservancy.

Early JW, Dugdale JS 1994. *Fustiserphus* (Hymenoptera: Proctotrupidae) parasitises Lepidoptera in leaf litter in New Zealand. New Zealand Journal of Zoology 21: 249–252.

Early JW, Masner L, Naumann ID, Austin AD 2001. Maamingidae, a new family of proctotrupoid wasp (Insecta : Hymenoptera) from New Zealand. Invertebrate Taxonomy 15: 341–352.

Edwards CA 1991. The assessment of populations of soil-inhabiting invertebrates. Agriculture, Ecosystems and Environment 34: 145–176.

Foord SH, Ferguson JWH, van Jaarsveld AS 2003. Coleopteran assemblages in Afromontane grasslands reflect fine-scale variation in vegetation. Environmental Entomology 32: 797–806.

Fuller RM 1987. Vegetation establishment on shingle beaches. Journal of Ecology 75: 1077–1089.

Gardner SM 1991. Ground beetle (Coleoptera: Carabidae) communities on upland heath and their association with heathland flora. Journal of Biogeography 18: 281–289.

Gibb JG 1978. Rates of coastal erosion and accretion in New Zealand. New Zealand Journal of Marine and Freshwater Research 12: 429–456.

Gonzalez A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281: 2045–2047.

Hansen RA 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81: 1120–1132.

Harris RJ, Berry JA 2001. Confirmation of the establishment of three adventive ants (Hymenoptera: Formicidae) in New Zealand: *Cardiocondyla minutior* Forel, *Ponera leae* Forel, *Mayriella abstinens* Forel. New Zealand Entomologist 24: 53–56.

Hartley SE, Gardner SM, Mitchell RJ 2003. Indirect effects of grazing and nutrient addition on the hemipteran community of heather moorlands. Journal of Applied Ecology 40: 793–803.

Hodkinson ID, Webb NR, Coulson SL 2002. Primary community assembly on land - the missing stages: why are heterotrophic organisms always there first? Journal of Ecology 90: 569–577.

Koehler H, Munderloh E, Hofmann S 1995. Soil microarthropods (Acari, Collembola) from beach and dune: characteristics and ecosystem context. Journal of Coastal Conservation 1: 77–86.

Leathwick J, Wilson G, Rutledge D, Wardle P, Morgan F, Johnston K, McLeod M, Kirkpatrick R 2003. Land environments of New Zealand. Auckland, David Bateman for the Ministry for the Environment.

McGeogh M 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73: 181–201.

Morris MG 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biological Conservation 95: 129–142.

Morris R, Parsons M 1993. Dungeness – a shingle beach and its invertebrates. British Wildlife 4: 137–144.

Osler GHR, Cole L, Keith AM 2006. Changes in oribatid mite community structure associated with the succession from heather (*Calluna vulgaris*) moorland to birch (*Betula pubescens*) woodland. Pedobiologia 50: 323–330.

Packham JR, Spiers T 2001. Plants along the prom: an account of shingle vegetation associated with coastal defence works at Brighton, Sussex, UK. In: Packham JR, Randall JM, Barnes RSK, Neal A eds Ecology and geomorphology of coastal shingle. Otley, West Yorkshire, Westbury. Pp. 174–190.

Packham JR, Randall RE, Barnes RSK, Neal A eds 2001. Ecology and geomorphology of coastal shingle. Otley, West Yorkshire, Westbury. 459 p.

Patrick B 1994. Lepidoptera of Kaitorete Spit, Canterbury. New Zealand Entomologist 17: 52–63.

Patrick BH, Dugdale JS 2000. Conservation status of the New Zealand Lepidoptera. Science for Conservation 136. Wellington, Department of Conservation. 33 p.

Quinn MA, Walgenbach DD 1990. Influence of grazing history on the community structure of grasshoppers of a mixed-grass prairie. Environmental Entomology 19: 1756–1766.

R Development Core Team 2010. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.

Randall RE 1992. The shingle vegetation of the coastline of New Zealand: Nelson Boulder Bank and Kaitorete Spit. New Zealand Journal of Geography 93: 11–19.

Rusek J 1998. Biodiversity of Collembola and their functional role in the ecosystem. Biodiversity and Conservation 7: 1207–1219.

Sakchoowong W, Nomura S, Ogata K, Chanpaisang J 2007. Comparison of extraction efficiency between Winkler and Tullgren extractors for tropical leaf litter macroarthropods. Thai Journal of Agricultural Science 40: 97–105.

Sanderson RA, Rushton SP, Cherrill AJ, Byrne JP 1995. Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. Journal of Applied Ecology 32: 506–518.

Schaffers AP, Raemakers IP, Sýkora KV, ter Braak CJF 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89: 782–794.

Seyd EL, Seaward MRD 1984. The association of oribatid mites with lichens. Zoological Journal of the Linnean Society 80: 369–420.

Shardlow MEA 2001. A review of the conservation importance of shingle habitats for invertebrates in the United Kingdom (UK). In: Packham JR, Randall JM, Barnes RSK, Neal A eds Ecology and geomorphology of coastal shingle. Otley, West Yorkshire, Westbury. Pp. 355–377.

St.John MG, Bagatto G, Behan-Pelletier V, Lindquist EE, Shorthouse JD, Smith IM 2002. Mite (Acari) colonization of vegetated mine tailings near Sudbury, Ontario, Canada. Plant and Soil 245: 295–305.

St.John MG, Wall DH, Behan-Pelletier VM 2006a. Does plant species co-occurrence influence soil mite diversity? Ecology 87: 625–633.

St.John MG, Wall DH, Hunt HW 2006b. Are soil mite assemblages structured by the identity of native and invasive alien grasses? Ecology 87: 1314–1324.

St.John MG, Crossley DA Jr, Coleman DC 2012. Microarthropods. In: Huang PM, Li YC, Sumner ME eds Handbook of soil sciences. Vol. 1. Boca Raton, FL, Taylor and Francis.

Editorial Board member: Michael Winterbourn
Received 28 April 2012; accepted 4 September 2012

Stanton NL 1988.The underground in grasslands. Annual Review of Ecology and Systematics 19: 573–589.

Tait NN, Briscoe DA 1995. Genetic differentiation within New Zealand Onychophora and their relationships to the Australian fauna. Zoological Journal of the Linnean Society 114: 103–113.

Vestergaard P 2001. Geomorphology and vegetation of Danish shingle. In: Packham JR, Randall JM, Barnes RSK, Neal A eds Ecology and geomorphology of coastal shingle. Otley, West Yorkshire, Westbury. Pp. 277–288.

Wardle DA, Chase J 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9: 870–886.

Watt JC 1961. The New Zealand Onychophora. Tane 8: 95–103.

Werner FG, Chandler DS 1995. Anthicidae (Insecta: Coleoptera). Fauna of New Zealand 34. Lincoln, Manaaki Whenua Press. 64 p.

Williams PA, Wiser S, Clarkson B, Stanley MC 2007. New Zealand's historically rare terrestrial ecosystems set in a physical and physiognomic framework. New Zealand Journal of Ecology 31: 119–128.

Wiser SK, Buxton RP, Clarkson BR, Richardson SJ, Rogers GM, Smale MC, Williams PA 2010. Climate, landscape and microenvironment interact to determine plant composition in naturally discrete gravel beach communities. Journal of Vegetation Science 21: 657–671.

Appendix 1. Numbers of invertebrates in different taxonomic groups found at 51 gravel beach sites in New Zealand. Grid reference display coordinates (metric; longitude/latitude – WGS84 datum). Region codes in accordance with geographic boundaries defined by Crosby et al. (1998): BP, Bay of Plenty; CL, Coromandel; HB, Hawke's Bay; TK, Taranaki; WN, Wellington; BR, Buller; FD, Fiordland; KA, Kaikoura; MC, Mid-Canterbury; NC, North Canterbury; NN, Nelson; SC, South Canterbury; SD, Marlborough Sounds; SL, Southland.

Region	Locality	Grid reference	Acari	Amphipoda	Annelida	Araneae	Blattodea	Chilopoda	Coleoptera	Collembola	Dermaptera	Diplopoda	Diplura	Diptera	Gastropoda	Hemiptera	Hymenoptera	Isopoda	Lepidoptera	Onychophora	Opiliones	Orthoptera	Pseudoscorpionida	Psocoptera	Thysanoptera	Thysanura
CL	Kuaotunu	36°43.44S, 175°43.26E	13	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
CL	Stony Bay	36°30.52S, 175°25.39E	105	0	0	1	0	0	13	0	0	0	0	0	0	0	14	0	3	0	0	0	6	2	2	0
CL	Tuateawa	36°39.15S, 175°34.05E	10	0	0	0	0	0	0	12	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
CL	Wairotoroto	36°55.53S, 175°26.72E	6	0	0	0	0	1	0	20	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	4
BP	Motu West	37°52.43S, 177°34.52E	94	1	1	0	0	1	1	10	0	0	0	5	0	0	0	1	0	0	0	0	0	1	0	0
BP	Raukokore West	37°38.86S, 177°52.24E	235	0	0	4	1	0	4	75	0	7	0	4	0	0	2	0	8	0	0	0	6	0	1	0
BP	Te Hanoa Bay, Torere East	37°55.42S, 177°31.43E	160	45	0	0	0	0	2	2	0	0	0	13	0	0	2	2	0	0	0	0	1	0	0	0
BP	Te One Bay, Torere South	37°57.03S, 177°28.94E	6	0	0	0	0	0	1	25	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0
TK	Bell Block	39°01.75S, 174°07.10E	450	21	1	1	0	3	15	150	1	10	0	6	0	5	2	2	0	0	0	0	0	0	0	0
TK	Cape Egmont	39°16.03S, 173°45.56E	190	13	0	5	0	2	1	80	0	2	0	6	0	2	10	11	1	0	0	0	1	7	13	0
TK	Stent Rd, North Cape Egmont	39°13.64S, 173°46.71E	60	0	0	3	0	0	6	150	0	5	0	1	0	1	3	3	1	0	0	0	2	0	5	0
TK	Waiweranui Stream	39°13.10S, 173°46.78E	700	1	0	0	0	3	16	110	0	8	0	3	0	3	196	28	0	0	0	0	4	3	33	0
HB	Awatoto	39°32.76S, 176°55.15E	24	0	0	0	0	0	3	16	0	0	0	0	0	63	0	0	0	0	0	0	4	1	3	0
HB	Haumoana	39°36.94S, 176°57.49E	0	0	0	0	0	0	0	300	0	0	0	3	0	2	1	0	0	0	0	0	0	1	6	0
HB	Napier, West Shore	39°29.35S, 176°53.64E	1	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
HB	Te Awanga	39°37.91S, 176°59.29E	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	11	0
HB	Tangoio	39°20.81S, 176°55.25E	7	0	0	1	0	0	0	0	0	0	0	2	0	14	1	0	1	0	0	0	0	3	5	1
WN	Palmer Head	41°20.62S, 174°48.72E	15	0	0	9	0	0	5	0	2	0	0	0	0	0	21	0	0	0	0	0	1	1	0	1
WN	Turakirae Head	41°25.83S, 174°54.47E	6	0	0	12	1	2	7	20	0	2	0	28	0	7	17	0	1	0	0	6	0	0	2	0
SD	Long Island	41°06.56S, 174°17.53E	52	0	0	3	0	0	7	2	0	0	0	1	0	0	0	0	2	0	0	0	11	2	1	0
SD	Matarau Pt., Croiselles Hbr.	41°02.76S, 173°41.48E	188	0	0	0	0	0	2	50	0	1	0	1	1	2	0	2	0	0	0	0	4	0	0	0
SD	Pakiaka Pt., Croiselles Hbr.	41°02.39S, 173°41.05E	125	0	0	2	0	1	4	216	0	5	0	1	0	0	13	1	1	0	0	0	1	1	3	0
SD	Rarangi	41°24.22S, 174°02.89E	0	0	0	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	2	0	0
MB	Wairau Boulder Bank	41°28.89S, 174°03.76E	24	0	0	0	0	0	0	0	0	0	0	11	0	1	1	0	0	0	0	0	1	1	0	0
NN	Cable Bay	41°09.49S, 173°24.24E	260	0	1	10	0	5	8	315	0	46	0	5	0	7	463	5	3	0	0	0	11	12	19	3
NN	Glenduan	41°10.96S, 173°21.68E	70	0	1	2	0	0	18	100	0	12	0	3	0	3	5	0	0	0	0	1	5	15	200	0
NN	Nelson Boulder Bank	41°12.83S, 173°18.72E	200	0	0	7	0	3	2	50	3	15	0	2	0	5	100	27	1	0	0	0	26	10	12	0
KA	Mirza Creek	41°52.89S, 174°08.63E	1	0	0	0	0	0	0	12	0	0	0	2	0	0	0	0	0	0	0	0	0	4	0	0
KA	Mirza Platform	41°53.38S, 174°07.98E	0	0	0	0	0	0	1	15	0	0	0	6	0	0	0	0	0	0	0	0	0	6	0	0
KA	Kaikoura Township, North	42°24.42S, 173°41.05E	67	0	0	0	0	0	4	0	0	0	0	0	1	8	0	0	0	0	0	0	0	3	1	0
KA	Kaikoura Peninsula, South	42°25.50S, 173°41.32E	38	0	0	2	0	0	2	36	0	0	0	12	0	0	0	1	1	0	0	0	1	12	5	0
KA	Kaikoura South Bay	42°24.78S, 173°40.36E	30	0	0	1	0	0	1	10	0	0	0	2	0	0	1	0	0	0	0	0	2	0	1	0
BR	Pororari River Mouth	42°06.22S, 171°20.27E	10	0	0	12	0	0	3	60	1	1	0	135	0	0	9	2	1	0	0	0	1	0	0	0
BR	Pakiroa, South Punakaiki	42°11.51S, 171°18.93E	39	0	0	6	0	6	1	10	0	9	0	15	0	1	2	21	2	0	3	0	19	1	1	0
BR	Cobden Beach	42°24.40S, 171°12.76E	320	5	4	6	0	7	12	150	0	13	0	3	0	13	9	10	0	1	1	0	0	0	5	1
NC	Gore Bay	42°51.13S, 173°18.81E	32	0	0	0	0	0	0	16	0	0	0	0	0	1	1	0	0	0	0	0	0	1	5	0
NC	Napenape	42°56.62S, 173°15.01E	45	0	0	2	0	0	5	25	0	0	0	2	0	0	0	1	0	0	0	0	0	11	1	0
MC	Rakaia South	43°54.22S, 172°11.61E	29	0	0	5	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	6	0	0
MC	Hakatere	44°03.01S, 171°48.70E	34	0	0	3	0	0	9	22	1	0	0	1	0	17	1	0	2	0	0	0	0	0	24	0
SC	Wainono Lagoon	44°40.03S, 171°09.78E	60	0	0	2	0	1	6	52	0	20	0	4	0	0	0	0	0	0	0	0	14	2	4	0
FD	Big Bay South	44°19.52S, 168°05.93E	150	0	2	2	0	4	21	20	0	0	0	2	0	7	17	4	0	0	0	0	3	2	0	0
FD	Wilson River	46°11.34S, 166°38.87E	75	0	1	6	0	11	29	50	1	5	1	0	0	4	9	6	7	0	1	0	2	1	3	0
FD	Andrew Burn	46°12.86S, 166°48.42E	50	5	0	4	0	2	2	120	0	5	0	25	0	3	28	15	0	0	0	0	2	2	0	0
FD	Fred Burn-West	46°12.48S, 166°51.10E	17	0	0	0	0	1	4	13	0	1	1	0	0	5	47	1	0	0	0	0	4	0	0	0
FD	Westys Prices Harbour	46°13.30S, 166°56.61E	28	7	1	1	0	0	12	100	0	0	0	11	0	1	50	0	3	0	1	0	2	1	0	0
FD	Wairaurahiri West	46°15.68S, 166°12.84E	75	8	1	3	0	5	25	50	0	1	0	1	0	13	3	16	1	0	0	0	0	9	0	0
SL	Colac Bay	46°21.47S, 167°55.82E	90	0	1	0	0	0	8	50	0	1	0	0	0	22	2	0	1	0	0	0	0	1	0	0
SL	Oraka Point	46°23.41S, 167°52.85E	50	0	2	0	0	0	15	10	0	15	0	0	0	33	0	0	1	0	0	0	0	0	0	0
SL	Roaring Bay, Nugget Pt.	46°26.72S, 169°48.09E	200	11	3	7	0	0	6	500	0	4	0	3	0	5	2	4	0	0	2	0	0	0	2	0
SL	Fraser's Beach	46°35.94S, 168°49.07E	16	19	2	2	0	0	12	190	0	13	0	4	0	0	0	11	0	0	0	0	0	0	1	0
SL	Tiwai Peninsula	46°36.18S, 168°31.68E	27	1	1	3	0	5	6	28	0	0	0	6	0	1	0	31	2	0	1	0	0	0	0	0

Appendix 2. Invertebrates of special interest collected from New Zealand shingle beaches.

Organism	Group	Common name	No.	Locality	Reason for interest	Reference material
Caliobius littoralis	Coleoptera: Anthribidae	Fungus weevil	2	Cable Bay, Nelson	Collection rare	
Corticaria formicaephila	Coleoptera: Lathridiidae	Minute scavenger beetle	1	Wainono Lagoon, South Canterbury	Collection rare	
Floydwernerius gushi	Coleoptera: Anthicidae	Ant-like flower beetle	4	Napenape, North Canterbury	Collection rare, new locality	Werner & Chandler 1995
Undetermined	Coleoptera: Curculionidae: Cossoninae: Pentarthrini	Weevil	1	Colac Bay, Southland	Suspected new genus and species	
Moorea zealandica	Coleoptera: Staphylinidae	Rove beetle	n	Wellington Region	New genus and species, collection rare, specific to shingle beach	Ahn 2004
Nototorchus montanus	Coleoptera: Staphylinidae	Rove beetle	3	Colac Bay, Southland	Collection rare	
Nototorchus sp.	Coleoptera: Staphylinidae	Rove beetle	5	Oraka Point, Southland	Collection rare; unknown species	
Paratorchus sp.	Coleoptera: Staphylinidae	Rove beetle	5	Cobden Beach, Buller Region	Collection rare; unknown species	
Liriomyza sp.	Diptera: Agromyzidae	Leaf -miner fly	1	Turikirae Head, Wellington	Collection rare; unknown species	
Zalea sp.	Diptera: Tethinidae	Surge fly	2	Turikirae Head, Wellington	Collection rare; unknown species	
Cardiocondyla minutior	Hymenoptera: Formicidae	Ant	1	Tangoio, Hawke's Bay	Adventive species; new locality	Harris & Berry 2001
Hypoponera confinis	Hymenoptera: Formicidae	Ant	2	Turikirae Head, Wellington	New potentially invasive species; MPI Biosecurity notified	
Maaminga marrisi	Hymenoptera: Maamingidae	Proctotrupoid wasp	9	Turikirae Head, Wellington; Roaring Bay, Southland	New endemic family, genus and species, collection rare, gravel beach association	Early & Dugdale 1994; Early et al. 2001
Kiwaia jeanae	Lepidoptera: Gelechiidae	Mat daisy jumper moth	n	Kaitorete Spit, Canterbury	Rare genus; habitat threatened	Patrick 1994; Patrick & Dugdale 2000
Kiwaia sp.	Lepidoptera: Gelechiidae	Mat daisy jumper moth	n	Cloudy Bay, Nelson	Rare genus, unknown species; habitat threatened	Patrick & Dugdale 2000; Dugdale 2001
Ooperipatellus viridimaculatus	Onychophora: Peripatopsidae	Velvet worm	1*	Cobden Beach, Buller Region	Rare egg-laying species, first record for this habitat	Watt 1961; Tait & Briscoe 1995

*Two specimens were recovered from coarse woody debris at the same locality on two separate sampling occasions (one as part of this survey), indicating the likelihood of an established colony on this shingle beach. n = specimens not collected as part of this survey. MPI = Ministry for Primary Industries.