matches our conceptual description of what models without We develop a graphical description of interaction modification and HOIs to match the verbal description above. We start with two functions, *h* and *l*­, which give the population growth rate of species *i* (hereafter referred to as the ‘focal’ species) as a function of the density of competitor species one or two (*n*1 or *n*2),

|  |  |  |
| --- | --- | --- |
|  | = . | (10) |

If we are studying how the focal species responds to two competitor species in isolation these two functions are distinct and we plot them separately (Figures 1a and 1b). However, when both competitor species one and two are present together, we require a new multivariate function, *F*, which we can depict as a surface in three dimensions with the per capita growth rate of the focal species on the z-axis (fig. 1c).

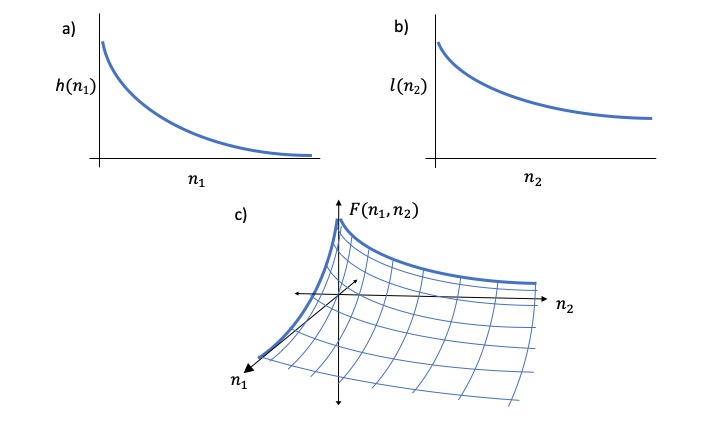


Figure 1 The per capita growth rate as a function of competitor densities.

While we originally described the response of the focal species to competition using separate functions, *h*, *l*, and *F*, these functions are related: the lines in figures 1a and b are slices through the three-dimensional surface in figure 1c. Assume that all three plots accurately capture the response of the focal species to the density of its competitors. How can we tell whether the surface in 1c implies an HOI? The relationship between the three-dimensional surface of function F and the two separate functions h and l is the central problem of HOIs.

One might first try to build up the function F from the separate functions h and l. Looking at figure 1c, this would entail producing the whole three-dimensional surface from the slices at the edges. If one could reproduce F from only studying the slices at the edges, captured by the functions h and l, then there would be no new information in the surface of F. In other words, F does not involve emergence in the region where more than species is present.

However, the separate density dependent functions h and l may not be enough on their own to specify the multidimensional function F—even when no new parameters are involved. Consider the specific functions for h and l,

|  |  |  |
| --- | --- | --- |
|  | . | (11) |

Knowing these two functions does not entail any specific multivariate function *F*(*n*1, *n*2). For instance, the function *F* could be , or it could be both of which have the same slices at *n*1 = 0 or *n*2 = 0.

However, knowing F does imply that of there were a definite way to produce the whole surface from the separate slices the single slices produced Unfortunately there is no general way to do this for any given set of functions. In facOne approach would be to build up the function F from the separate functions. Unfortunately there is no general way that we are aware of to build ssumption of pairwise competition models is that we can recreate the two-dimensional function *F* from the two separate functions, *h* and *l*, that define the perpendicular slices at the edges. Any HOIs between species one and two will produce a surface in figure 1c that cannot be recreated from two perpendicular slices through it. In an abstract way, a pairwise model of *m*-species competition can be compressed into *m*-dimensions, each representing the functional response to a separate competitor. In contrast, an *m*-species competition model with HOIs *cannot* be compressed into *m*-dimensions.

## A quantitative description of higher order interactions

Building on this visual understanding of HOIs we propose a quantitative definition for pairwise competition and higher order interactions. We start by defining the function *F* which gives the population growth rate of the focal species as a function of the density of competitor species one and two:

|  |  |  |
| --- | --- | --- |
|  |  | (12) |

For the pairwise understanding of multispecies competition to be correct, we need to be able to express population growth rate as some function of the two single species functions defining the cases where species one or two is absent. In mathematical terms,

|  |  |  |
| --- | --- | --- |
|  |  | (13) |

where *G* is a new function that combines the univariate competition functions *h* and *l* described in equation 1 and shown in figure 1. If we cannot re-write *F* in this way, then there would appear to be no way to recover the surface in figure 1 c from the single species functions in figures 1a and b. By our definition, the pairwise understanding of species composition is not adequate for the multispecies case. Interaction modification or HOIs are a particular case that causes the pairwise model to fail.

In this model, the interaction between a competitor and the focal species is defined by the sensitivity of the focal species to a change the in the density of the competitor species one, which is given by the partial derivatives: and . The partial derivative in terms of G,

|  |  |  |
| --- | --- | --- |
|  |  | (14) |

At this point we note that our definition of a non-pairwise model, coincides with the criteria for interaction modification developed by Adler and Morris (1994). A possible quantitative test for an interaction modification resulting in an HOI would be to take the partial derivative of the function *Fi* with respect to the density of each competitor, , and assess whether the partial derivative is a function, *Gij*, of any competitor’s density other than *j*.

|  |  |  |  |
| --- | --- | --- | --- |
|  |  | IM / HOI present | (15) |

While this test may appear adequate, Adler and Morris (1994) demonstrated that many standard models of density dependent growth that are not commonly thought to contain HOIs would test positive for HOIs according this test. For instance, a discrete time Hassel model for population growth (Hassell and Comins 1976),

|  |  |  |
| --- | --- | --- |
|  |  | (16) |

where *ri* is the intrinsic population growth rate, are the competition coefficients describing the effect of species *j* on species *i*, and *bi* determines how density dependent effects change with competitor density. The complicated partial derivative,

|  |  |  |
| --- | --- | --- |
|  |  | (17) |

includes the original function, *Fi*, for population growth and by extension the density of all competitors. While we understand this model not to have HOIs, the sensitivity of the model to density of any competitor, *j*, is a function of all competitor’s densities. How can we resolve this problem? A step taken by Adler and Morris (1994) was to make an exception for partial derivatives like the one above that are a function of the per capita population growth rate itself. Thus, they found a way to prevent models like the one above from testing positive for HOIs.

Nevertheless, the reasoning behind the Adler and Morris criteria was somewhat unclear and their specific test was developed to accommodate community models of trophic dynamics whereas we want to focus more strictly on HOIs among competitors.

Old Adler and Morris Section:

Here, we propose a new quantitative definition for HOIs based on an a definition first proposed by Adler and Morris (1994). We believe this definition provides a concise quantitative criteria for testing for HOIs while still retaining the intended meaning of the earlier verbal definitions. The goal of the Adler and Morris definition was to “distinguish simple non-additivity in the statistical sense from higher order interaction and interaction modification (IM) in the biological sense” (Adler and Morris 1994). Thus, they developed a definition of HOIs that could isolate how the density of one competitor species at a time affected the population growth rate of the focal species.

To understand the Adler and Morris definition and our slight revision of it, we start with a general model of density dependent population growth:

|  |  |  |
| --- | --- | --- |
|  |  | (18) |

where the per capita population growth rate of species *i* (the focal species) is a function, *Fi*, of the densities of all other *m* species (the competitors) in the community. Adler and Morris argue that one cannot determine if *Fi* involves HOIs simply by testing whether *Fi* is non-linear, because such nonlinearities are not necessarily the result of one species modifying the effect of another competitor. As a case in point, competition in commonly used models of density dependence, such as the Ricker, Beverton-Holt or Hassel, is non-additive but this is generally not thought of as an HOI (Mayfield and Stouffer 2017). A more specific test for an HOI requires examining the partial derivative of *Fi* with respect to the density of a competitor species *j* (for brevity, we refer to this as the sensitivity of the focal species to the competitor). If this partial derivative can be expressed as a function, *Gi*, which is itself a function of *Fi* and the density of the competitor species *j* and no other species, then the model does not contain HOIs. On the other hand, if the partial derivative involves the density of any other species *k* then there is an HOI. This is expressed mathematically as,

|  |  |  |  |
| --- | --- | --- | --- |
|  |  | HOI absent | (19) |
|  |  | HOI present |

Here we have slightly modified the definition provided by Adler and Morris and we discuss why later on. To contrast this definition with non-linearity, take the Lotka-Volterra model for competition between three species and apply the criteria in (2):

|  |  |  |
| --- | --- | --- |
|  | ). | (20) |

The sensitivity of species *i* to the density of species *j* is given by the partial derivative: This sensitivity is a constant and is not determined by the density of any other species’, so there are no HOIs. Adding a quadratic term, , to the same model,

|  |  |  |
| --- | --- | --- |
|  | ), | (21) |

and taking the partial derivative shows that the sensitivity of species *i* to competitor *j* now depends on the density of competitor *j*. However, according to our definition there is still no HOI because no *additional* competitor species are involved.

In contrast, adding the product of and to eq. (3) results in,

|  |  |  |
| --- | --- | --- |
|  | ). | (22) |

The sensitivity of the focal species to the competitor j is now expressed by the partial derivative . The partial derivative is now a function of an additional species, *k*, which means that the model includes an HOI. Specifically, the HOI is the modification of the effect of *j* on the per capita growth rate of *i* by the density of *k*.

To restate our criteria in one sentence, *a model does not contain an HOI if the sensitivity of the focal species to a change in the density of a competitor can be expressed as a function of the density of the competitor and the current population growth rate of the focal species, and does not involve the densities of any other competitor species*. It may appear that our criteria are more complicated than they need to be. Why is the current population growth rate, *Fi*, included in the definition? A simpler criteria for models without HOIs, would be requiring the sensitivity of the focal species to be a function of competitor species *j’s* density and nothing else. However, allowing the sensitivity to be function of the current per capita population growth rate, *Fi*, is a critical part of the definition. As Adler and Morris explain, *Fi* can be thought of as a proxy for all other limiting resources and interactions. Allowing the partial derivative to be a function of *Fi* means that we are isolating how one competitor species at a time affects the focal species while accounting for all other competitor densities (see Box 1 for a graphical interpretation). A practical consequence of this is that the standard version of discrete time competition models such as Beverton-Holt and Ricker do not test positive for HOIs, despite being non-additive (Adler and Morris 1994). In these models, the sensitivity of per capita growth rate to each additional competitor declines as more competitors are added (Hassell and Comins 1976). This could be interpreted as a kind of HOI, an interaction modification among *individuals within* species. However, the standard versions of these models are widely understood not to contain HOIs (Mayfield and Stouffer 2017) and our criteria are consistent with this (Adler and Morris 1994).

Our test is slightly less restrictive for the presence of HOIs than that of Adler and Morris. We stipulate that the partial derivative in eq. (2) must be a function of another competitor other than *j* for there to be an HOI. This means that an HOI can involve the modification of intraspecific density dependence by interspecific density, or vice versa. Consider a variation on eq. (3) above,

|  |  |  |
| --- | --- | --- |
|  | ), | (23) |

Taking the partial derivative of the growth rate with respect to species *j*, we find, , which shows that the sensitivity of species *i* to the competitor *j* depends on the density of species *i* itself. Our definition says this is an HOI, whereas the original Adler and Morris criteria required models to be sensitive to the density of some competitor other than the focal species. In essence, we treat intraspecific competition no differently than interspecific competition in our models. This matches the definitions for HOIs in earlier papers as well (Billick and Case 1994, Mayfield and Stouffer 2017). This difference in interpretation may be due to the fact that Adler and Morris discussed a larger set of population models including both trophic and competitive dynamics. It is only among trophic models that the sensitivity of the focal species was a function of its own density.