Disturbance and diversity in a continental archipelago: a mechanistic framework linking area, height, and exposure

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Abstract. Species–area relationships (SARs) are among the most general patterns in nature. Yet, significant variation in species richness often remains after accounting for area, especially for small islands. One factor thought to influence species richness on small islands is disturbance from the combined influence of tides and waves. Here, we derive a quantitative framework for determining how ocean disturbance impacts island communities, which we then test in plant communities in a temperate island archipelago. We do so by applying some well-developed techniques honed in the marine intertidal zone but rarely applied to studies on land. By estimating and adjusting for the effect of wave exposure on habitable island area, we dramatically improved the fit of the SAR for small islands, nearly doubling the amount of variation in species richness explained (from 37% to 69%). Our predictions of island occupancy also improved using this method. Our approach predicts that small islands (<100,000 m²) are the most affected by ocean-borne disturbance. Given that many archipelagos are susceptible to wave disturbance, future studies should consider how ocean-borne disturbances arising from the matrix might interact with sampling area to influence patterns of species richness on small islands.

Key words: disturbance; diversity; habitat; plants; small-island effect; species–area relationship; supralittoral zone; zonation.

Received 3 August 2017; accepted 15 August 2017. Corresponding Editor: Debra P. C. Peters. Copyright: © 2017 Neufeld et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. † E-mail: cneufeld5@gmail.com

INTRODUCTION

Species–area relationships (SARs) are one of the most ubiquitous patterns in nature (Lawton 1999) and are a hallmark of island systems. To better understand these relationships on islands, many recent studies have debated and improved the methodology for fitting statistical (Lomolino and Weiser 2001, Triantis et al. 2006, 2012, Burns et al. 2009, Sfenthourakis and Triantis 2009, Dengler 2010, Tjorve and Tjorve 2011, Morrison 2014, Burns 2016) and dynamical models (Chisholm et al. 2016) to island SARs. One pattern to emerge from this body of work is that area alone is often insufficient to explain variation in species richness for small islands in many archipelagos (Morrison 2014, Chisholm et al. 2016). In other words, after accounting for the effect of area, islands in these systems often vary widely in species richness (a pattern known as the small-island effect). As a result, some recent studies have argued that future efforts should move beyond simply fitting models to island SARs and instead develop new methods to focus directly on other factors, beyond area, thought to influence diversity on small islands (Triantis and Sfenthourakis 2012, Morrison 2014).

One promising hypothesis for patterns of species richness on small islands relates to
disturbance. According to this hypothesis, small islands should be particularly susceptible to disturbance (resulting in periodic local extinction and lower average species richness) because they contain more low-lying edge habitat vulnerable to storms and hurricanes (MacArthur and Wilson 1967, McGuinness 1984)—indeed, most visitors to the seashore have likely noticed that plants often grow further from the water’s edge in wave-exposed places. Some of the best efforts to explore this hypothesis come from a series of studies of plant communities in the Bahamas (Morrison 2002, 2011, 2013, 2014). Collectively these studies show that similar-sized islands can vary in the amount of land occupied by plants (i.e., vegetated area), that islands with more vegetated area generally have more species, and that vegetated area and disturbance may be negatively correlated.

This previous work has found some intriguing patterns, but many gaps remain. First, without a mechanistic framework to be able to model how exposure impacts habitable land, we can never be sure that we understand the underlying processes responsible for the observed patterns of occupied area. Second, a drawback of simply measuring vegetated area is that we are stuck assuming that all habitable land is inhabited at the time of census. This assumption will be violated every time a patch of habitat opens up due to a local extinction, an event that should be common given the dynamic nature of extinction and colonization on islands predicted by the Theory of Island Biogeography (MacArthur and Wilson 1967). The amount of inhabited land is also likely to vary depending on the taxa included; the inhabited area of an island that considers purely terrestrial forest species, for example, will differ from a study of the same island when including mangroves or other species that are resistant to wave disturbance. By studying additional processes thought to influence habitable land and species diversity on small islands, we can advance our understanding of both the patterns of diversity on islands as well as their causes. This effort may also contribute to the broader goal of understanding species persistence and extinction in the many increasingly fragmented landscapes worldwide (Haddad et al. 2015).

Here, we describe a mechanistic hypothesis for patterns of species richness on small islands that links disturbance and island area into a single predictive framework based on simple physical characteristics of islands. We then test this approach on an island plant community in Barkley Sound, British Columbia, Canada. We focused specifically on small islands because these islands are predicted to experience the greatest effects of disturbance, and because they are the class of islands where SARs show the most unexplained variation (Morrison 2014, Chisholm et al. 2016). Our approach hinges on two simple observations: (1) that the boundary between marine and terrestrial communities is affected by disturbance from waves (Bird et al. 2013), and (2) that not all islands are equally susceptible to this disturbance (Spiller et al. 1998).

In the marine intertidal zone, the physical stress of aerial exposure created by tides and waves influences the upper limits of most intertidal marine species (Harley 2007), yet this well-developed body of theory—and associated methods—has not been applied to adjacent island communities that may experience a similar (but opposite) effect of ocean waves and storms. Consider the lower reaches of land on a high tide (Fig. 1). For islands in sheltered waters, where a lack of large waves creates a narrow transition between marine and terrestrial ecosystems, the habitable land may be mere centimeters from the highest reaches of the intertidal zone. When an island is exposed to the full force of the ocean, however, land at the same elevation above the high-tide mark may be regularly washed over by incoming waves (Bird et al. 2013). Although this may not provide enough emersion to allow for high intertidal species to live, it should prevent the persistence of terrestrial species, leading to a band of uninhabited shoreline (Fig. 1).

Owing to variability in the frequency and severity of waves, this boundary between land and water may not be a strict border but instead may reflect a gradient of increasing stress moving toward the intertidal zone, especially in ocean archipelagos where salt spray and inundation could severely reduce habitat quality for terrestrial species. Furthermore, because species differ in their abilities to tolerate stress (Gupta and Huang 2014), this gradient may also be one of habitability, where taller islands of a given exposure may allow for persistence of less salt-tolerant species. Additionally, disturbance and island size should interact: Small islands should be more
affected by storms than large ones. Together, these predictions imply that disturbance from ocean waves should reduce the amount and/or quality of available land on islands, thereby influencing species diversity (Fig. 1).

In this study, we first assessed the vertical zonation in nearshore terrestrial plants across a wave exposure gradient to measure how the lower limit of plants is affected by exposure to onshore waves. We did this for terrestrial plants in general, and for the eight most common species individually. After quantifying the relationship between wave exposure and plant lower limit, we incorporated this information into a quantitative framework to predict the height of an island and the accompanying area expected to be able to support plant life (referred to here as habitable height and habitable area, respectively; Fig. 1). We then assessed whether estimates of habitable height and habitable area improved models of plant species richness and island occupancy.

**METHODS**

**Study region**

All data were collected between 2011 and 2015 in Barkley Sound, British Columbia, Canada. Located on the outer edge of Vancouver Island approximately 150 km northwest of Victoria (Fig. 2a), this region is ideal for studying the role of marine disturbance on terrestrial communities. Strong storms arising from the southwest occur frequently during winter months, with winds that can reach hurricane force and incoming waves that can exceed 12 m in height (Ruggiero et al. 2010). Furthermore, the region contains hundreds of small islands that vary in their exposure to the open ocean; some islands are protected by headlands and other islands, while others are perched at the edge of the Sound (Fig. 2b), exposed to the full force of incoming storms. Plant communities on these islands consist of salt-tolerant herbs and grasses at the

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**Fig. 1.** The predicted distribution of plants on mainland and island sites across a gradient of wave exposure. (a) The region above the highest intertidal organism but below the lowest plant (i.e., the bare rock gap) should increase in vertical extent at sites exposed to stronger ocean waves because the lower limit of plants should move up the shore faster than the upper limit of intertidal organisms. Furthermore, some plant species may persist lower on the shore than others (e.g., if some species are more salt-tolerant), especially at more wave-exposed sites. Two simple metrics can be calculated easily for any island once the relationship between plant presence and wave exposure has been quantified for an archipelago: habitable height and habitable area. If wave exposure limits plant distribution on islands, these simple metrics should predict island plant presence and plant species richness. Specifically, a wave-protected island (b) should have more species than a wave-exposed island of the same surface area above the high tide line (c). Furthermore, a small wave-exposed island should be absent of plants if its height falls below the predicted lower limit of plants (i.e., if its habitable height is zero).
margins of the seashore, while the prevailing vegetation type on the inside of larger islands is coastal coniferous forest dominated by a small number of canopy-forming conifers (Cody 2006). Bird-dispersed shrubs and small trees occur in the forest understory and dominate the forest edge habitat closer to the shoreline (Burns 2005).

Estimating wave exposure

We estimated the degree to which each island or mainland site was exposed to disturbance from incoming waves following the approach used by Burns and Neufeld (2009). This metric uses the log of the angle of exposure (in degrees) of an island to the predominant swell direction, in this case coming from the southwest, as a proxy for onshore exposure.

Fig. 2. (a) A map of southern Vancouver Island, showing the location of Barkley Sound, where this study was conducted. (b) A map of the vertical elevation survey sites (N = 15) and the island sites (N = 106) sampled in this study. In this archipelago, swell approaches from the west and southwest.
water velocity of breaking waves. The benefit of this simple approach is that exposure measurements can be made with nothing more than a map and compass, or a computer connected to the internet. A potential drawback is that the metric may not be precise enough to quantify important variation between islands. Therefore, to validate this simple metric, we tested whether this exposure angle (on a log scale) accurately predicted published longer-term onshore water velocity measurements for five sites in Barkley Sound (Arsenault et al. 2001, Marchinko and Palmer 2003). Our simple metric (the log10 exposure angle) predicted most of the variation in measured onshore intertidal wave force at these sites (linear regression, adjusted $R^2 = 0.87, P_{4.1} = 0.004$). Therefore, we used the log10 exposure angle as a measure of incoming wave velocity in all subsequent analyses (Appendix S2: Fig. S1).

Vertical elevation surveys

To assess the lower elevation limits of plants, we surveyed 15 sites in July 2015 (Fig. 2b). We chose sites that (1) varied in exposure to incoming waves ranging from completely protected sites to those exposed to the full force of incoming wind and waves (exposure index range: 0–2.26), (2) faced approximately southwest, (3) had a consistent slope of ~15–35°, and (4) were free of obstructions below the low tide line that could impede the shoreward movement of incoming waves. Some of these sites occurred on mainland Vancouver Island ($n = 6$), and others occurred on other islands in Barkley Sound ($n = 9$; Fig. 2b). The inclusion of both island and mainland sites in our estimates of vertical elevation for each species allowed us to increase the sample of sites that met our selection criteria, and there is no reason to believe that including these sites could bias our estimates of minimum vertical elevation of plants at a particular exposure. If a species was absent from a particular site (either because it had not dispersed there or because it could not persist there), we simply did not use that site to predict the lower limit of that particular species. In other words, although dispersal limitation could restrict which species are found at some island sites, this is not expected to bias our results.

At each site, we assessed species elevation along 1–3 vertical transects depending on availability of suitable habitat ($n = 31$ transects in total). Where the horizontal range of sites allowed, we ran three transects spaced at least 10 m apart. In sites where the suitable habitat was limited, we fit as many transects as possible while maintaining the 10-m spacing.

We recorded the upper limit of intertidal groups (barnacles, Balanus glandula, and seaweed, usually Fucus distichus) and the lower limit of each terrestrial plant species encountered 1 m on either side of each transect. Elevation measurements were made using stadia rods and sight levels in relation to local tide predictions (relative to the Canadian Hydrographic Service standard, Lower Low Water, Large Tide; LLWLT). Grasses were included in the terrestrial species pool when considering the lower limit of plant species, but excluded from our analyses of species-level patterns due to the challenge of identifying grasses to species in the field when flowers and seeds are absent.

Each transect extended up the shore from the highest reaches of intertidal barnacles to 3 m above the lowest occurrence of a terrestrial plant, or to where the lower limit of the first 10 new plant species had been reached if this limit occurred <3 m above the lowest plant on that transect. We used this 10-species limit to avoid sampling too far into the forest understory at wave-sheltered sites and because forest understory is not representative of the habitat on the islands whose plant communities we sought to predict.

Testing model predictions for habitable height

In order to validate our estimates of inhabited island height, we compared predictions of the habitable height of islands from our vertical elevation surveys (Fig. 3) to measured habitable heights of 37 islands in Barkley Sound (Fig. 4). In 2011, islands were selected to represent a range of sizes and exposures to incoming waves (area range: 100–1000 m²; exposure index range: 0–1.46). To obtain predicted habitable height, we measured the height of the islands above the upper limit of the intertidal zone (defined by the highest intertidal alga) and subtracted model predictions of bare rock gap height from the best-fit model of bare rock gap against exposure (Fig. 3). Inhabited island height (i.e., observed habitable height) was determined by measuring the vertical distance from the lowest plant to the
top of the island on a uniform section of shoreline on the southwest side of each island.

**Island species surveys**

In July 2015, we surveyed 106 small islands (area range: 1–4000 m²; exposure index range: 0–2.26) in Barkley Sound to investigate how island size and exposure to waves influenced (1) whether an island was occupied by plants, (2) how many species were present, and (3) which species were present. The height of each island was measured using standard surveying techniques and recorded as the height above LLWLT. The land area of each island above the intertidal zone was approximated as the conical area above the highest barnacles following Burns (2007). Each island was then surveyed exhaustively to compile a species list of vascular plants. As above, grasses were included in the terrestrial species pool (treated as a single species) when considering whether an island was occupied, but excluded from our analyses of species-level patterns.

**Statistical analyses**

All statistical analyses were conducted in R 3.1.2. To test whether some species generally occurred lower on the shore than others, we fit an ANCOVA to the log-transformed lower limits of the eight most common plant species found in the vertical elevation surveys. An ANCOVA was fit in two ways: using the site as the unit of replication (with transects averaged for each site) and using transect as the unit of replication. In both cases, the response variable was elevation above LLWLT and the predictor variables were species (categorical) and exposure index (continuous). To predict whether each island was tall enough to be able to support plant life, we calculated habitable height using the best-fit relationship between wave exposure and lowest plant height from the vertical elevation surveys (Fig. 3). We tested both linear and
exponential models and determined the best fit using AICc. Then, by assuming that each island was approximately conical (as in Burns 2007), we estimated habitable area \( (A_{hab}) \) of each island by substituting the habitable height \( (h_{hab}) \) of each island into the following equation where \( h \) is the height of each island above the barnacle line and \( r \) is the back-calculated radius of each island (see Appendix S1 for a thorough derivation of this equation):

\[
A_{hab} = \pi \frac{h_{hab}r}{h} \sqrt{\left(\frac{h_{hab}}{h}\right)^2 + (h_{hab})^2}.
\]

In order to determine the best predictors of species richness, we fit exhaustive linear models between species richness and island area, height, wave exposure, habitable height, and habitable area, as well as their interactions. We then used AICc model selection criteria to determine the best non-redundant predictive model. To prevent the overrepresentation of zero-values in the dataset (as suggested by Morrison 2014), species richness models included only the 97 islands that were larger than the smallest islands known to contain plants. The nine excluded islands were all under 2 m² in area and under 5 m (above LLWLT) in elevation. When models were run on all 106 islands for completeness (Appendix S2: Table S8), interpretation of results did not differ. To enable comparisons with previous studies of diversity on small islands, we also compared simple linear regressions to zero-slope and two-slope piecewise linear regressions (Appendix S2: Table S4) following the approach used by Morrison (2014).

To predict the suitability of small islands for plants at all, and for the eight common plant species (Appendix S2: Table S1) on their own, we fit models to data from vertical elevation surveys to assess the relationship between minimum shore height and wave exposure. Habitability was determined by estimating wave exposure for each island and using these regressions to predict the minimum island height required to support plants. An island was deemed habitable unless habitable height was equal to or less than 0. We tested these predictions of habitability using chi-square tests and binomial logistic regressions. We compared two different predictions of habitability for the eight most common plant species. The first set of predictions was generated using the lower limit of plants in general. The second set of predictions was generated using species-specific relationships between wave exposure index and minimum occupied shore height from vertical elevation surveys. Models were then compared using AICc model selection criteria.

**Results**

**Vertical elevation surveys**

At more wave-exposed sites, the lower limit of terrestrial plants moved further up the shore than those at wave-protected sites. This asymmetry created a region of bare rock that was more than seven times greater on more wave-sheltered sites (the lowest plant was attached 8 m above the highest intertidal organism on average at the most wave-exposed sites; Fig. 3). This relationship was best fit by an exponential model (Appendix S2: Table S2), with wave exposure explaining 72% of the variation in the size of the bare rock gap among sites. Similarly, wave exposure explained 82% of the variation in the lower limit of plants among sites when fit with an exponential model. Lower elevation limits also varied among species (ANCOVA results shown in Appendix S2: Table S3), with some species generally occurring lower on the shore than others (Appendix S2: Fig. S3). Finally, wave exposure had an effect on the number of species that were found in the first meter of our vertical elevation surveys; more than twice as many species were found in this zone at wave-protected sites than at wave-exposed sites on average (Appendix S2: Fig. S4).

**Predicting habitable height and habitable area**

The vertical extent of habitable land on islands (habitable height) predicted by our model very closely aligned with the measured inhabited height in an independent set of 37 islands measured (Fig. 4). Although there was no significant difference between predicted and observed values (paired t test: \( t_{36} = 1.94, P = 0.0591 \)), the slope of this relationship differed significantly from 1 (linear model: Observed = 0.75 Predicted + 0.12; \( F_{1,35} = 15.4, P = 0.0004 \)), such that...
predictions of habitable height from our vertical elevation surveys tended to slightly overestimate what was observed, and this difference was most pronounced on the tallest small islands.

When model predictions were applied to hypothetical islands (Appendix S2: Fig. S2), the most exposed islands were predicted to contain no habitable land until uncorrected island area exceeded approximately 1000 m². When comparing predictions between island shapes, relatively flat islands were predicted to contain less habitable area than were steep conical islands when wave exposure was incorporated into estimates of habitable land. Islands up to approximately 100,000 m² were significantly affected by exposure; exposed islands smaller than this threshold had >10% of their area that was deemed uninhabitable when compared to similar-sized wave-protected islands (Appendix S2: Fig. S2).

**Island species richness**

The linear model containing habitable area alone was the top-ranking model according to AICc (Fig. 5, Table 1), and explained 69% of the variation in species richness (compared to only 37% for the model containing total uncorrected area). The closest top-ranking three-variable model (which included height, area, and exposure and their interactions) explained 64% of the variation in species richness (Fig. 5, Table 1). Wave exposure index was not a significant predictor of species richness on its own (Table 1), but was included in interaction terms of the best two- and three-variable models. Fitting piecewise regressions to the data in Fig. 5a, c produced similar qualitative results to those obtained using simple linear regression; piecewise models of the uncorrected SAR (R² = 0.46) were a poorer fit than for the SAR using habitable area (R² = 0.72), and the difference in model fit between piecewise and simple linear regression diminished markedly for the habitable SAR (Appendix S2: Table S4, Fig. S5).

**Island occupancy**

When island height was corrected for the known effect of wave exposure based on best-fit models from the vertical elevation surveys, these
Habitable height estimates were a good predictor of whether islands were occupied by plants in general, and by individual species (Fig. 6; Appendix S2: Table S5). Only five out of 50 islands that were deemed uninhabitable (i.e., habitable height < 0) were occupied by plants (Fig. 6; Appendix S2: Table S5), and many of these fell within the confidence intervals of our estimates. However, islands predicted to be habitable (i.e., habitable height > 0) only sometimes supported plants (64% for plants in general; Appendix S2: Table S5). For all eight species examined individually, as well as for plants in general, habitable height had a strong and significant effect on observed island occupancy (Table 2; Appendix S2: Table S6). Species-specific predictions of lower limits were better predictors of species-specific island occupancy than predictions based on the lower limit of plants in general (Appendix S2: Table S7).

**DISCUSSION**

We devised a simple quantitative framework for how disturbance should alter the amount of habitable land available on islands and show how this framework can dramatically improve predictions of species diversity in a temperate island plant community. Our result that plants move up the shore in more wave-exposed areas is unlikely to surprise most ecologists—or most visitors to the seashore for that matter. The pattern itself is intuitive and is probably widely observed (though to our knowledge ours is the first attempt to systematically quantify the shape of this relationship). What should surprise most ecologists, however, is that by incorporating this pattern into a simple quantitative framework, we were able to nearly double the ability of area to explain patterns of species richness on small islands.

These findings have important implications for how the area of small islands should be measured and reported. Most strikingly, our results suggest that a large proportion of land above the high tide line is not habitable on exposed small islands (Appendix S2: Fig. S2). Consider a hypothetical island that is roughly conical, has a 45° slope, and rises 8 m above the high tide line (Appendix S1). Based on our measurements in Barkley Sound (Fig. 3b), this hypothetical island would contain approximately 217 m² of land available to plants in a wave-protected region but only 4 m² of habitable land in a wave-exposed region (<2% of the land above the high tide line). According to our simulations, the most exposed islands should be inhospitable to plants until they exceed approximately 7 m in height and 160 m² in area. At the other end of the size spectrum, islands as large as 100,000 m² should lose more than 10% of their habitable area in exposed locations (Appendix S2: Fig. S2). Importantly, if the effect of exposure is ignored, islands are predicted to contain the same land area and support the same number of species regardless of their exposure to waves. These findings suggest that wave disturbance can significantly influence the amount of habitable land on islands as large as 100,000 m².

### Table 1. AICc values from model testing performed to determine the best predictor of species richness on small islands in Barkley Sound.

| Parameters | AICc  | Δi | F-statistic | Adjusted $R^2$ | df  | P-value   |
|------------|-------|----|-------------|----------------|-----|-----------|
| Habitable area | 517.2522 | 0  | 214.9       | 0.69           | 95  | <0.0001   |
| Height × Exposure + Area | 536.1753 | 18.9231 | 43.13       | 0.64           | 92  | <0.0001   |
| Area × Height × Exposure | 538.5453 | 21.2931 | 25.68       | 0.64           | 89  | <0.0001   |
| Height × Exposure | 541.2098 | 23.9576 | 51.66       | 0.61           | 93  | <0.0001   |
| Area × Exposure + Height | 551.9139 | 34.6617 | 33.23       | 0.57           | 92  | <0.0001   |
| Habitable height | 571.4617 | 54.2095 | 82.22       | 0.46           | 95  | <0.0001   |
| Area + Height | 577.2375 | 59.9853 | 37.48       | 0.43           | 94  | <0.0001   |
| Area × Exposure | 583.9386 | 66.6864 | 22.21       | 0.40           | 93  | <0.0001   |
| Area | 586.3723 | 69.1201 | 56.97       | 0.37           | 95  | <0.0001   |
| Height | 593.5327 | 76.2805 | 46.16       | 0.32           | 95  | <0.0001   |
| Exposure | 631.1415 | 113.8893 | 0.7892 | 0.00           | 95  | 0.3766 |

Notes: df, degrees of freedom. Data tested include only islands larger than the smallest island with plants (N = 96 islands). AICc is the small-sample Akaike information criterion; Δi is the difference in AICc between current and best model.
So how have previous studies measured area? A variety of approaches have been used, but none have directly captured the effect of exposure that we document here. In decades of research in Barkley Sound (the same archipelago we studied), Cody (2006) used the surface area above the high tide line (delineated by the upper limit of the intertidal alga *Fucus distichus*) as a measure of available land. Researchers studying patterns of species richness on small islands in the Bahamas have measured the two-dimensional area above the high tide line and have also tested the explanatory power of the actual vegetated area occupied by plants in some models (Morrison 2002, Morrison and Spiller 2008). The two most common metrics of area reported—area above the high tide line, and vegetated area—are problematic for opposite reasons. Area above high tide includes area that is uninhabitable on wave-exposed islands as described in detail earlier. In contrast, vegetated area leaves out potentially habitable land by failing to distinguish between permanently inhospitable land and land that is habitable but temporarily unoccupied. Finally, in many other cases, descriptions of methods are simply not detailed enough to know what approach was used (Panitsa et al. 2006, Sfenthourakis and Triantis 2009). Given the large documented effects of wave disturbance on the amount of habitable land available on small islands, future studies should quantify habitable area much more carefully, especially for size classes of islands predicted to be most affected (Appendix S2: Fig. S2).

Fig. 6. Logistic regressions of plant presence vs. habitable height ($h_{hab}$) for (a) all plants, (b) *Gaultheria shallon*, (c) *Fragaria chiloensis*, (d) *Achillea millefolium*, (e) *Picea sitchensis*, (f) *Vaccinium ovatum*, (g) *Potentilla villosa*, (h) *Lonicera involucrata*, and (i) *Plantago maritima* for 106 small islands in Barkley Sound, British Columbia. Dotted lines indicate $h_{hab}$ equals zero, above which islands are predicted to be habitable for a given taxon. In panel (a), light green data points have confidence intervals that include zero, while dark green points exclude zero.
Table 2. Logistic regressions of plant occupancy as a function of habitable island height for 106 small islands.

| Species                  | Pseudo-$R^2$ | z-value | df | P-value |
|--------------------------|--------------|---------|----|---------|
| All plants               | 0.4674       | 4.691   | 104| <0.0001 |
| Vaccinium ovatum         | 0.2464       | 3.781   | 104| 0.0001  |
| Fragraia chiloensis      | 0.4603       | 3.777   | 104| 0.0001  |
| Gaultheria shallon       | 0.3719       | 3.867   | 104| 0.0001  |
| Lonicera involucrata     | 0.2401       | 3.749   | 104| 0.0002  |
| Potentilla villosa       | 0.2173       | 3.737   | 104| 0.0002  |
| Plantago maritima        | 0.1841       | 3.698   | 104| 0.0002  |
| Picea sitchensis         | 0.2902       | 3.751   | 104| 0.0002  |
| Lonicera involucrata     | 0.2401       | 3.749   | 104| 0.0002  |
| Potentilla villosa       | 0.2173       | 3.737   | 104| 0.0002  |
| Vaccinium ovatum         | 0.3227       | 3.837   | 104| 0.0001  |

Note: df, degrees of freedom.

area—we also compared our best estimate of habitable island area against other combinations of explanatory variables thought to influence species richness on islands (e.g., island height, uncorrected area, and exposure index; Table 1). One important outcome of this approach was that habitable area outperformed all other combinations of explanatory variables in predicting species richness (Table 1). Furthermore, in the best-ranking multivariable models, exposure index was not included as an important factor on its own, but instead remained tied up in complex interactions with other variables. This is noteworthy because it shows that our estimate of habitable area—which encompasses a mechanistic connection between wave exposure and uncorrected area—captured important variation beyond what could be captured by other purely statistical models used in previous studies. Together, these results are relevant to the ongoing debate surrounding the small-island effect (Triantis and Sfenthourakis 2012, Morrison 2014, Chisholm et al. 2016). We were able to significantly reduce the amount of unexplained variation in species richness of small islands and thus largely account for the small-island effect simply by more precisely quantifying the area of islands relevant to the community under study.

While the primary focus of the current study was on species richness, we also explored the ability of our approach to predict plant occupancy on islands. Overall, we successfully predicted the occupancy state of plants on 77% of surveyed islands. Of the 25 incorrect predictions, most (20) were false positives (i.e., islands that were deemed habitable but lacked plants). In contrast, only five of the incorrect predictions were false negatives (i.e., islands predicted to lack plants but were occupied), and all but one of these islands had habitable height estimates with confidence intervals that included positive values. These results clearly suggest that our estimates of habitable land better predicted plant absence than plant presence. This outcome provides some additional evidence for why vegetated area is a poor predictor of habitable land. Just because land is potentially habitable does not mean it is inhabited at any given time (Spiller et al. 1998). Beyond possessing habitable land, many other factors may influence whether an island contains plants (e.g., dispersal limitation, establishment, stochastic extinction, habitat diversity, and ecological subsidies). Therefore, positive habitable heights should be thought of as a first-pass filter upon which to consider other factors known to have an influence on island occupancy. By better quantifying and accounting for the role of exposure to waves in estimates of habitable land, future studies of small islands may be better able to study these other factors known to influence island communities.

One hypothesis that follows from our approach is that habitable land at the edge of exposed islands (i.e., land just above the lowest plant) may be prone to disturbance during periodic storm events making this lower quality habitat suitable to a restricted number of species. Results from the current study and some previous work support this view. First, some species occurred higher on the shore than others (Appendix S2: Table S3, Fig. S3); and species-level occupancy (i.e., whether a particular species occurred on a particular island) was better predicted by species-specific occurrence curves from vertical elevation surveys than by the curve for plants in general (Appendix S2: Table S7). We also found fewer species on average in the first vertical meter of land at exposed sites than at protected sites in the vertical elevation survey (Appendix S2: Fig. S3). In a previous study in Barkley Sound, plant extinction rate was higher on more exposed islands and extinctions outnumbered colonizations overall during a 10-yr period of intense storm events (Burns and Neufeld 2009). On Kapingamarangi Atoll, some species common to the interior of large islands had extensive leaf damage when found on the exterior of the same islands (Niering
While our approach to quantifying plant zonation relative to a standard datum is novel as applied to island SARs, the existence of patterns of vertical zonation (and the approach we use to document them) should be familiar to most practicing intertidal ecologists. The vertical upper limits of many intertidal organisms are known to be affected by the duration of exposure to air and water, and these limits are thought to structure many aspects of these marine communities (Harley 2007). For example, even geographically proximate intertidal shorelines can have dramatically different species if sites vary in exposure to incoming waves (Ricketts et al. 1985). Horizontal and vertical variation in wave force also interact, such that marine species live higher on the shore at more wave-exposed sites (Robles and Desharnais 2002, e.g., Harley and Helmuth 2003). Our study suggests that these long-standing observations of intertidal systems may be broadly applicable to terrestrial species found at the land–sea boundary.

Although the simplicity of our overall approach provides many benefits, it is not without limitations. First, although our simple exposure index metric appears to correlate relatively well with the more precise approach of measuring maximum incoming wave velocity (albeit with a very small sample size for this comparison), our simpler metric no doubt fails to capture much about how islands are exposed to disturbance. Exceptions to our predictions of occupancy support this view. Of the five islands that were predicted to be uninhabitable but observed to have plants, all occurred in moderately wave-exposed environments. In particular, one island which was predicted to have no plants was found to have 12 species. This island was surrounded by other islands and behind multiple large reefs suggesting that it was likely much less exposed than our objective method predicts. This suggests that our simple wave exposure index may be too coarse to capture more fine-scale variation in exposure at intermediate values and may have limitations when considering some islands with more complex local topography. Our approach also does not take into account the complex variation in physical factors as waves and storms wrap around the back of each island (Liu et al. 1995). Another simplifying assumption of our approach is that each island is modeled as a cone, ignoring variation in shoreline topography and island shape. Indeed, some islands in our study violated this assumption; one island was four times as long...
(40 m) as it was wide (10 m). In future studies, we may be able to refine our understanding of how disturbance interacts with island topography by more carefully measuring each island’s shape using rapidly developing remote sensing technology (Klemas 2015, Nijland et al. 2017), and by more carefully measuring physical gradients in salinity, temperature, and water velocity associated with variation in exposure to ocean waves. Yet, despite this long list of possible refinements, the fact that our approach works as well as it does shows that this simple approach captures important variation in each island’s exposure to disturbance that has been ignored by previous studies.

Given the long history of using islands as models for other fragmented landscapes, our findings are also relevant to a broader literature aimed at predicting species distributions in an increasingly fragmented landscape worldwide (Jiménez-Valverde et al. 2008, Kearney and Porter 2009, Haddad et al. 2015). In environments where habitat is marginal or in short supply, disturbance may cause local extinction of a particular species or functional group which in turn could lead to large effects on communities and biodiversity. Understanding factors that influence vertical range limits is particularly important in light of the shifting abiotic conditions under climate change. For example, in Pacific rocky intertidal communities, barnacles and mussels have been squeezed into a progressively narrower band of the shore over the last 50 yr as their upper limit has been pushed down by rising temperatures while their lower limit (set by predation) remained unchanged (Harley 2011). In areas where the mussel bed was lost, species richness dropped by nearly 50% (Harley 2011). Terrestrial species restricted to the edge of the shoreline (e.g., Plantago maritima in this study) may be similarly vulnerable to uncoupled changes in lower and upper limits.

One such change predicted to affect the lower limit of plants in our system appears already to be occurring. Storm intensity and accompanying wave height have been rising in the Northeast Pacific (Ruggiero et al. 2010) and are expected to continue to do so into the next century (Barnard et al. 2015). These forecasted changes in wave height and intensity could further reduce the area available to plants on small islands in affected archipelagos. Although such changes to a community on a single island may seem insignificant, the impact of rising wave disturbance on nearshore habitat may be much more substantial when one extrapolates the effects to a whole archipelago (or a whole coastline). This may be especially true where at-risk species depend on the viability of many interconnected small populations on islands (González-Mancebo et al. 2012).

**Conclusions**

Here, we developed a framework that relates each island’s susceptibility to disturbance to the amount of habitable land available for terrestrial species. By using this framework to refine estimates of habitable land for small islands, we were able to nearly double the amount of variation in species richness explained compared to a commonly used estimate of island area that ignores the role of disturbance. Given the prevalence and heterogeneity of disturbance events in ecological communities, studies of species richness in small, fragmented habitats would benefit from incorporating disturbance into estimates of habitable area, and we provide a simple framework for doing so that should be applicable in many archipelagos and across a range of taxa. By more carefully quantifying and predicting habitable areas, we may be able to better study the relative importance of other factors thought to influence diversity in fragmented communities such as those on small islands.

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Supporting Information

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