

## **Gone with the wind: is it always true for invasive plants and, if not, why not?**

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### **INTRODUCTION**

Factors that can either speed up or slow down the spread of invasive species are of considerable current interest, and their identification and proper understanding are expected to lead to efficient management and control. In order to reveal the relevant factors, the main mechanisms of species transport must first be identified. In the case of plant species, it is widely accepted that local seed-spread is attributable to the impact of wind (Okubo & Levin, 1989). However, estimates based on this mechanism often appear to be at variance with field data. In particular, wind-driven seed dispersal would imply that invasive plants are strongly affected by wind pattern, which is not always the case. This apparent discrepancy is sometimes interpreted as the manifestation of certain specific features of wind mixing (Clark *et al.*, 1998), but it may also indicate that some additional or alternative mechanisms of seed transport have not been taken into account. In this paper, we assume that, at least in the case of some tree species, such a mechanism can be avian-based: birds eat seeds, but they do not assimilate all of them so that a part of the seed population is then egested at a different location. In order to study the impact of this mechanism, we apply a simple conceptual mathematical model, and show that avian-based dispersal can significantly modify the pattern of invasion by plant species.

### **MATHEMATICAL MODEL**

We consider a plant species  $A$ , presumably an arbor, described by its population density  $a(x,t)$ . We assume that species  $A$  dwells in an unbounded, one-dimensional domain, with the following conditions at infinity:  $a(\infty,t) = K$ ,  $a(-\infty,t) = 0$ . These conditions imply that the species range has a boundary situated at a certain  $x_0$ . Species invasion or colonization takes place if, with each new generation,  $x_0$  moves to the left. Redistribution of species  $A$  in space takes place due to dispersal of its seeds which, having neglected the impact of other species, happens through wind mixing.

Next, we consider an avian species  $B$ , described by its population density  $b(x,t)$ . We assume that seeds of plant species  $A$  provide an essential source of food for avian species  $B$ . The relation between  $A$  and  $B$  is, therefore, one of the ‘resource-consumer’ or ‘predator-prey’ type. We then make use of the observation that a higher density of resource (or prey) often leads to a higher density of consumer (or predator), and assume that, within the range of species  $A$ , their densities are linearly related:

$$b(x,t) = \eta a(x,t). \quad (1)$$

Apparently, dispersal of avian species is not affected by wind to the same extent as that of plant species, because of a bird's ability of self-motion. Moreover, some avian species are known to exhibit two-mode dispersal: a short-distance dispersal due to everyday round-about motion (which we assume to be random), and a long-distance dispersal due to small-scale migrations by individuals or groups of individuals (Hengeveld, 1989). The colonies created by groups of migrating birds are outside of the main range of species  $A$ , and thus relation (1) would not seem to be applicable. However, before migrating, the birds would have been feeding on seeds of  $A$ , and it is likely that some of these seeds would be transported to the place where a new colony is formed. Moreover, the more birds that have migrated the more seeds are transported; thus, we can assume that relation (1) also holds outside the species  $A$  range, albeit with a different coefficient.

The issue of species  $A$  invasion is, therefore, reduced to the issue of species  $B$  invasion. In order to describe the dynamics of population  $B$ , we use the model earlier developed by Petrovskii & Li (2003):

$$\frac{\partial b(x,t)}{\partial t} + \frac{\partial}{\partial x} [S(b)b] = D \frac{\partial^2 b}{\partial x^2} + F(b) \quad (2)$$

where  $D$  is the species diffusivity responsible for the short-term dispersal,  $S(b)$  describes the intensity of small-scale density-dependent migrations responsible for the long-distance dispersal, and  $F(b)$  describes local population growth of species  $B$ .

## RESULTS

For a biologically reasonable parameterization of  $S(b)$  and  $F(b)$ , equation (1) appears to be exactly solvable. Its solution describes the propagation of a population front, which apparently corresponds to the advance of the species range boundary. We calculate the speed of the front and show that, when seed dispersal is enhanced by an avian-based mechanism, the direction of the propagation front does not necessarily coincide with the direction of the wind. Moreover, the speed of the front appears to be several times greater, compared with that observed in the case of simple wind-driven dispersal. The latter result can, in some cases, account for the phenomenon of rapid plant invasion, both in ongoing ecological observations and in historical data.

## REFERENCES

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