



Using experimental indices to quantify the strength of species interactions

Mark Novak and J. Timothy Wootton

M. Novak (*mnovak1@ucsc.edu*) and J. T. Wootton, *Dept of Ecology and Evolution, Univ. of Chicago, Chicago, IL 60637, USA; Present address for MN: Dept of Ecology and Evolutionary Biology, Univ. of California, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060-5730, USA*

Few methods for demonstrating the effects of species interactions rival that of the manipulative experiment (Kareiva and Levin 2002). The now commonly performed removal or addition of predators, competitors, or mutualists to experimentally replicated populations of recipient species has irrefutably shown that species can have important effects on each other's populations, and that the strengths of these effects can vary considerably across environmental contexts and species identities. A large body of research is directed towards understanding this variation to forecast community dynamics and dissect how species interactions regulate community structure (Chesson 2000, McCann 2000, Stachowicz 2001, Duffy 2002). It has frequently been pointed out that progress in this field will require more explicit connections between ecological theory and the realities of nature (Laska and Wootton 1998, Parker et al. 1999, Berlow et al. 2004, Agrawal et al. 2007). This requires that interaction strengths measured experimentally be appropriate to the biology of our study systems and the mathematical abstractions we ascribe to them.

Here we clarify some of the assumptions made in the application of the two most commonly used indices for measuring the strengths of species interactions with manipulative removal/addition experiments: Paine's index and the dynamic index. We explain how the values these indices are intended to measure – the per capita interaction strength between two species – are typically not estimated in common currencies. We then introduce extensions to these indices that alleviate a subset of previously made assumptions and limitations. These include a reformulation of Paine's index appropriate for an open-recruitment system, and an extension of the dynamic index applicable to interactions of a particular nonlinear form. While we focus our language on predator–prey interactions, our discussions are pertinent to the measurement of species effects in other types of interactions as well (Mitchell and Wass 1996, Freckleton et al. 2009).

Defining per capita interaction strengths

We define an estimate of a per capita interaction strength between two species as a measure of the direct effect that one individual of the first species has on one individual of the second species per unit time, or vice versa (Laska and Wootton 1998). Per capita interaction strength estimates thereby scale out differences in species' population size. This makes estimates immediately comparable across species and environmental contexts when population abundances vary. Indeed, per capita interaction strengths underlie all other measures of interaction strength, including the species-level effect rates that empirical ecologists typically intend to compare (Wootton 1997, Laska and Wootton 1998). Seen simplistically, the actual effect that an interaction produces in an experiment arises from the combination of the species' abundances, the per capita interaction strength of their individuals, and the other environmentally-dependent factors that affect a recipient species' recovery rates (e.g. population growth or immigration rates).

In the parallel theoretical framework of a typical model (e.g. Lotka–Volterra or individual-based), per capita interaction

strengths are ostensibly equivalent to interaction coefficients. In fact, much of our theory investigating multi-species interactions, built largely on Lotka–Volterra type models, has used empirical patterns of per capita interaction strengths as motivation. In a predator–prey model this would be the number of prey eaten per predator per prey available per unit time (a.k.a. the per capita attack rate, encounter or discovery rate, assuming all encountered prey are eaten). Note that this definition differs from that of a second usage of the term to denote elements of the Jacobian matrix (May 1973, de Ruiter et al. 1995, Kokkoris et al. 2002). These correspond to the effect of one predator individual on the prey's population growth rate typically evaluated at equilibrium (Laska and Wootton 1998, Berlow et al. 2004).

Experimental estimates of per capita interaction strengths

The juxtaposition of the empirical effect rate-based description and the theoretical attack rate-based definitions of per capita interaction strengths is central to our discussion. Most experimental interaction strength indices used to infer per

capita interaction strengths were devised with an empirical perspective, the underlying theoretical framework remaining unstated (Paine 1992). However, the biological insights gained from their application have subsequently informed a plethora of mathematical models and simulations (reviewed by Chesson 2000, McCann 2000, Duffy 2002, Berlow et al. 2004, Wootton and Emmerson 2005). Furthermore, even when model-based predictions of community dynamics are not envisioned (Abrams 2001), mathematical theory can ensure that we are not contrasting apples with oranges when comparing empirical interaction strength estimates.

Two experimental indices have seen particularly frequent use: Paine's index (Paine 1992, Fagan and Hurd 1994, Raffaelli and Hall 1995, Moran and Hurd 1997, Berlow 1999) and the dynamic index (Wootton 1997, Sala and Graham 2002, Navarrete and Castilla 2003, Emmerson and Raffaelli 2004, O'Gorman et al. 2008, Kordas and Dudgeon 2009, McCluney and Sabo 2009, O'Connor 2009), with a number of variations having also been used (Navarrete and Menge 1996, Sanford 1999, Harley 2003, Navarrete and Berlow 2006). Both indices have been used to compare the interaction strengths of different predators on the same focal prey species (Paine 1992), of focal predators on different prey species (Raffaelli and Hall 1995), and of specific predator-prey pairs across space and time (Navarrete and Berlow 2006) and environmental gradients such as temperature (O'Connor 2009). As we explain below, the interpretation of many of these studies is rendered difficult by the indices' underlying assumptions.

Paine's index

The index proposed by Paine (1992) for estimating the top-down per capita interaction strength between a predator and a single prey species using a caging experiment is

$$PI = \frac{N_{+P} - N_{-P}}{PN_{-P}} \quad (1)$$

where P is the abundance of the predator (held constant), and N is the abundance of the prey in the manipulated presence (+ P) or absence (− P) of the predator at the end of the experiment. Paine's index estimates $-\alpha$ if the prey's dynamics are adequately characterized by a Lotka-Volterra predator-prey model formulated as

$$\begin{aligned} \frac{dN}{dt} &= rN \left(1 - \frac{N}{K} - \alpha P \right) \\ &= rN - \frac{rNN}{K} - r\alpha NP \end{aligned} \quad (2)$$

where r is the prey populations' intrinsic per capita growth rate, and K is its carrying capacity assuming logistic growth. Under this characterization, prey reproduction, self-limitation, and predator consumption are assumed to occur continuously through time. Though not originally conceived of in the context of such a mathematical model, the theoretical justification of Paine's index proceeds as follows: assume that prey populations have reached equilibrium abundance N^*

at the end of the experiment, such that prey populations are no longer changing in both the presence and absence of the predator ($dN/dt = 0$). Rearranging Eq. 2 to isolate N^* leads to the prediction that the prey's population size will reach its carrying capacity

$$N_{-P}^* = K \quad (3)$$

in the predator-exclusion treatment (where $P = 0$), and

$$N_{+P}^* = K - \alpha PK \quad (4)$$

due to predation in the predator-enclosure treatment. Thus, if prey populations have reached their equilibria in the two experimental treatments (i.e. we can substitute observed prey abundances N for the two N^* s), then the application of Paine's index leads to the cancellation of all parameters except the per capita interaction strength $-\alpha$ (Laska and Wootton 1998). This applies only when individual predator-prey pairs are manipulated in isolation such that no indirect effects between species can occur. Indirect effects by such mechanisms as intraguild predation, for example, will produce per capita estimates of net effects that are likely to show little correspondence with the direct strength of a species pair's interaction.

This model formulation (Eq. 2), however, implicitly treats the per capita attack rate as being scaled to the prey's per capita growth rate. Paine's index does not, therefore, produce estimates equivalent to per capita attack rate estimates (i.e. number of prey eaten per predator per prey available per unit time). This is seen more easily by formulating prey dynamics as

$$\begin{aligned} \frac{dN}{dt} &= rN \left(1 - \frac{N}{K} \right) - \alpha NP \\ &= rN - \frac{rNN}{K} - \alpha NP \end{aligned} \quad (5)$$

where α is not implicitly scaled to r . An application of Paine's index to this formulation leads to an estimate of $-\alpha/r$ (Abrams 2001). Note that interpretation of Paine's index as a loosely defined per capita interaction strength under either model formulation is not incorrect. The effect that a predator has on a prey population is directly dependent upon the rate at which the prey is able to recover from such disturbance. However, direct comparisons of Paine's index across multiple prey species, or across environmental contexts where a prey species' per capita growth rates may differ (e.g. productivity regimes), is rendered difficult since the index does not tease apart the effects of the predator from those of the prey population. The use of Paine's index to estimate per capita interaction strengths in a standardized manner therefore requires additional independent measurement of the prey population's per capita growth rate.

The type of predator-prey model that is assumed to characterize the prey dynamics of an empirical system is also of importance in regards to the application of Paine's index under other model formulations. While Paine's index was originally

applied to an intertidal system (Paine 1992), and marine biologists have been among its most frequent subsequent users, the index is in fact not appropriate to situations open to outside prey recruitment or immigration. Application of Paine's index to models with prey immigration leads to very different estimates that make simple comparisons across prey species with different life histories impossible (Table 1). The index's per capita interaction strength estimates are confounded by the other factors that affect the prey population's response. A subtle reformulation of Paine's index as

$$PI_{Im} = \frac{N_{+P} - N_{-P}}{PN_{+P}} \quad (6)$$

provides a means to isolate $-\alpha/r$ in a simple immigration model that assumes only density-independent mortality in the prey (Table 1). No such simple index can estimate α in the other open-recruitment models of Table 1.

The dynamic index

The second interaction strength index frequently used to estimate per capita interaction strengths is the dynamic index (a.k.a. the log-ratio method, Billick and Case 1994, Wootton 1994, Osenberg et al. 1997, Wootton 1997, Berlow et al. 1999). This index is classically written as

$$DI = \frac{\ln\left(\frac{N_{+P}}{N_{-P}}\right)}{P\Delta t} \quad (7)$$

where Δt is the time period over which interaction strengths are to be estimated (i.e. the elapsed time between two censuses of the experiment). The index is derived from a Ricker-type predator-prey model, analogous to Eq. 2 but formulated in discrete-time, where the dynamics of the prey

in the presence (N_{+P}) and absence (N_{-P}) of the predator are respectively assumed to be characterized by

$$N_{t+\Delta t} = N_t e^{(r-N_t/K-\alpha P)\Delta t} \text{ and } N_{t+\Delta t} = N_t e^{(r-N_t/K)\Delta t} \quad (8)$$

The exponential terms of these equations are used to account for serial changes in the prey's abundance between time points. Laska and Wootton (1998) present a multispecies formulation that assumes independence of the predator's attack rates on alternative prey.

Simulations have suggested that the dynamic index performs best at estimating α when prey population sizes are closest to their starting conditions (Laska and Wootton 1998, Berlow et al. 1999). This observation has erroneously been interpreted to mean that, in contrast to Paine's index, the dynamic index is best applied when population dynamics are far from equilibrium (Berlow et al. 1999). In fact, the index can perform just as well at prey abundances near equilibrium as it does when abundances are far from equilibrium (Fig. 1). Rather, the index estimates $-\alpha$ accurately only when prey abundances in the two treatments are exactly equal at time t , and Δt is sufficiently small that changes in abundance during this time period do not have a substantially different effect on the two prey populations' growth rates (via density-dependence). Increasing divergence of prey abundances over time leads to bias. This is because of the discrete-time nature of the model on which the index is based (Eq. 8) which assumes that population trajectories depend only on conditions at time t (Laska and Wootton 1998). The dynamic index assumes that any continuous-time changes in population size between censuses have no effect on the population growth rate of the species over the census interval (Deng 2008).

The dependence on initial conditions is problematic since prey abundances are rarely equal across treatments at the beginning of a field experiment even when the use of the index is otherwise appropriate (i.e. prey recruitment occurs episodically and censuses are performed at the appropriate

Table 1. Values estimated by applying Paine's index (Eq. 1) and the classic dynamic index (Eq. 7) to systems open to outside prey recruitment with the intention of measuring the per capita strength, α , of a predator-prey interaction. Shown are the estimates produced under various assumed model characterizations of observed prey dynamics.

	Immigration (I) with...		
	Density-independent mortality (m) [†]	Density-dependent self-limitation (n) ^{††}	Mortality and self-limitation
Paine's index			
Model:	$\frac{dN}{dt} = I - mN - \alpha NP$	$\frac{dN}{dt} = I - nNN - \alpha NP$	$\frac{dN}{dt} = I - mN - nNN - \alpha NP$
Estimate:	$\alpha / (m + \alpha P)$	$\frac{\alpha P + 2\sqrt{I\sqrt{n}} + \sqrt{\alpha^2 P^2 + 4In}}{2P\sqrt{I\sqrt{n}}}$	$\frac{\alpha P - \sqrt{m^2 + 4In} + \sqrt{m^2 + 2\alpha mP + \alpha^2 P^2 + 4In}}{mP + P\sqrt{m^2 + 4In}}$
Dynamic index			
Model:	$N_{t+\Delta t} = N_t e^{(I/N_t - m - \alpha P)\Delta t}$	$N_{t+\Delta t} = N_t e^{(I/N_t - nN_t - \alpha P)\Delta t}$	$N_{t+\Delta t} = N_t e^{(I/N_t - m - nN_t - \alpha P)\Delta t}$
Estimate:	α	α	α

[†]m = -r (the prey population's intrinsic growth rate). ^{††}n = 1/K (the prey population's carrying capacity). See main text for other variable and parameter definitions.

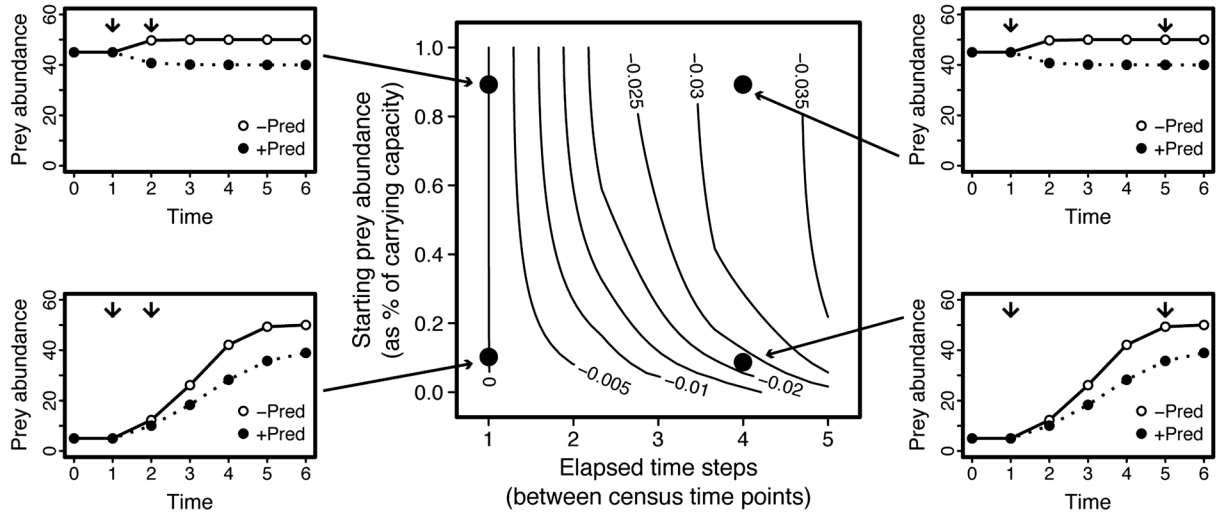


Figure 1. Accuracy of the dynamic index (Eq. 7) in estimating the per capita interaction strength, α , of a predator–prey interaction. Shown is the difference between the index estimate and the true α as a function of the proximity of the prey's abundance to its carrying capacity K at the start of the experiment on the y-axis, and the elapsed time Δt (the number of reproductive episodes) between two successive censuses of the experiment on the x-axis. Insets illustrate prey dynamics in the manipulated presence and absence of predation, with arrows indicating the times at which censuses were performed. Simulations performed using Eq. 8, with $r = 1$, $K = 50$, $\alpha = 0.05$, and $P = 4$, with predators introduced at $t = 1$.

frequency). If abundances at time t are sufficiently similar however, such that treatment differences in the effects of intraspecific density-dependence can be assumed to be relatively unimportant, then a practical formulation of the dynamic index that estimates $-\alpha$ more faithfully is

$$DI_{\text{growth}} = \frac{\ln\left(\left(\frac{N_{+P,t+\Delta t}}{N_{+P,t}}\right) / \left(\frac{N_{-P,t+\Delta t}}{N_{-P,t}}\right)\right)}{P\Delta t} \quad (9)$$

This DI_{growth} index uses not the difference in final prey abundances but rather the difference in prey growth rates between the two treatments. Note that Eq. 9 reduces to the classic dynamic index (Eq. 7) if starting prey abundances are in fact equal ($N_{-P,t} = N_{+P,t}$). Unlike Paine's index, the log-ratio method need not be affected by the inclusion of outside immigration (Table 1).

Nonlinear interaction strengths

To this point we have assumed that our manipulated predators exhibit linear functional responses; their feeding rates changing in constant proportion to changes in the density of their focal prey (Holling 1959). In using our empirical estimates to parameterize a mathematical model we would therefore implicitly assume that a predator's feeding rate could be unlimited. Taken to the extreme, this assumption may make little logical sense. Indeed, the potential for feeding rates to become saturated is observed quite commonly (Jeschke et al. 2004).

If nonlinearities are suspected of having strong effects, then formulations for experimental comparisons can be developed to properly estimate the interaction strength function, just as they have been for linear effects. For example, the log-ratio method of the dynamic index can be extended

to situations where the predator's feeding rate exhibits a single-species type II functional response (Holling 1959). We assume that prey dynamics in the presence of the predator (N_{+P}) can be described by

$$N_{t+\Delta t} = N_t e^{\left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t}\right)\Delta t} \quad (10)$$

which is a slight simplification of the model used in the simulations of Berlow et al. (1999), written in discrete time. The extension requires a total of four experimental treatments: the standard $+P$ and $-P$ treatments where prey densities are left un-manipulated, and two additional $+P$ and $-P$ treatments in which prey densities are reduced by proportion δ . Letting R_x stand for the log-ratio of prey abundances at time $t+\Delta t$ and time t (i.e. $\ln(N_{t+\Delta t}/N_t)$) in treatment x ,

$$DI_{\text{TypeII}} = \frac{(R_{-P,\delta} - R_{+P,\delta})(R_{+P} - R_{-P})(1-\delta)}{(\delta(R_{-P,\delta} - R_{+P,\delta}) - (R_{-P} - R_{+P}))P\Delta t} \quad (11)$$

(see Appendix 1 for details). This DI_{TypeII} index estimates c , the attack rate constant that describes the rate at which a predator's feeding rate approaches the saturation point of its functional response (Holling 1959). We denote this per capita attack rate estimate by c to distinguish it from α which assumes a linear functional response (Novak and Wootton 2008). Note that c is not itself the per capita interaction strength of the predator on the prey, but rather is a parameter that contributes to the per capita interaction strength function (i.e. $c/(1+chN_t)$). This index shares all other assumptions implicit in the DI_{growth} index. With four treatments it is also possible to derive estimates of the other parameters assumed to characterize the prey population's dynamics (Table 2, Appendix 1). While the DI_{TypeII} index may also be appropriate for systems open to

Table 2. Uses of the log-ratio method to estimate parameters when predators exhibit single-species type II functional responses and prey dynamics are assumed to follow Eq. 10. Four treatments are required to isolate each parameter. (See main text and Appendix 1 for details.)

Parameter estimated	Index [†]
Per capita attack rate, c	$\frac{(R_{-P,\delta} - R_{+P,\delta})(R_{+P} - R_{-P})(1 - \delta)}{(\delta(R_{-P,\delta} - R_{+P,\delta}) - (R_{-P} - R_{+P}))P\Delta t}$
Time spent handling all prey, ch	$\frac{R_{+P,\delta} - R_{-P,\delta} - R_{+P} + R_{-P}}{(R_{+P} - R_{-P} + \delta(R_{-P,\delta} - R_{+P,\delta}))N_t}$
Prey intrinsic growth rate, r	$\frac{\delta R_{-P} - R_{-P,\delta}}{(\delta - 1)\Delta t}$
Prey carrying capacity, K	$\frac{(R_{-P,\delta} - \delta R_{-P})N_t}{R_{-P,\delta} - R_{-P}}$

[†] R_x denotes the log-ratio of prey abundances at time $t + \Delta t$ and time t in treatment x , where treatments are the presence (+P) or absence (-P) of predators given the unmanipulated or proportional reduction (δ) of the starting prey abundance N_t .

immigration, further treatments would be needed to isolate the prey population's intrinsic growth rate from its immigration rate.

What to compare?

Empirical ecologists have often expressed frustration over the use of experimental indices to compare the strengths of different species effects because the indices have not intuitively described the relative effect sizes observed. In part this may be because other differences between species (e.g. prey growth or immigration rates) have confounded previous comparisons (Table 1). More ostensibly, however, this occurs when a given predator's abundance (i.e. P in the denominator of the indices) is very small, leading to very large per capita interaction strength estimates.

We posit that per capita interaction strengths as estimated by the appropriate index are still the correct measures to compare when pairs of interacting species are contrasted. This is the intent of most empirical studies, particularly those investigating the community-wide frequency distribution of interaction strengths that have been widely used to inform theoretical studies. A contrasting interest is the comparison of the effects of different predators alone on a single focal prey species at a given location and time. When the starting abundances of focal prey are indeed constant across these comparisons, a more intuitive measure to compare different predators is likely to be the product of the estimated per capita interaction strength and the predator's abundance (i.e. αP). For a nonlinear interaction such as Eq. 10, the appropriate comparison is of $cP/(1 + chN)$.

Conclusions

The juxtaposition of empirical and theoretical interaction strength definitions illustrates the implicit assumptions made

in applying Paine's index and the dynamic index to manipulative experiments. It should be noted that our discussion has assumed that the key parameters contributing to a per capita interaction strength (i.e. α , c , h) are constants. In nature these parameters may themselves be functions of predator and prey densities, which may require further density-manipulations to be adequately characterized. While the true functional form of species interactions is arguably unknown (Abrams and Ginzburg 2000), further careful consideration is also needed to ensure that implicit system characterizations preserve interaction strength estimates that are comparable across focal interactions (Laska and Wootton 1998). Methods for connecting mechanistic statistical models with data may alleviate some of these difficulties in simple, logistically feasible systems by allowing some of the assumptions of experimental indices to be considered explicitly (Hilborn and Mangel 1997, Johnson and Omland 2004, Novak in press). These methods are equally useful for assessing the adequacy of a model formulation in characterizing a particular prey's dynamics in the first place. Nevertheless, problems associated with the duration of between census time intervals do not disappear entirely with these methods, particularly when difference equations are used (Deng 2008). There may also exist multiple, equally plausible model parameterizations when differential equations are used. When explicit model-fitting is impractical, we recommend using the dynamic index based on growth rates (Eq. 9) to estimate interaction strengths in the typical removal/addition experiment due to its increased flexibility.

Our discussion in no way diminishes the power of manipulative experiments to disentangle the effects of species interactions (Paine 1980); models themselves are merely abstractions of the empirical insights we have previously made (Levins 1966). Both should be seen as important to theoreticians and empiricists alike, for the continued alignment of theory and empirical approaches will bring us closer to understanding the imposing complexity of whole communities in nature.

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References

- Abrams, P. A. 2001. Describing and quantifying interspecific interactions: a commentary on recent approaches. – *Oikos* 94: 209–218.
- Abrams, P. A. and Ginzburg, L. R. 2000. The nature of predation: prey dependent, ratio dependent or neither? – *Trends Ecol. Evol.* 15: 337–341.
- Agrawal, A. A. et al. 2007. Filling key gaps in population and community ecology. – *Front. Ecol. Environ.* 5: 145–152.
- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. – *Nature* 398: 330–334.
- Berlow, E. L. et al. 1999. Quantifying variation in the strength of species interactions. – *Ecology* 80: 2206–2224.
- Berlow, E. L. et al. 2004. Interaction strengths in food webs: issues and opportunities. – *J. Anim. Ecol.* 73: 585–598.

- Billick, I. and Case, T. J. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? – *Ecology* 75: 1529–1543.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- de Ruiter, P. C. et al. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. – *Science* 269: 1257–1260.
- Deng, B. 2008. The time invariance principle, the absence of ecological chaos, and a fundamental pitfall of discrete modeling. – *Ecol. Modell.* 215: 287–292.
- Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. – *Oikos* 99: 201–219.
- Emmerson, M. C. and Raffaelli, D. 2004. Predator–prey body size, interaction strength and the stability of a real food web. – *J. Anim. Ecol.* 73: 399–409.
- Fagan, W. F. and Hurd, L. E. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. – *Ecology* 75: 2022–2032.
- Freckleton, R. P. et al. 2009. Measuring the importance of competition in plant communities. – *J. Ecol.* 97: 379–384.
- Harley, C. D. G. 2003. Species importance and context: spatial and temporal variation in species interactions. – In: Kareiva, P. et al. (eds), *The importance of species: perspectives on expendability and triage*. Princeton Univ. Press, pp. 44–68.
- Hilborn, R. and Mangel, M. 1997. *The ecological detective. confronting models with data*. – Princeton Univ. Press.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. – *Can. Entomol.* 91: 385–398.
- Jeschke, J. M. et al. 2004. Consumer–food systems: why type I functional responses are exclusive to filter feeders. – *Biol. Rev.* 79: 337–349.
- Johnson, J. B. and Omland, K. S. 2004. Model selection in ecology and evolution. – *Trends Ecol. Evol.* 19: 101–108.
- Kareiva, P. and Levin, S. A. (eds) 2002. *The importance of species: perspectives on expendability and triage*. – Princeton Univ. Press.
- Kokkoris, G. D. et al. 2002. Variability in interaction strength and implications for biodiversity. – *J. Anim. Ecol.* 71: 362–371.
- Kordas, R. and Dudgeon, S. 2009. Modeling variation in interaction strength between barnacles and fucoids. – *Oecologia* 158: 717–731.
- Laska, M. S. and Wootton, J. T. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. – *Ecology* 79: 461–476.
- Levins, R. 1966. The strategy of model building in population biology. – *Am. Sci.* 54: 421–431.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. – Princeton Univ. Press.
- McCann, K. S. 2000. The diversity–stability debate. – *Nature* 405: 228–233.
- McCluney, K. E. and Sabo, J. L. 2009. Water availability directly determines per capita consumption at two trophic levels. – *Ecology* 90: 1463–1469.
- Mitchell, S. F. and Wass, R. T. 1996. Quantifying herbivory: grazing consumption and interaction strength. – *Oikos* 76: 573–576.
- Moran, M. D. and Hurd, L. E. 1997. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. – *Oecologia* 113: 126–132.
- Navarrete, S. A. and Berlow, E. L. 2006. Variable interaction strengths stabilize marine community pattern. – *Ecol. Lett.* 9: 526–536.
- Navarrete, S. A. and Castilla, J. C. 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. – *Oikos* 100: 251–262.
- Navarrete, S. A. and Menge, B. A. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. – *Ecol. Monogr.* 66: 409–429.
- Novak, M. and Wootton, J. T. 2008. Estimating nonlinear interaction strengths: an observation-based method for species-rich food webs. – *Ecology* 89: 2083–2089.
- O'Connor, M. I. 2009. Warming strengthens an herbivore–plant interaction. – *Ecology* 90: 388–398.
- O'Gorman, E. et al. 2008. Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. – *Oecologia* 158: 557–567.
- Osenberg, C. W. et al. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. – *Am. Nat.* 150: 798–812.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. – *J. Anim. Ecol.* 49: 667–685.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. – *Nature* 355: 73–75.
- Parker, I. M. et al. 1999. Toward a framework for understanding the ecological effects of invaders. – *Biol. Invas.* 1: 3–19.
- Raffaelli, D. and Hall, S. J. 1995. Assessing the relative importance of trophic links in food webs. – In: Polis, G. A. et al. (eds), *Food webs*. Springer, pp. 185–191.
- Sala, E. and Graham, M. H. 2002. Community-wide distribution of predator–prey interaction strength in kelp forests. – *Proc. Natl Acad. Sci. USA* 99: 3678–3683.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. – *Science* 283: 2095–2097.
- Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. – *Bioscience* 51: 235–246.
- Wootton, J. T. 1994. Putting the pieces together: testing the independence of interactions among organisms. – *Ecology* 75: 1544–1551.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. – *Ecol. Monogr.* 67: 45–64.
- Wootton, J. T. and Emmerson, M. 2005. Measurement of interaction strength in nature. – *Annu. Rev. Ecol. Evol. Syst.* 36: 419–444.
- Novak, M. Estimating interaction strengths in nature: experimental support for an observational approach. – *Ecology* in press.

Appendix 1

Derivation of the DI_{typell} index and the equations of Table 2

The DI_{typell} index for estimating the per capita attack rate c of a predator exhibiting a single-species type II functional response to its prey assumes that prey dynamics are described by

$$N_{t+\Delta t} = N_t e^{\left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t}\right)\Delta t}$$

in the presence of the predator (see main text). This index is derived following the same principles as used to arrive at the DI_{growth} index and is complicated only by the additional number of parameters that must be cancelled. The same is true for the other indices of Table 2 which estimate parameters r , K , and ch in the above scenario.

Four treatments are required:

- +P – predator and prey are unmanipulated (a control treatment).
- P – predator is removed and prey is unmanipulated (the classic experimental treatment).
- +P, δ – predator is unmanipulated and prey is reduced by proportion δ .
- P, δ – predator is removed and prey is reduced by proportion δ .

Each treatment's prey dynamics between time t and time $t+\Delta t$ are therefore assumed to take the following form:

$$N_{+P} = N_t e^{\left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t}\right)\Delta t}$$

$$N_{-P} = N_t e^{\left(r - \frac{N_t}{K}\right)\Delta t}$$

$$N_{-P,\delta} = \delta N_t e^{\left(r - \frac{\delta N_t}{K} - \frac{cP}{1+ch\delta N_t}\right)\Delta t}$$

$$N_{-P,\delta} = \delta N_t e^{\left(r - \frac{\delta N_t}{K}\right)\Delta t}$$

Take the log-ratio of prey population sizes at time $t+\Delta t$ and time t within each treatment. For simplicity we denote this by R_x for treatment x . Thus,

$$R_{+P} = \ln \left(\frac{N_{+P(t+\Delta t)}}{N_{+P(t)}} \right) = \left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t} \right) \Delta t$$

$$R_{-P} = \ln \left(\frac{N_{-P(t+\Delta t)}}{N_{-P(t)}} \right) = \left(r - \frac{N_t}{K} \right) \Delta t$$

$$R_{+P,\delta} = \ln \left(\frac{N_{+P,\delta(t+\Delta t)}}{N_{+P,\delta(t)}} \right) = \left(r - \frac{\delta N_t}{K} - \frac{cP}{1+ch\delta N_t} \right) \Delta t$$

$$R_{-P,\delta} = \ln \left(\frac{N_{-P,\delta(t+\Delta t)}}{N_{-P,\delta(t)}} \right) = \left(r - \frac{\delta N_t}{K} \right) \Delta t$$

The remainder of the derivation is a matter of using these equations to cancel-out the unwanted parameters. We provide two examples.

Estimating r requires only the –P and –P, δ treatments:

$$\begin{aligned} r &= \frac{\delta R_{-P} - R_{-P,\delta}}{(\delta - 1)\Delta t} \\ &= \frac{\delta \left(r - \frac{N_t}{K} \right) \Delta t - \left(r - \frac{\delta N_t}{K} \right) \Delta t}{(\delta - 1)\Delta t} \\ &= \frac{\delta r \Delta t - \frac{\delta N_t \Delta t}{K} - r \Delta t + \frac{\delta N_t \Delta t}{K}}{(\delta - 1)\Delta t} \\ &= \frac{(\delta - 1)r \Delta t}{(\delta - 1)\Delta t} \end{aligned}$$

Estimating c requires all four treatments:

$$\begin{aligned} c &= \frac{(R_{-P,\delta} - R_{+P,\delta})(R_{+P} - R_{-P})(1 - \delta)}{(\delta(R_{-P,\delta} - R_{+P,\delta}) - (R_{-P} - R_{+P}))P\Delta t} \\ &= \frac{\left(\left(r - \frac{\delta N_t}{K} \right) \Delta t - \left(r - \frac{\delta N_t}{K} - \frac{cP}{1+ch\delta N_t} \right) \Delta t \right)}{\left(\delta \left(\left(r - \frac{\delta N_t}{K} \right) \Delta t - \left(r - \frac{\delta N_t}{K} - \frac{cP}{1+ch\delta N_t} \right) \Delta t \right) - \left(\left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t} \right) \Delta t - \left(r - \frac{N_t}{K} \right) \Delta t \right) \right)} P\Delta t \\ &= \frac{\left(\left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t} \right) \Delta t - r - \frac{N_t}{K} \Delta t \right) (1 - \delta)}{\left(\left(r - \frac{N_t}{K} \right) \Delta t - \left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t} \right) \Delta t \right) P\Delta t} \\ &= \frac{\left(\frac{cP\Delta t}{1+chN_t} \right) \left(\frac{-cP\Delta t}{1+chN_t} \right) (1 - \delta)}{\left(\left(\frac{\delta cP\Delta t}{1+ch\delta N_t} \right) - \left(\frac{-cP\Delta t}{1+chN_t} \right) \right) P\Delta t} \\ &= \frac{c^2 P^2 \Delta t (\delta - 1)}{(1+chN_t)(1+ch\delta N_t)} \\ &= \frac{\left(\frac{cP\Delta t (\delta - 1)}{(1+chN_t)(1+ch\delta N_t)} \right) P\Delta t}{\frac{c^2 P\Delta t (\delta - 1)}{cP\Delta t (\delta - 1)}} \\ &= c \end{aligned}$$

The equations to estimate parameters ch and K are obtained in likewise manner.

Erratum

Novak, M. and Wootton, J. T. 2010. Using experiemntal indices to quantify the strength of species interactions. – Oikos 119:1057–1063.

The fourth equation of Table 2 is incorrect, having inadvertently been swapped with a different equation. Rather than estimating the carrying capacity, K, the provided equation estimates rK.

The correct equation for estimating K is:

$$\frac{(1-\delta)N_t\Delta t}{R_{-P,\delta}-R_{-P}}$$

Mark Novak