

## Adaptive Walks on Changing Landscapes: Levins' Approach Extended

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The assumption that trade-offs exist is fundamental in life-history theory. In 1962 R. Levins introduced a widely adopted graphical method for analyzing evolution towards an optimal combination of two quantitative traits, which are traded off [1]. His approach explicitly excluded the possibility of density-dependent and frequency-dependent selection. While simple forms of density-dependence can easily be incorporated into Levins' approach, this is not possible when populations are structured and density-dependence is such that selection becomes frequency-dependent. Here we extend Levins' method towards models, which include these selection regimes.

When selection is density-dependent and frequency-dependent, fitness landscapes change with population state. In the presence of frequency-dependence the invasion success of a given mutant not only depends on its traits but also on the densities of the various stages of the resident population. We derive the dynamics of evolution from the same types of curves Levins used: trade-off curves and fitness contours. However, fitness contours are not fixed but a function of the resident traits and we only consider those that divide the trait space into potentially successful mutants and mutants which are not able to invade. By means of the behavior of these two curves we can identify points where the fitness gradient is zero ('evolutionarily singular points' [2]) and assign them to the four possible

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types: Continuously Stable Strategies, Repellers, Branching Points and Gardens of Eden.

Based on the shape of the trade-off and fitness contours our approach allows us to derive a priori predictions about the evolutionary dynamics and about the bifurcation of singular points. This will be illustrated by applying the method to several models from the literature.

## References

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