

Encroaching forests decouple alpine butterfly population dynamics

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Over the past 50 years, the rising tree line along Jumpingpound Ridge in the Rocky Mountains of Alberta, Canada, has reduced the area of alpine meadows and isolated populations that reside within them. By analyzing an 11-year data set of butterfly population sizes for 17 subpopulations along the ridge, we show that forest habitat separating alpine meadows decouples the dynamics of populations of the alpine butterfly *Parnassius smintheus*. Although the distance between populations is often negatively correlated with synchrony of dynamics, here we show that distance through forest, not Euclidean distance, determines the degree of synchrony. This effect is consistent with previous results demonstrating that encroaching forest reduces dispersal among populations and reduces gene flow. Decoupling dynamics produces more smaller independent populations, each with greater risk of local extinction, but decoupling may produce a lower risk of regional extinction in this capricious environment.

population synchrony | spatial dynamics | alpine fragmentation

The tree line is rising in alpine areas of the world, including the Rocky Mountains of North America (1). The rise in tree line has been ascribed to global warming and fire suppression (2, 3). One consequence of forest encroachment into the alpine zone is the fragmentation of alpine meadows. Fragmentation of habitat by natural or anthropogenic causes creates a greater number of smaller isolated populations, which can increase the risk of local extinction compared with that in the previous continuous population (4, 5); the effects of fragmentation depend on the degree to which subpopulations function as independent populations (6). Here, we investigate the effects of forest encroachment into alpine meadows (Fig. 1) on the dynamics of closely neighboring subpopulations of the Rocky Mountain apollo butterfly, *Parnassius smintheus* (Papilionidae).

Our long-term study of populations of *P. smintheus* in alpine meadows at Jumpingpound Ridge, Alberta, Canada (Fig. 1), has demonstrated that movement (7–9) and gene flow (10, 11) are severely limited by encroaching forests. These butterflies are restricted to open alpine meadows in the Rocky Mountains where their larval host plant, lance-leaved stonecrop, *Sedum lanceolatum*, and adult nectar resources are present (12). By monitoring the population size of *P. smintheus* over an 11-year interval in a series of alpine meadows, we determine whether population growth is most similar between meadows close to each other, suggesting that local dispersal synchronizes nearby populations, and identify the components of landscape that determine the degree of synchrony, in particular the effect of encroaching forest.

Results and Discussion

Subpopulations close to each other and separated by a small amount of forest, such as meadows F and G (Fig. 1), showed patterns of population change that were very similar to each other (Fig. 2 *a* and *b*), whereas populations separated by larger distances were more dissimilar, such as meadow R vs. F and G (Fig. 2 *a* and *c*). Among all meadows along the 8-km ridge (Fig. 1*b*), there were strong correlations in dynamics if pairs were close

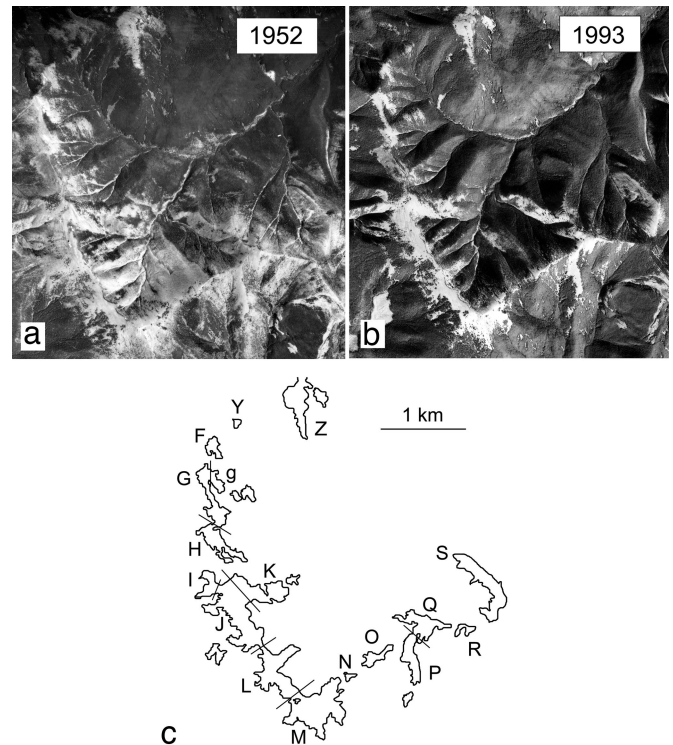


Fig. 1. Change in forest and meadow structure between 1952 and 1993. Aerial photos from (a) 1952 and (b) 1993 of alpine meadows at Jumpingpound Ridge, Alberta, Canada. Photos and (c) schematic map of the individual meadows in 1993 from which total distance, distance through meadow, and distance through forest between subpopulations were estimated. Dark areas are conifer forests; lighter areas are open alpine meadows. Large meadows are arbitrarily separated into smaller submeadows indicated by straight line segments.

to each other, declining in similarity as the total distance between them increased (black diamonds in Fig. 3, $\beta = -0.053$, $SE = 0.017$, $r^2 = 0.23$, $F_{1,34} = 10.21$, $P = 0.03$). When total distances are partitioned into distance through forest and distance through meadow, it is clear it is the amount of forest between them that largely determines the degree to which population dynamics are correlated (red squares, $\beta = -0.25$, $SE = 0.048$, $r^2 = 0.44$, $F_{1,34} = 26.21$, $P < 0.001$), not the amount of open meadow (blue diamonds, $\beta = -0.05$, $SE = 0.022$, $r^2 = 0.13$, $F_{1,34} = 5.01$, $P = 0.032$). Based on multiple regression analysis, the partial effect of intervening forests on synchrony is

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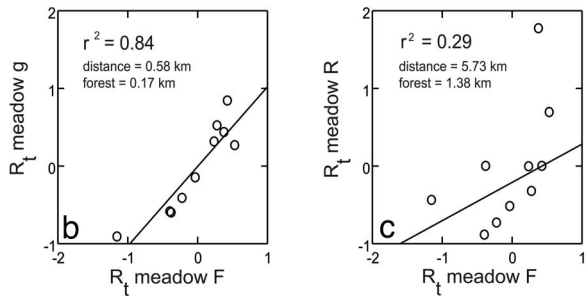
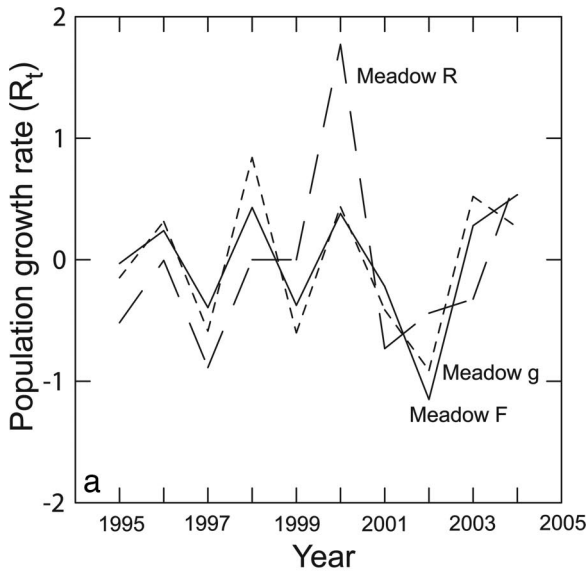


Fig. 2. Pattern of population change for *P. sintheus* butterflies in 3 of 26 alpine meadows. (a) Butterfly population change (R_t) from one year (t) to the next in two subpopulations separated by 0.17 km of forest (meadows F and g) and two subpopulations separated by 1.38 km of forest (meadows F and R), and (b) and (c) the correlation in R_t for the respective meadow pairs.

much greater ($\beta = -0.26$, $t = -4.26$, $P < 0.001$) than the effect of an equivalent distance through open meadow ($\beta = 0.008$, $t = 0.350$, $P = 0.73$; r^2 for the overall model = 0.44). When the potential for a lack of independence of data is taken into account (Mantel's test), correlated dynamics are still significantly related to total distance between subpopulations ($r_m = -0.480$, $P = 0.004$), distance through meadow ($r_m = -0.358$, $P = 0.031$), and particularly distance through forest ($r_m = -0.660$, $P < 0.0001$). When the effect of forest is held constant (partial Mantel's test), the effect of distance through meadow on correlated dynamics is not significant ($r_m = 0.061$, $P = 0.732$). In contrast, when the effect of meadow is held constant, the effect of distance through forest is very strong ($r_m = -0.595$, $P < 0.0001$). Again, virtually all of the effect of distance in decoupling dynamics is distance through forest as a component of the landscape, not distance through meadow. The above patterns are all consistent with the known effect of forest, compared with meadow, in limiting dispersal (7, 8) and in reducing gene flow (10, 11) and underscore the impact that this rapidly changing component of alpine landscapes has on alpine populations.

Parnassius dispersal can link populations in close proximity to each other, but this linkage almost disappears if there is >1 km of forest separating two populations (Fig. 3). Thus, populations with >1 km of forest habitat between them are effectively isolated and function independently. The relatively fine spatial scale over which dynamics are synchronized implies there is sufficient fine-scale dispersal (<1 km) linking populations. The

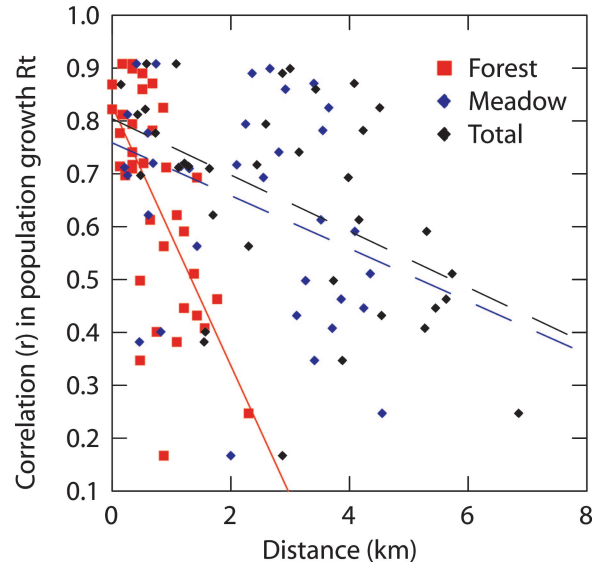


Fig. 3. Effect of distance between pairs of meadows (subpopulations) on the degree to which annual rates of population growth (R_t) of the alpine butterfly, *P. sintheus*, are correlated (r) for all alpine meadow pairs. Effect of total distance between subpopulations (\blacklozenge), distance through open meadow (blue diamond), and distance through intervening forest (red square) on population change are estimated separately. Regression statistics are provided in the text.

linkage may be direct via dispersal between populations or less direct via “stepping-stone” dispersal to and from an intervening population (13). Potentially, dispersing natural enemies or a key environmental variable that fluctuates locally at the scale of only a couple of kilometers could produce similar patterns (14), but this seems unlikely. That intervening forest is far more important in explaining the degree of similarity in dynamics than is distance through meadow or even total distance, combined with the fact that amount of forest is the best explanatory landscape variable both for *Parnassius* movement (7, 8) and gene flow (10, 11), indicates it is dispersal that produces this correlated dynamics rather than a spatially correlated exogenous factor such as weather.

At our study sites, the tree line has risen by 100–200 m over the past 40 years (Fig. 1). A continued rise in the elevation of the tree line will have several consequences for butterflies and likely other alpine organisms. The risk of local extinction via stochastic events (15) or through inbreeding depression (16) is expected to increase as meadows shrink, population sizes decrease, and populations become more isolated. As we show here, the potential for a “rescue effect” (17) via immigration from other meadows declines severely as forests intervene among subpopulations. In temporally unpredictable environments such as the alpine zone, the potential for local extinction because of stochastic events is high. We are beginning to see such effects, with local extinctions occurring in the smallest and most-isolated populations. For the five extinctions that have occurred, all were recolonized in one or two generations. This result, combined with a relatively low overall extinction rate, suggests that currently the rate of colonization remains higher than the rate of extinction; there is a high likelihood of persistence under current conditions.

Despite the large effect of forests in decoupling dynamics, weak correlations are still apparent at distances >4 km. This may result from small but sufficient amounts of dispersal at such distances either within a generation or over several generations but likely also from broadly correlated weather across the study area. Our results indicate that, even when habitat fragmentation

occurs on a relatively small spatial scale, the consequences for population dynamics can be severe if movement is correspondingly reduced. A continued rise in tree line will no doubt fill in some meadows entirely. Many meadows on Jumpingpound Ridge have disappeared completely in just 40 years (7). Further disappearance of meadows not only will result in lost habitat but also will remove “stepping stones” that currently facilitate some dispersal among neighboring meadows. Immigration to the remaining populations will thus be further curtailed.

Although the loss of synchronization through reduced dispersal might increase the risk of local extinction, it could potentially lower the risk of larger-scale extinction (6), particularly in an environment as capricious as the alpine for small ectotherms. In the current case, we view a loss of synchrony as a negative symptom of the progression from a large population with relatively low risk of extinction to a series of smaller more independent populations, each now with a higher risk of extinction. It remains to be seen whether loss of synchrony will be a benefit (lower regional extinction risk) or a detriment (higher local extinction risk) for *Parnassius* populations.

Methods

Abundance of *P. smintheus* was estimated for each of 17 alpine meadows each year from 1995 through 2005 along Jumpingpound Ridge, Alberta, Canada (Fig. 1). This ridge is characterized by a series of meadows delineated by forest encroachment into a previously large area of meadow created by forest fire in 1938. We searched each meadow four to five times each year during sunny warm conditions. At each of these sampling times, butterflies were netted and marked on the wing with a unique three-letter code by using a fine-point permanent marker (7). In most years, population size for each meadow was estimated based on Craig’s method (18). Alternatively, butterfly abundance was estimated from standardized transect counts of butterflies in each meadow (19). All estimates were converted to a common scale based on the known relationship between the estimates (20). In most years, we made >2,000 captures of >1,000 individuals, averaging over two captures per individual. The maximum estimate for each year among the repeated estimates for each meadow was used as the population estimate for that year.

Change in population size from one year to the next (R_t) was calculated as the change in \log_{10} abundance between each year (t) and the next ($t + 1$):

$$R_t = \log N_{t+1} - \log N_t,$$

such that positive values indicate population growth, and negative values indicate population decline. The degree to which dynamics in two meadows were similar to each other was estimated by the correlation coefficient (r) in R_t among years for each meadow pair. Only those meadows that had a continuous record of abundance estimates over the 11-year interval were included in the analysis (nine meadows, resulting in 36 meadow pairs). Correlations in population change (r) did not deviate from normality (21) in either skewness ($n = 36, g_1 = -0.625$) or kurtosis ($g_2 = -0.534, ns$).

Landscape characteristics were determined from 1:40,000 scale aerial photos taken in 1993 (Fig. 1a). Although population studies were conducted from 1995 to 2005, change in meadow boundaries since 1993 has been minimal, although tree seedlings have continued to become established since 1993. We estimated the distance (kilometers) between the centroid of butterfly capture for a given meadow to those in each other meadow (7). We also separated total distance between centroids into the portions through forest and through meadow. In doing so, we acknowledge that not all meadow is, in fact, butterfly habitat; distances through meadow include habitat used by *Parnassius* butterflies and nonforested area with very few butterflies, in effect, open meadow matrix. We therefore imply there are two types of matrix. Linear regression was used to estimate the effect of distance on the correlation in dynamics between pairs of subpopulations. The effects of total distance, distance through forest, and distance through meadow were assessed separately. We also assessed the relative importance of forest and meadow by including both as terms in multiple regression analysis of the between-meadow correlations in R_t . Because of concern that data are not independent (the same distances between subpopulations are used repeatedly for several meadow pairs), we performed Mantel’s test and partial Mantel’s test on the matrix of correlations in population dynamics to the respective matrices of distances (total, meadow and forest) between meadow pairs.

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