

Can the mass effect explain the mid-altitudinal peak in vascular plant species richness?

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Abstract

A mid-altitudinal peak in species richness is commonly observed and the mass effect (or source–sink effect) has been suggested as a possible cause. We test the importance of the mass effect for generating altitudinal patterns of plant species richness at two grain sizes using a simple estimate of sterility/fertility to indicate sinks and sources. To do this we identified species with fertile specimens (fertile species) and species with only sterile specimens (sterile species) in each sampling unit along altitudinal transects and assumed that the number of sterile species indicated the relative number of sink species, correspondingly that the number of fertile species indicated the relative number of source species when looking at the overall pattern of species richness along a transect. To evaluate this approach, we investigated the distribution of sterility and fertility of each species along the altitudinal transects. We found that sterile species are found more often at the edges and fertile species more often in the centre of the species altitudinal ranges than expected by chance. Using a fine grain, sterile species richness had a humped altitudinal pattern on all transects investigated at this scale, whereas using a coarse grain two of the three transects investigated had a humped pattern. At the fine grain, sterile species richness had a more pronounced peak than fertile species richness in two of the three transects investigated supporting the hypothesis of the mass effect, but this pattern did not persist at coarser grain. The observations at the fine grain are in accordance with the idea that the mass effect is important in shaping the mid-altitudinal peak in species richness, whereas the observations from the coarser grain are ambiguous.

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Zusammenfassung

Üblicherweise wird ein Höchstwert der Artenvielfalt bei mittleren Höhen beobachtet und der Masseneffekt (oder Quellen-Senken-Effekt) als mögliche Ursache vermutet. Wir testeten auf zwei Skalengrößen, wie wichtig der Masseneffekt für die Bildung des Höhenmusters der Artenvielfalt ist und benutzten eine einfache Abschätzung von Sterilität/Fertilität um Senken oder Quellen zu bestimmen. Um dies zu tun, identifizierten wir fertile Exemplare (fertile Arten) und Arten, die nur sterile Exemplare umfassten, in jeder Probeinheit entlang von Höhengradienten. Wir nahmen an, dass die Anzahl der sterilen Arten die relative Anzahl der Senkenarten angibt, und entsprechend die Anzahl der fertilen Arten die relative Anzahl der Quellenarten angibt, wenn das gesamte Muster der Artenvielfalt

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entlang eines Transektes betrachtet wird. Um diesen Ansatz zu bewerten, untersuchten wir die Verteilung von Sterilität und Fertilität für jede Art entlang der Höhengradienten. Wir fanden heraus, dass im Vergleich zu einer zufälligen Verteilung sterile Arten eher an den Rändern und fertile Arten eher im Zentrum der Höhenverbreitung der jeweiligen Art zu finden sind. Bei der Betrachtung auf einer feinen Skala zeigte die Artenvielfalt der sterilen Arten auf allen Transekten, die untersucht wurden, ein Höhenmuster mit Maximalwert, während auf einer größeren Skala zwei von den drei Transekten ein Muster mit Maximalwert zeigten. Bei einer feinen Betrachtung zeigte die Artenvielfalt steriler Arten in zwei von den drei untersuchten Transekten einen deutlicheren Höchstwert als die Artenvielfalt der fertilen Arten und stützt damit den Hypothese des Masseneffekts. Dieses Muster blieb allerdings bei einer Betrachtung auf größerer Skala nicht bestehen. Die Beobachtungen auf der feinen Skala stimmen mit der Idee überein, dass der Masseneffekt wichtig für die Ausbildung des Höchstwertes der Artenvielfalt in mittleren Höhen ist, während die Beobachtungen auf einer größeren Skala mehrdeutig sind.

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Introduction

The local distribution of a species is influenced by environmental factors, species interactions, and dispersal of the species. Patterns of species richness are simple summaries of species distributions. The effects of environmental factors and species interactions on richness patterns have been discussed extensively (Huston, 1994). In addition, an increasing number of studies now focus on the effect of dispersal on local species richness (e.g. Hubbell, 2001; Leibold et al., 2004). Dispersal mainly influences species distributions in two ways. Suitable habitats may not be colonised by a species because of dispersal limitations (Eriksson & Ehrlén, 1992; Tilman, 1997; Turnbull, Crawley, & Rees, 2000), or species may extend their range to habitats where they are able to survive for some time but are unable to produce enough offspring to sustain a viable population (Dias, 1996; Pulliam, 1988, 2000; Shmida & Wilson, 1985). Such populations are dependent on receiving propagules from source populations to survive over time. As early as 1869, Blytt, while describing the vegetation in a fjord area of Norway, noted the large number of alpine species in the lowlands. He explained this by the short distance between the fjord and the mountain top and proposed that seeds and roots are easily transported downwards by rivers, avalanches, etc. resulting in the establishment of alpine species in the lowlands. MacArthur (1965) described such species as “species having no business” in the area. Van Steenis (1961) compared the altitudinal distributions of species on several mountains in Java, which differed in maximum height. He noted that species were absent on some lower mountains even though their ranges on other mountains extended below the highest point on the lower mountains. Van Steenis suggested that the lower mountains did not have “zones of permanent establishment” (i.e. source areas) for the species. The establishment of populations at sites in which the

species cannot maintain viable populations without the constant input of propagules from other populations is referred to as both the mass effect by Shmida and Wilson (1985) and source–sink dynamics by Pulliam (1988, 2000).

The mass effect (or source–sink dynamics) is currently discussed as an important factor contributing to altitudinal richness patterns. In particular, it has been proposed as an explanation for the commonly observed mid-altitudinal peak in species richness (Grytnes, 2003a, b; Grytnes & Vetaas, 2002; Kattan & Franco, 2004; Kessler, 2000; Lomolino, 2001; Rahbek, 1997; Shmida & Wilson, 1985). The mass effect may create a mid-altitudinal peak in species richness because so-called hard boundaries restrict dispersal into an area (Grytnes, 2003b; Grytnes & Vetaas, 2002). The presence of hard boundaries can result in more sink populations at mid-altitudes because this area receives sink populations from sources both above and below. In contrast, the uppermost or lowermost parts of the gradient receive sink populations from one direction only (Grytnes, 2003b; Rahbek, 1997). Alternatively, the mass effect may cause a peak in richness around a transition zone (ecotone) somewhere along the gradient (Kunin, 1998; Lomolino, 2001; Shmida & Wilson, 1985). For instance, a peak has been demonstrated to occur around the forest line (Grytnes, 2003a).

It has proved difficult to assess the importance of the mass effect because it is difficult and time-consuming to identify sources and sinks correctly in nature (Dias, 1996; Diffendorfer, 1998). However, source populations usually have higher reproductive rates than sink populations (Hansen & Rotella, 2002; Kessler, 2000; Pulliam, 1988; Robinson, Thompson, Donovan, Whitehead, & Faaborg, 1995). This suggests that the presence or absence of fertile individuals within an area may be used as an estimate of sources and sinks. Species with fertile specimens in an area are more likely to have their source in that area than species with only sterile

individuals in that area. The fertility/sterility approach is not able to identify sink and source populations exactly as it is only a probabilistic approach, but the sterility/fertility averaged over many populations and many species can be used as an estimate of relative distribution of sources and sinks along altitudinal transects.

The main aim of this study is twofold. First, we want to evaluate if the simple approach of using fertility/sterility as an indicator of the source/sink status of species is valid; and second, we want to use this approach to evaluate the mass effect as a potentially important factor in creating a mid-altitudinal peak in vascular plant species richness along four altitudinal transects in Norway. This is done on two different sampling scales to see if the methods are robust to differences in grain size. For the first part of the aim, we specifically test if fertile individuals of species are found more often in the core part of their altitudinal ranges or if the fertile individuals are randomly distributed with respect to altitude. The importance of the mass effect is then evaluated by, first, quantifying the sterile species richness alone and, second, testing if the sterile species richness has a more pronounced hump than fertile richness. Finally, we will test if ecotones, together with the mass effect, are important in creating the observed peak in species richness, and discuss the possible importance of hard boundaries.

Assumptions and predictions

Population dynamics can be described by a simple equation: $N_{t+1} = N_t + b + i - d - e$, where N is number of individuals at time t or $t+1$, b is number of births, i is number of individuals immigrating, d is number of individuals dying, and e is number of individuals emigrating. If a local population is a source population $b > d + e$, i.e. the population is independent of immigration (i). If a local population is a sink population $b < d + e$, meaning that the sink population is dependent on immigration (i) to persist. The critical assumptions made in this study are that there exists a positive relationship between b and the frequency of fertility and that $d + e$ does not increase more than b with a higher frequency of fertility. Then a higher frequency of fertility will be positively related to the number of source populations. As populations tend to be larger and thrive better in the central part of a species range (Brown, 1984; Gaston, 2003; Hengeveld, 1990), source populations should in general be found in the central part of a species altitudinal range (Shmida & Wilson, 1985). An altitudinal gradient represents a strong environmental gradient and sink populations, if present, would be expected to be located towards the

altitudinal range margins of the species. Hence, if fertility/sterility is a good way of estimating source/sink, we expect that fertile specimens are found more frequently in the core part of their altitudinal ranges than at the range margins, but if $d + e$ alone is determining sources and sinks along the altitudinal gradient the fertility/sterility will be randomly distributed along altitude.

For the mass effect to contribute significantly to a mid-altitudinal peak in species richness, we would expect that sterile species richness has a mid-altitudinal peak. The existence of a humped sterile species richness pattern does not in itself provide strong support for the mass effect as this pattern would also arise if sterile species richness was a constant proportion of the total species richness at each altitude. On the other hand, the absence of such a peak would be a strong indication that the mass effect is not important. A stronger indication of the importance of the mass effect in creating a humped altitudinal pattern would be if the peak were found to be more pronounced for the sterile species richness than for the fertile species richness.

As mentioned above, the mass effect may enhance species richness in the middle of the transect either due to hard boundaries (Grytnes, 2003b; Grytnes & Vetaas, 2002) or due to an ecotone effect. An ecotone is an abrupt change in environment resulting in different species associations at either side of the ecotone (Brown & Lomolino, 1998). Sink species may inflate the richness around an ecotone due to dispersal over the ecotone (Brown & Lomolino, 1998; Lomolino, 2001; Shmida & Wilson, 1985;). Because two different species associations meet around the ecotone, the species turnover around the ecotone is expected to be higher in this area. Presence of sink species is expected to dampen the observed species turnover around the ecotone and we therefore hypothesise that using only the fertile species to quantify the turnover will result in a more pronounced turnover around the ecotone than if all species are used. We use two different definitions of the ecotone. First, the peak in species richness is hypothesised to be caused by an ecotone and we therefore assume that an ecotone is found in the area of the observed maximum in species richness. Second, Grytnes (2003a) suggested that the forest-line ecotone was partly responsible for the observed pattern of species richness along the seven transects studied because species from below the forest line could establish sink populations above, whereas alpine species could not establish sink species in the shady conditions below the forest line. We therefore use both the observed forest line and the area of maximum species richness to test if the ecotone together with mass effect is important for the observed mid-altitudinal peak in species richness.

Materials and methods

Sampling

The four transects sampled for this study (Tronfjellet, Grjothøi, Horndalsnuten, and Kvitingskjølen) are four of the seven transects described in detail in Grytnes (2003a). Data on fertility and sterility of the species were sampled for these four transects only. Samples were placed along the transects starting at as low an altitude as possible and avoided areas clearly influenced by human activity. The highest altitude sampled is either a local peak or where vegetation cover becomes discontinuous.

Along each transect, plots of $5 \times 5 \text{ m}^2$ ($10 \times 10 \text{ m}^2$ at the Grjothøi transect) were placed approximately every 20 m. The number of plots per transect varies from 43 at Horndalsnuten to 48 at Grjothøi. Within each plot five subplots of $0.5 \times 0.5 \text{ m}^2$ (four subplots at the Grjothøi transect) were placed systematically. Hereafter, these two grain sizes are referred to as *plot scale* and *subplot scale*. The two grain sizes are used to determine if the results are scale dependent.

Species that are observed with flowers or fruits within an area are more likely to belong to a source population than species with no flowers or fruits in an area. For each plot and subplot each species was recorded as either fertile or sterile. A fertile species had at least one individual with signs of sexually reproductive organs (plus vivipary), while sterile species only had specimens lacking signs of sexually reproductive organs in the plot or subplot.

Since the sampling was done in late August or September, it is assumed that all specimens that were going to set seed that season had at least visible flowers. Fertility/sterility was analysed at the subplot scale for three transects (Grjothøi, Tronfjellet, and Horndalsnuten) and three transects where plots are analysed (Kvitingskjølen, Tronfjellet, and Horndalsnuten).

Statistics

We first tested if fertile specimens were found more frequently in the core part of their altitudinal ranges than at the range margins. Only species that were found in at least three plots with fertile specimens and at least three plots of only sterile specimens were used in this analysis. For each species, the plots where the species was present were divided into quartiles along the altitudinal gradient, assuming that the two central altitudinal quartiles of a species range represent source populations and the first and fourth quartiles represent the assumed sink populations. To evaluate if the observed fraction of fertility was higher in the central quartiles, we developed a permutation test where the

same number of plots with fertile specimens as observed for each species was randomly distributed among the plots where the species were present. This was done for all species separately and for each permutation the number of species with a higher fraction in the central half of the plots was counted. Permutation was conducted 999 times and an exact Monte Carlo *p*-value derived (Manly, 1997).

The presence or absence of a hump-shaped pattern of sterile species richness was evaluated by testing if the second term of a second-order polynomial was statistically significant and a peak appeared using regression. Two different regression models were used depending on the grain size. At the plot scale, we used a Generalised Linear Model assuming a Poisson distribution and log link (McCullagh & Nelder, 1989). Due to dependency (autocorrelation) between the subplots within plots, we used another approach at the subplot scale. Here we used a mixed-effect model to account for the spatial dependency between the subplots within the whole plots, in addition to the fixed effects of the predictor variables (i.e. altitude and the fertility/sterility variable described below) (Pinheiro & Bates, 2000). As the residuals were assumed to follow a Poisson distribution, i.e. increasing variance, we utilised a penalised quasi-likelihood approach to Generalised Linear Mixed Models (using the *glmmPQL* function of the R library MASS, Venables & Ripley, 2002). The significance of the different terms was tested with *F*-statistics for the plot-scale analyses (McCullagh & Nelder, 1989), and for the subplot scale the coefficients of the mixed-effect models was tested by a sequential *t*-test (Pinheiro & Bates, 2000).

To test if sterile species richness has a more humped altitudinal pattern than fertile richness, we used a test analogous to ANCOVA. First, we combined the two richness variables into one new response variable. A dummy variable was made, which indicates if the data point relates to sterile richness (value 0) or fertile richness (value 1). The actual test was done by examining the interaction term between altitude and the dummy variable. The same regression models, i.e., a GLM with Poisson distribution at the plot scale and a mixed-effect model at the subplot scale were used for these analyses. A model including a second-order polynomial of altitude plus the effect of the fertility/sterility dummy variable was used as a null model. This model was subsequently compared to models including the interaction term between the two predictor variables. Statistically significant interaction terms indicate a difference in the relationship between richness and altitude for the two groups (fertile and sterile). The second-order interaction term is expected to be positive indicating less curvature for the fertile richness (i.e. giving a more pronounced peak in the sterile richness pattern).

One problem when using a log link may appear when testing the models; since species richness is highest in the middle of the altitude gradient a log link in GLM will produce a more pronounced peak when looking at the fitted lines on the original scale (i.e. when the fitted values are back-transformed to be plotted on a natural scale [McCullagh & Nelder, 1989]). This will create a more pronounced peak for the line that has most species on average, even though no statistically significant interaction term is found. To see the potential influence of using log link we made additional analyses testing the same patterns assuming a Gaussian distribution and an identity link (McCullagh & Nelder, 1989).

Null models evaluating the effect of hard boundaries have been developed in many previous studies (see reviews in Colwell, Rahbek, & Gotelli, 2004; Zapata, Gaston, & Chown, 2003). We have, however, not been able to develop satisfactory or realistic null models for a direct test of the hard boundaries in this study as this would require a better estimation of species ranges than is available from the data sampled here.

Koleff, Gaston, and Lennon (2003) recommend, among other estimators, β_{sim} as an estimate of species turnover (Lennon, Koleff, Greenwood, & Gaston, 2001). β_{sim} is defined by $1 - a / (\min[b, c] + a)$, where a is the total number of species occurring in both plots, b is the number of species occurring in only the neighbouring plot but not in the focal one, and c is the number of species occurring in only the focal plot. Turnover estimates were made at the plot scale only, because the species number at the subplot scale was insufficient to obtain reliable estimates of species turnover. Turnover between all neighbouring plots along the altitudinal gradient was estimated using all species. We arbitrarily chose an altitude interval of 100 m above and below the forest line to be the “ecotone interval”. A simple one-way ANOVA was applied to test for the difference in turnover between the plots in the ecotone interval vs. the other plots. A Gaussian distribution is assumed for the response variable. When checking the diagnostic plots, no trend in the residual variance was found with the estimated means, confirming the assumption of the Gaussian distribution.

Turnover estimates are known to be dependent on plot species richness (Heegaard, 2004; Magurran, 2004; Wilson & Shmida, 1984), so prior to using the turnover estimates we checked if these estimates correlated strongly with the total species number in the two quadrats together. This was not the case for any of the transects. We also plotted the turnover estimates towards the species richness of the two adjacent plots used to estimate turnover and checked for outliers at either high or low species richness, but no outliers were found. We therefore made no attempt to account for species richness before using the turnover estimates in the analyses.

New turnover estimates were made based on fertile species only using the same β_{sim} . We used a two-way ANOVA to test if the turnover estimates based on fertile species had a stronger response than the turnover estimates based on all species together by investigating the interaction term between the ecotone dummy variable and a dummy variable identifying if the turnover estimates were based on all species or on fertile species only.

Results

For the Horndalsnuten transect, 12 out of 15 species analysed were more frequent in the central part of the species range ($p = 0.037$). At the Tronfjellet transect, 48 species were analysed and 31 of these had more frequently fertile specimens in the middle of their altitudinal range ($p = 0.020$). At the Kvitingskjølen transect, 29 out of a total of 45 species had more fertile specimens in the central half ($p = 0.010$).

Sterile richness has a statistically significant unimodal relationship with altitude for all transects at both scales, except for the Horndalsnuten transect at the plot scale (Table 1). At the subplot scale there is a statistically significant interaction term between altitude and the fertility/sterility variable for all three transects tested (Table 2, Fig. 1). Further, the model including both the first- and second-order polynomial interaction term fits the data significantly better than a model not including a second-order polynomial interaction term or the null model for two of the transects (Horndalsnuten and Grjøthøi), but for the Tronfjell transect only a first-order polynomial interaction term is significant (Table 2). Considering the fixed effects, the sign of the second-order interaction term is positive for all three transects (Table 2). When a Gaussian distribution and identity link is assumed, the second-order interaction term is also significant for the Tronfjellet transect ($p < 0.001$). For the other two transects the second-order interaction term remained significant when a Gaussian distribution was assumed. These results indicate that sterile species richness has a more pronounced peak than fertile species richness when the subplot scale is considered.

At the plot scale, sterile richness and fertile richness altitudinal patterns differ on two of the three transects (Tronfjellet and Kvitingskjølen), as indicated by significant interaction terms for these transects (Table 2). However, the best model does not include the second-order interaction term but only the first-order interaction (Table 2, Fig. 2). Assuming a Gaussian distribution of the response variable and an identity link did not change the conclusions at the plot scale. These results therefore give no indication of a more pronounced hump for the sterile species than for fertile species at the plot scale.

Table 1. Summary statistics of the regressions with sterile species richness as response and altitude as predictor variables

Location (scale)	Model	Coefficient	Test	<i>t</i> -value	<i>p</i> -value
Horndalsnuten (subplot)	1	0.005	1 vs. NULL	3.242	0.002
	2	−3.4e-6	2 vs. 1	−3.802	<0.001
Tronfjellet (subplot)	1	0.011	1 vs. NULL	7.092	<0.001
	2	−5.0e-6	2 vs. NULL	−7.063	<0.001
Grjothøi (subplot)	1	0.006	1 vs. NULL	4.09	<0.001
	2	−2.7e-6	2 vs. 1	−3.740	<0.001
	Model	Residual deviance	Test	<i>F</i> -value	<i>p</i> -value
Horndalsnuten (plot)	NULL	48.93			
	1	48.93	1 vs. NULL	0.0002	0.989
	2	48.89	2 vs. NULL	0.021	0.979
Tronfjellet (plot)	NULL	151.45			
	1	151.03	1 vs. NULL	0.136	0.714
	2	73.84	2 vs. NULL	25.565	<0.001
Kvitingskjølen (plot)	NULL	53.50			
	1	42.82	1 vs. NULL	10.402	0.002
	2	37.026	2 vs. 1	6.423	0.015

Model indicates the complexity of the model: Null is the null model of no trend, Model 1 is a linear model and Model 2 is a unimodal model. The Test column indicates which models were tested against each other. At the subplot scale the coefficient of the mixed effect model was tested by a sequential *t*-test, and at the plot scale the amount of deviance explained was tested with an *F*-test.

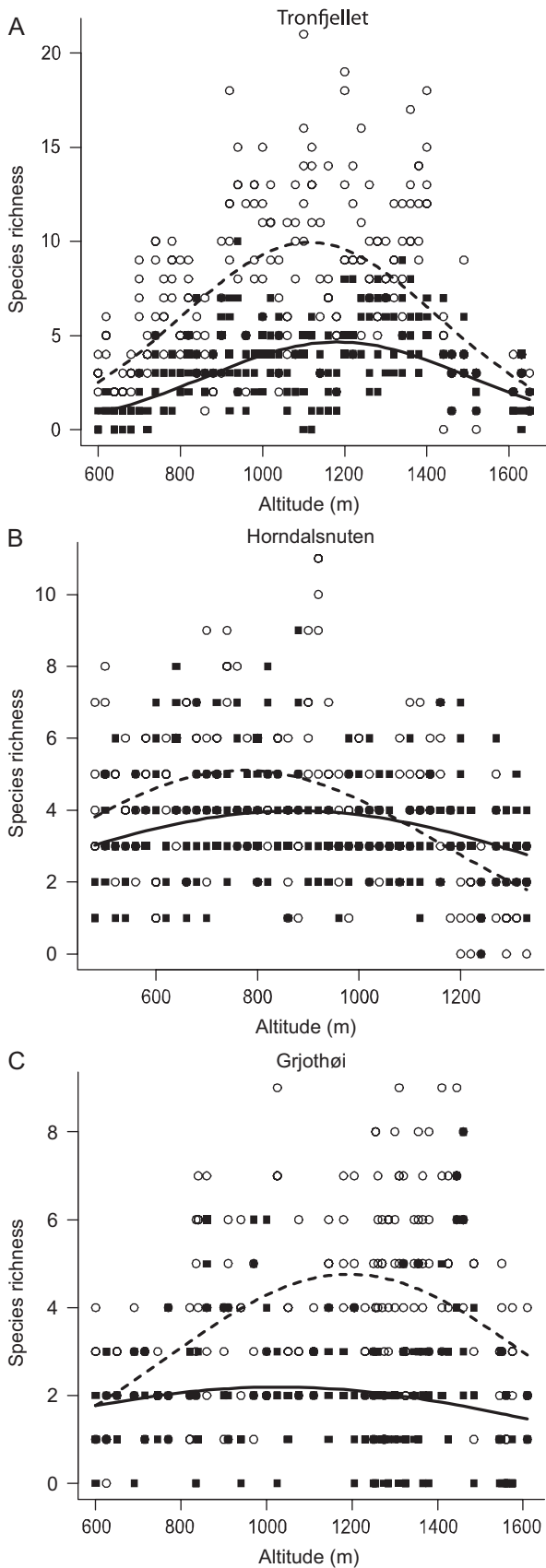
Table 2. Summary statistics of tests evaluating if sterile richness and fertile richness patterns are different

Location (scale)	Model	Coefficient	Test	<i>t</i> -value	<i>p</i> -value
Tronfjellet (subplot)	1	6.6e-4	1 vs. NULL	4.034	0.001
	2	0.0e-6	2 vs. 1	0.411	0.682
Horndalsnuten (subplot)	1	7.4e-4	1 vs. NULL	4.175	<0.001
	2	1.6e-6	2 vs. 1	2.103	0.036
Grjothøi (subplot)	1	−6.7e-4	1 vs. NULL	−3.256	0.001
	2	1.6e-6	2 vs. 1	2.04	0.041
	Model	Residual deviance	Test	<i>F</i> -value	<i>p</i> -value
Tronfjellet (plot)	NULL	181.35			
	1	164.81	1 vs. NULL	9.632	0.003
	2	164.79	2 vs. 1	0.013	0.909
Horndalsnuten (plot)	NULL	77.72			
	1	76.51	1 vs. NULL	1.377	0.244
	2	75.62	2 vs. NULL	1.194	0.308
Kvitingskjølen (plot)	NULL	112.87			
	1	95.12	1 vs. NULL	16.530	<0.001
	2	94.68	2 vs. 1	0.401	0.528

Model indicates the complexity of the model: NULL is the model accounting for a second-order polynomial for altitude plus the dummy variable (sterile–fertile), Model 1 adds an interaction term with a first-order polynomial with altitude and sterile–fertile to Model 0, and Model 2 adds an interaction term between a second-order polynomial for altitude and sterile–fertile to Model 1. The Test column indicates which models were tested against each other. At the subplot scale the coefficient of the mixed effect model was tested by a sequential *t*-test, and at the plot scale the amount of deviance explained was tested with an *F*-test. Note the sign of the coefficients for Model 2 where a positive coefficient indicates that the mass effect hypothesis is supported.

We did not find evidence of a higher species turnover in the ecotone interval than in the remaining part of the transects when using all species to estimate the species

turnover, and sterile species did not have a more pronounced turnover at the ecotone than all species together (Table 3). These results were independent of



whether the ecotone was defined as the forest line or whether the ecotone was assumed to be where maximum species richness had been observed.

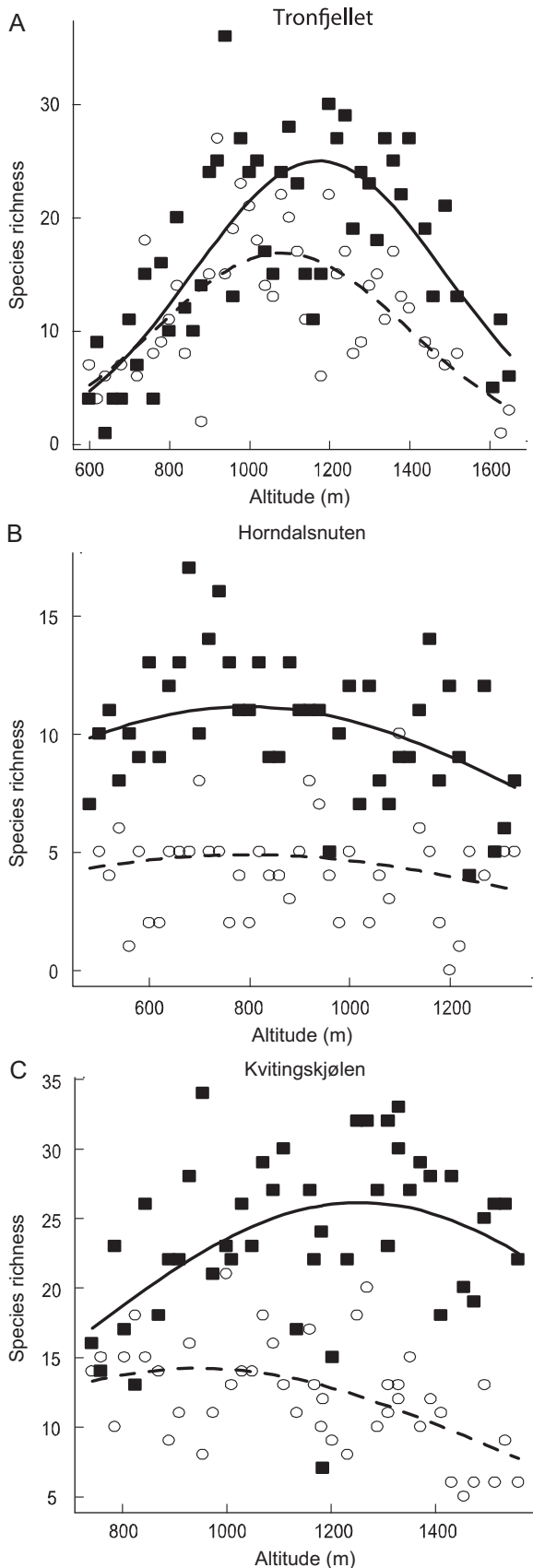
Discussion

Ideally, we need to observe the population dynamics over long time periods to determine whether a population is a source or a sink (Dias, 1996; Diffendorfer, 1998). For long-living perennial plants, this becomes an impossible task. We therefore need alternative ways to evaluate the impact of the mass effect on observed species-richness patterns of such organisms. The overall evaluation of the simple approach used here shows that the altitudinal distribution of fertility/sterility was non-random. Significantly more species than expected had fertile specimens in the central half of the species altitudinal distribution. Species are in general assumed to be more common and perform better in the middle of their range (Brown, 1984, 1995; Gaston, 2003; Hengeveld, 1990; Whittaker, 1967), i.e., they are most likely to be source species there. The finding that the estimated sources are more commonly found in the middle of the ranges supports our approach of using sterility/fertility as indicators of sinks and sources, and, looking at the total pattern over all species and all plots, a crude indication may give valuable insight into a process that are difficult to approach in an ideal way.

Having established that our assumptions regarding the estimation of sources and sinks are likely to hold, at least when averaged over many observations, we tested if fertile richness had a unimodal relationship with altitude. This was the case for two of the three transects at the plot scale and for all three transects at the subplot scale. The Horndalsnuten transect at the plot scale was the only one that did not show this pattern. Horndalsnuten is the most oceanic transect in this study and it is probably the transect with the poorest true alpine flora relative to the lowland flora (Moe, 1995). A relatively poor flora from either the upper or lower part of the transect should result in the sinks from the poor end having only a small influence on the species richness pattern, i.e., the effect may be too weak to be detected with these methods.

The predictions generated by assuming that the mass effect is important are clearly supported when analysing the data at the subplot scale, as all sterile species richness patterns are humped and sterile species richness is more

Fig. 1. The subplot-based richness distribution of sterile (circles) and fertile (squares) species along the altitudinal gradients at three sites: ((A) Tronfjellet, (B) Horndalsnuten, (C) Grjøthøi). Continuous lines (fertile richness) and broken lines (sterile richness) are based on the “best” model from Table 2.



humped than the fertile richness (for the Tronfjellet transect this is, however, found to be statistically significant only when an identity link is used). The mass effect was not supported at the plot scale. The different results from the two sampling scales may reflect problems with the fertility/sterility approach to test for mass effect. One specimen with badly developed reproductive organs is enough to categorise that species as a fertile species, and as larger areas are sampled many actual sink species may have been classified as source species. Similarly, when searching larger areas some of the more inconspicuous sterile specimens may be overlooked; hence the number of sink species may be underestimated. Both overlooking sterile species and the finding of actual sink species with fertile specimens more often will result in an increased probability of refuting the mass effect hypothesis even though the hypothesis may be correct. This is analogous to inflating the Type II error. Despite these problems, we believe that the method applied here has the potential to give valuable insights into questions that are extremely difficult to tackle by experiments in natural communities.

The test of an ecotone effect along the three transects at the plot scale shows that the turnover is actually not significantly higher around the area of highest estimated species richness along the transects or around the forest-line ecotone than in other parts of the transect. This lack of increased turnover around the forest line has been noted in other studies along transects in Norwegian mountains (Hofgaard, 1997). Hofgaard also noted that there was no evident increase in species richness around the forest-line ecotone. A similar conclusion was reached by Odland and Birks (1999) as they observed no increase in species richness of vascular plants at the forest-line ecotone. A lack of increased species richness around proposed ecotones has also been found for small mammals (McCain, 2004). Terborgh (1985) studied the potential role of ecotones on birds altitudinal ranges in the Andes and found that a relatively small number of range terminations were caused by ecotones.

The test of whether fertile species showed a more pronounced turnover around the ecotone than all species showed no statistical significance for any of the three transects analysed and the explanatory power of the interaction term was so small for all three transects and for both definitions of ecotone used that there was not even a weak indication that an ecotone together with the mass effect is responsible for creating the unimodal altitudinal pattern along these three transects. Based on

Fig. 2. The plot-based richness distribution of sterile (circles) and fertile (squares) species along the altitudinal gradients at three sites: ((A) Tronfjellet, (B) Horndalsnuten, (C) Kvitingskjølen). Continuous lines (fertile richness) and broken lines (sterile richness) are based on the “best” model from Table 2.

Table 3. Summary statistics of the tests of whether turnover is higher at the ecotones (either forest line or at altitudes of observed maximum species richness) and whether turnover is more pronounced at the ecotone for fertile species than for all species

Location (ecotone)	Question 1		Question 2	
	<i>F</i> -value	<i>p</i> -value	<i>F</i> -value	<i>p</i> -value
Tronfjellet (forest line)	3.385	0.072	0.001	0.969
Tronfjellet (max richness)	0.594	0.445	0.645	0.424
Horndalsnuten (forest line)	0.034	0.854	0.001	0.970
Horndalsnuten (max richness)	0.104	0.749	0.346	0.558
Kvitingskjølen (forest line)	0.311	0.580	0.671	0.415
Kvitingskjølen (max richness)	0.681	0.414	0.498	0.482

The *F*-value and the corresponding *p*-value refer to the test of the interaction term between the ecotone dummy variable and the fertile-species/all-species dummy variable in explaining turnover (see text for further explanation). Question 1: Is turnover higher at the ecotone? Question 2: Is turnover more pronounced for fertile species than for all species at the ecotone?

qualitative observations of reproducing animals at the mid-altitudes, Kelt (1999) reached the same conclusions and suggested that the ecotone effect is not important for shaping a unimodal species richness pattern with altitude for small mammals in California.

Hard boundaries restrict dispersal and may create a mid-domain effect (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Colwell et al., 2004; Grytnes & Vetaas, 2002). Grytnes (2003b) suggests that the mass effect is one of the ecological causes that may actually create this Mid-Domain Effect. Due to hard boundaries, sink populations cannot be invaded from source populations outside the domain. This will create a unimodal pattern with maximum species richness in the centre of the domain, because there will be sink populations from either side in the middle of the gradient but from only one side as we move close to the boundaries (Rahbek, 1997; Grytnes & Vetaas, 2002). We have not made a direct test of the hard boundaries in this study, but given the importance of the mass effect and the absence of an ecotone effect, the mid-domain effect as interpreted by Grytnes (2003b) is potentially important in shaping these patterns.

We conclude that the results from this study give indications for the mass effect as an important factor in causing the mid-altitudinal peak in species richness, but that the recognition, perception and/or relative strength of the mass effect is scale-dependent, probably as an effect of accuracy of estimating sources and sinks.

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