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Community ecology

Climate change and elevational diversity capacity: do weedy species take up the slack?

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Climate change leads to species range shifts and consequently to changes in diversity. For many systems, increases in diversity capacity have been forecast, with spare capacity to be taken up by a pool of weedy species moved around by humans. Few tests of this hypothesis have been undertaken, and in many temperate systems, climate change impacts may be confounded by simultaneous increases in human-related disturbance, which also promote weedy species. Areas to which weedy species are being introduced, but with little human disturbance, are therefore ideal for testing the idea. We make predictions about how such diversity capacity increases play out across elevational gradients in non-water-limited systems. Then, using modern and historical data on the elevational range of indigenous and naturalized alien vascular plant species from the relatively undisturbed sub-Antarctic Marion Island, we show that alien species have contributed significantly to filling available diversity capacity and that increases in energy availability rather than disturbance are the probable underlying cause.

1. Introduction

With climate change, the timing of biological events is shifting, the body size of many taxa is declining and species ranges are moving, commonly with extensions into higher latitudes and/or elevations [1–3]. Species range shifts have also been forecast to lead to changes in local and regional diversity [4]. Among these forecasts is the idea that in areas that are not water-limited, diversity capacity will increase with increasing resource capacity, such as net primary productivity [5,6]. However, owing to relatively slow rates of speciation and movement of most species, this capacity (e.g. for plant species richness) will typically be taken up by cosmopolitan, weedy species that are rapidly moved around by humans [5]. Documenting weedy take up of diversity capacity in most of these systems is likely to be confounded by human development and disturbance, which also promote the establishment of weedy species [7], and are increasing, even in regions that are already developed [8,9]. Thus, for many regions, it might not be clear whether an increase in diversity is a consequence of climate change or of increasing human disturbance [10].

One way of distinguishing among these drivers is to find a non-water-limited region where human disturbance is minimal, but where climate is changing, and then to test the hypothesis that diversity capacity is mostly being taken up by weedy species. The sub-Antarctic islands provide exemplars of such systems. They are not water-limited, richness is related to energy input, their climates are changing rapidly and they have typically been invaded by European weedy species, which continue to be introduced at relatively low

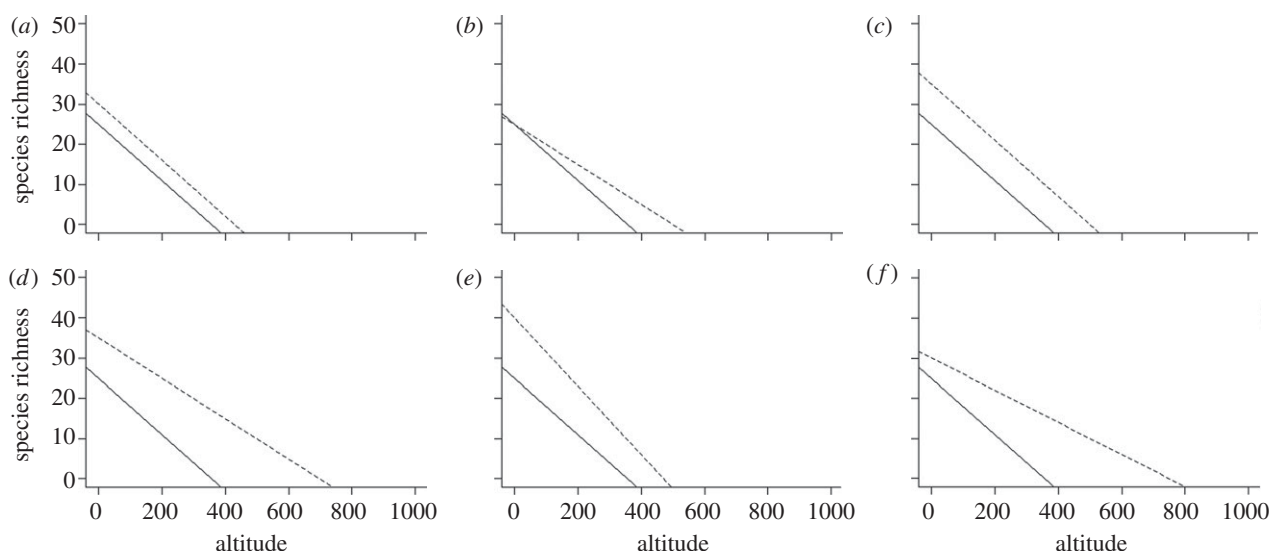


Figure 1. General predictions for changes in diversity capacity along non-water-limited elevational gradients (the species richness and altitude values are examples only). The solid line indicates the original situation and the dashed line the forecast or realized change. (a) Forecast increase in diversity capacity. (b) Realized response by indigenous species in the absence of colonization of the local species pool by new species; (c) change owing to colonization of the local species pool by alien species; (d) a combination of responses in (b) and (c); (e) alien colonization rate of the local species pool exceeds the rate of change of diversity capacity; (f) owing to contingent local extinction responses of some indigenous species, richness does not change significantly at lower elevations, but increases at higher elevations as expected with increasing diversity capacity.

rates [11,12]. Moreover, the extent of terrestrial human disturbance at these islands is very low [13]. This is true of Marion Island, which we use here to test the hypothesis that weedy invasive plants are taking up diversity capacity as climate changes [14]. Specifically, we developed several general hypotheses regarding the ways in which energy increases alter the relationship between species richness of vascular plants and elevation, given the decline in energy with elevation, and climate change-related increases in energy availability. The simplest prediction is an increase in richness at all elevations because of increasing energy availability (figure 1a). However, because isolation limits colonization and speciation is uncommon over sub-century timescales, the richness–elevation relationship for indigenous species should show no intercept change, but a decline in the magnitude of the slope, because increasing energy levels lead to higher richness at high elevations (figure 1b). For introduced species, the intercept should increase, but the slope remains unchanged (figure 1c), because new alien species colonize both lowland and upland areas. An increase in the intercept and decline in the magnitude of the slope should characterize the total richness–elevation relationship (figure 1d). Alternative, colonization rate-dependent and contingent outcomes, such as local species extinctions, are also possible (figure 1e,f).

2. Material and methods

Marion Island has a tundra-type vegetation that varies from sea level tussock grasslands to high-elevation polar desert [15]. Since 1947, the mean annual temperature has increased by approximately 1.8°C (approx. 1.5° since 1965–1966) [14]. A recent study showed that following the original 1965–1966 survey of vascular plants [16], their elevational extent has on average increased by 70 m [14]. During the original survey, 14 naturalized alien species were already present, with some being widespread, having been established since the late 1800s. This number has subsequently increased (to 17), with many of the

naturalized alien species having increased their ranges and abundances in the lower elevations of the island [15,17].

Here, we used the previous survey data on indigenous species [14,16] and supplemented them with information on the altitudinal distribution of all naturalized alien species in 1965–1966 based on new surveys of the distribution of all naturalized species in 2006–2010. In brief, all geo-referenced records of alien species were used to calculate richness per 100 m altitudinal band. The major survey consisted of a grid-based search method at 0.5 arc-min intervals, where all alien species were recorded at and *en route* to these grids, ensuring comprehensive coverage. Ad hoc records were also obtained during censuses of indigenous species distributions and as part of other surveys (see electronic supplementary material).

Richness of naturalized alien species and indigenous species was calculated per 100 m altitudinal band. Our hypotheses depend on a strong negative relationship between elevation and energy availability (for which temperature is a reasonable proxy in non-water-limited systems [18]). Thus, we investigated the relationship between average elevation and mean annual temperature (MAT) for each band using simple linear regression in R v. 2.15.1 [19]. MAT was calculated from hourly temperature recordings made since 2002 by Thermochron iButton data loggers placed just below the surface of the soil (see electronic supplementary material). To test the general predictions we developed for elevational gradients (figure 1), we determined whether the slopes and intercepts of the relationships differed among the two survey periods (1965–1966 and 2006–2010). All relationships were examined using generalized linear models assuming a negative binomial distribution, using a log-link function, and run in R v. 2.15.1 [19], using the MASS library [20].

3. Results

Mean annual temperature and elevation show a strong, significant negative relationship ($r^2 = 0.979$, $F_{(1,7)} = 384$, $p < 0.0001$). Over time, indigenous species richness increased at most elevations, but declined at the lower three bands, with no significant change in the intercept of the elevation–richness relationship and a significant decline in the magnitude of the

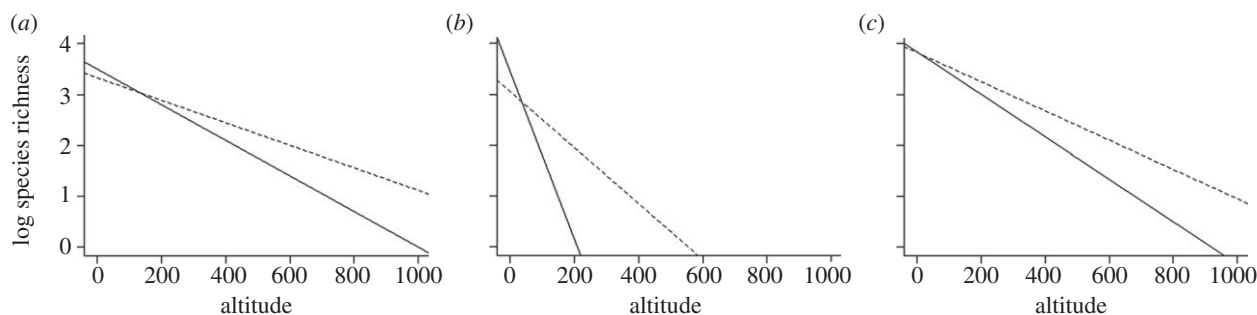


Figure 2. Fitted lines from the models summarized in table 1 illustrating the change in richness across elevation for the indigenous, alien and total species at sub-Antarctic Marion Island between 1965–1966 (solid lines) and 2006–2010 (dashed lines). The original data are provided in the electronic supplementary material. (a) Indigenous species, (b) alien species, (c) total species.

Table 1. The relationship between species richness and elevation on Marion Island for indigenous, naturalized alien and all species for two periods (years: 1965–1966; 2006–2010) (generalized linear models, negative binomial distribution, log-link function [19,20]). A significant interaction term indicates a change in slope between years and a non-significant year effect indicates no change in intercept among survey periods.

relationship	year	elevation	interaction (year \times elevation)	slope estimates
	<i>z</i> , <i>p</i>	<i>z</i> , <i>p</i>	<i>z</i> , <i>p</i>	1965, 2010
indigenous	−0.74, 0.46	−6.90, <0.001	1.97, 0.048	−0.0035, −0.0022
alien	−0.83, 0.40	−3.69, <0.001	2.38, 0.018	−0.017, −0.0056
total	−0.10, 0.92	−8.32, <0.001	2.12, 0.034	−0.0042, −0.0029

slope, reflecting upward range expansion (table 1, with model fits illustrated in figure 2). Alien species richness increased (though the intercept did not change significantly) at all low elevations, and these species appeared above 300 m for the first time in the later survey period, resulting in a substantial decline in the magnitude of the elevation–richness slope (table 1, figure 2). Total richness showed no change in intercept among years, but the magnitude of the slope of the richness–elevation relationship declined significantly (figure 1*f* rather than 1*d*).

4. Discussion

Significant upslope expansion by several indigenous species and the consequent increases in indigenous richness in most elevational bands [14] explain the significant decline in the magnitude of the elevation–indigenous richness relationship between 1965–1966 and 2006–2010, in keeping with the primary prediction made for the indigenous species as a consequence of increasing energy availability (figure 1*b*). The isolation of the island means that no new species have colonized naturally, and the short period has precluded speciation, thus explaining the absence of a change in richness among years, in keeping with previous predictions [5]. Nonetheless, a few species have vacated the lower elevations, although the exact reasons for this change remain poorly understood [14].

Over the period examined, alien species richness has increased at all elevations up to 600 m, but more so at the higher altitudes. Although the overall change in intercept among years was not significant, the magnitude of the slope of the richness–elevation relationship has declined substantially and significantly. The increase in richness at most elevations is in keeping with predictions that alien species will take up diversity capacity in non-water-limited systems [5,6].

The combined outcome of these changes is that between the two periods, richness has typically not changed significantly at the lower elevations on Marion Island, but the magnitude of the slope of the elevation–richness relationship has declined substantially (approx. 30%). Although richness of both indigenous and alien species has increased at mid-to-high elevations (figure 2), increases in alien, typically weedy, species richness at all altitudes up to approximately 600 m have contributed most to the significant, predicted decline in the slope of the total richness–elevation relationship. These results match one of the contingent predictions for the outcome of increasing elevational diversity capacity (figure 1*f*). They also illustrate how weedy species, in this case alien to the island, may show the most prominent responses to climate change, and hence demonstrate the importance of considering biological invasion in general models forecasting the impacts of such change [6]. Moreover, because the Marion Island terrestrial ecosystem has always been largely undisturbed by human activities (e.g. by exploitation/urbanization/agriculture) [15], the current results further demonstrate that realized increases in diversity capacity are due to growing energy availability and not due to increasing disturbance, thus supporting previous predictions [5,6]. An alternative explanation for the current findings is that the alien species are simply expanding their ranges over time. However, in that case and given the small absolute area of the island (approx. 290 km²), there is no expectation of a simultaneous increase in the elevational range of the indigenous species, which, as we demonstrate, is currently underway.

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