



cxr: A toolbox for modelling species coexistence in R

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Handling Editor: Timothée Poisot**Abstract**

1. Recent developments in modern coexistence theory (MCT) have advanced our understanding of how species interactions among themselves and with the environment influence community dynamics.
2. Although the formulation of MCT is mathematically clear, its application to empirical cases is still challenging, which precludes its adoption by a large range of ecologists and evolutionary biologists interested in broad questions related to community assembly and the maintenance of species diversity.
3. We developed *cxr*, an R package that provides a complete toolbox for calculating species vital rates and interaction parameters, from which the user can obtain estimates of coexistence outcomes based on stabilizing niche differences and average fitness differences.
4. Our aim is to offer a highly versatile package to accommodate different research needs. This means that the user can define population models, use different optimization algorithms and include the effect of external covariates on species interactions, which may include environmental variables (e.g. temperature, precipitation, salinity) and biotic controls (e.g. predation, pollination, mycorrhizae).
5. To illustrate the functionality and versatility of *cxr*, we provide a complete set of population dynamic models and a dataset from a highly diverse grassland community.
6. By building bridges between MCT formulation and its implementation, we provide tools to obtain a deeper mechanistic understanding of how species interactions determine basic patterns such as species abundances and dominance, which are core information for many applied fields, such as conservation, restoration and invasion biology.
7. Finally, the package is not limited taxonomically to any particular group. The application of tools derived from MCT to a wide range of different systems can create feedbacks between empirical and theoretical studies in a way that stimulates a better understanding of the processes maintaining biodiversity.

KEYWORDS

competitive abilities, interaction matrix, Lotka–Volterra models, multitrophic interactions, species coexistence, stabilizing niche differences

1 | INTRODUCTION

Modern coexistence theory (MCT) is a highly influential framework for understanding how species are able to coexist, at varying abundances, across space and time. Broadly speaking, MCT, mostly developed by P. Chesson over several decades (see Chesson, 2000 for the foundational paper), is expressed in the tension between two components of species coexistence. *Stabilizing niche differences* occur when intraspecific competition exceeds interspecific competition, and (stabilizing niche differences) reduce exclusion by favouring species that drop to low relative abundances (Adler, HilleRisLambers, & Levine, 2007). In contrast, *average fitness differences* drive competitive exclusion by favouring one competitor over others and in the absence of niche differences determine the competitive superior regardless of their commonness or rarity. These two processes arising from pairwise interactions, combined with other insights from MCT, provide a solid theoretical foundation to understand and predict coexistence patterns between pairs of species from the same trophic guild.

The application of MCT to empirical studies is gaining momentum, as in the last few years several research groups have studied the importance of environmental variation (Bimler, Stouffer, Lai, & Mayfield, 2018; Lanuza, Bartomeus, & Godoy, 2018), species traits (Angert, Huxman, Chesson, & Venable, 2009; Kraft, Godoy, & Levine, 2015; Pérez-Ramos, Matías, Gómez-Aparicio, & Godoy, 2019) or multitrophic interactions (Chesson & Kuang, 2008; Maron, Hajek, Hahn, & Pearson, 2018) in modulating niche and average fitness differences between species pairs. Yet, the vast majority of these studies come from a small set of ecological communities, namely, annual plant communities from Mediterranean grasslands and microcosm communities under experimental conditions (e.g. Letten, Dhami, Ke, & Fukami, 2018). The simplicity and versatility of MCT allows the study of many other ecological systems in terrestrial (e.g. perennial plant communities, tree communities, pollinator and herbivore insects) and water environments (e.g. marine invertebrates, freshwater fishes, seaweed grasses). In order to expand the field of application of MCT and to narrow the gap between theory and empirical studies, we introduce *cxr* (acronym for *CoeXistence analyses in R*). This R package has two main aims. First, it provides numerical tools to obtain estimates of the per capita strength of interactions between pairs of species, which form the interaction matrix of the community (Wootton & Emmerson, 2005). Second, it combines these estimates with mathematical models describing the population dynamics of interacting species to obtain estimates of fluctuation-independent coexistence metrics (e.g. stabilizing niche and average fitness differences) and the outcome of species interactions according to the MCT formulation.

2 | *cxr* DATA REQUIREMENTS

The core information needed to estimate pairwise per capita interaction strengths is the variation of individual performance in relation to the density of other individuals within a community. Crucially,

the choice of what to measure as *performance* depends on both the species' biology and the model describing their population dynamics. As an example, for plants, viable seed production has been the traditional measurement of performance in MCT when estimating per capita interactions. As a general guideline, the performance an empiricist should care about is the one that contributes to the population growth rate of the interacting species. For animal species, an example would be the number of viable offspring that reach maturity and reproduce. Similarly for a perennial plant species, an appropriate measure of performance is the amount of biomass produced that contributes to further biomass production. Regardless of the performance measure used, users can consult the *Data formats* vignette in the package for an overview of the specific data requirements and formatting accepted by the different *cxr* functions. Furthermore, we include with the package a complete dataset consisting of abundances and performance estimates of plant species in a highly diverse Mediterranean grassland, alongside measurements of an external covariate, soil salinity (see Lanuza et al., 2018 for details on the dataset).

3 | POPULATION DYNAMIC MODELS

We have designed *cxr* in a flexible way to provide users an interface to fit their own models and data (see vignette 4 in the R documentation of the package). Aside from this flexibility, the package includes the formulation of four different families of population dynamics models (Table 1). The models included, and in general, those that can be used with the *cxr* functions, are of the form:

$$\frac{N_{i,t+1}}{N_{i,t}} = f(\lambda_i, A, N_{*,t}, C_{*,t}, \theta, \phi), \quad (1)$$

where λ_i is the per capita fecundity of species i in the absence of competition, A is the interaction matrix with coefficients α_{ij} , $N_{*,t}$ is the set of species abundances at time t , $C_{*,t}$ is the set of covariates at time t , θ is the set of parameters giving the effect of each covariate over λ_i and ϕ is the set of parameters giving the effect of each covariate over A . This set of parameters allows implementing a wide variety of functional

TABLE 1 Model families implemented by default in *cxr*. Here, for simplicity, we describe models without effects of covariates over λ_i or α_{ij} . These variations are exemplified, for the Beverton–Holt family, in Table 2

Model family	Acronym in <i>cxr</i>	Formulation
Beverton–Holt	BH	$\frac{N_{i,t+1}}{N_{i,t}} = \frac{\lambda_i}{1 + (\sum_{j=1}^n \alpha_{ij} N_j)}$
Law–Watkinson	LW	$\frac{N_{i,t+1}}{N_{i,t}} = \frac{\lambda_i}{1 + (\sum_{j=1}^n N_j^{\alpha_{ij}})}$
Lotka–Volterra	LV	$\frac{N_{i,t+1}}{N_{i,t}} = \lambda_i - \sum_{j=1}^n \alpha_{ij} N_j$
Ricker	RK	$\frac{N_{i,t+1}}{N_{i,t}} = \lambda_i e^{-\sum_{j=1}^n (\alpha_{ij} N_j)}$

TABLE 2 Five model formulations included in the package, here in their Beverton–Holt version. Parameters are defined in Table 3, and we assume a guild of n species with c relevant covariates. Note that other combinations of ‘alpha_form’, ‘lambda_cov_form’ and ‘alpha_cov_form’ are possible

Arguments in <i>cxr</i> functions	Formulation
alpha_form = none lambda_cov_form = none alpha_cov_form = none	$\frac{N_{i,t+1}}{N_{i,t}} = \lambda_i$
alpha_form = global lambda_cov_form = none alpha_cov_form = none	$\frac{N_{i,t+1}}{N_{i,t}} = \frac{\lambda_i}{1 + aN}$
alpha_form = pairwise lambda_cov_form = none alpha_cov_form = none	$\frac{N_{i,t+1}}{N_{i,t}} = \frac{\lambda_i}{1 + \left(\sum_{j=1}^n \alpha_{ij} N_j\right)}$
alpha_form = pairwise lambda_cov_form = global alpha_cov_form = global	$\frac{N_{i,t+1}}{N_{i,t}} = \frac{\lambda_i \left(1 + \sum_{k=1}^c \theta_{ik} C_k\right)}{1 + \left(\sum_{j=1}^n (\alpha_{ij} + \sum_{k=1}^c \phi_{jk} C_k) N_j\right)}$
alpha_form = pairwise lambda_cov_form = global alpha_cov_form = pairwise	$\frac{N_{i,t+1}}{N_{i,t}} = \frac{\lambda_i \left(1 + \sum_{k=1}^c \theta_{ik} C_k\right)}{1 + \left(\sum_{j=1}^n (\alpha_{ij} + \sum_{k=1}^c \phi_{jk} C_k) N_j\right)}$

forms for population models (Table 1). For now, models with more parameters cannot be implemented in *cxr*.

cxr is conceived in part as a response to the necessity of many empirical studies to not only estimate the effect of interaction strengths (α_{ij}), but also account for the role of external covariates influencing these parameters. Such covariates may include environmental variables (e.g. temperature, precipitation, resource amount) or interactions with other guilds (mutualisms, antagonisms), for naming two possibilities that have been shown to modify coexistence relationships (Bergholz et al., 2017; Lanuza et al., 2018). The package puts a strong emphasis on this question by explicitly incorporating C_{*t} , θ and ϕ in model formulation. For each of the four model families included by default in the package, we have implemented five models of increasing complexity, with different sets of parameters accounted for and different ways of dealing with covariates (Table 2).

4 | PARAMETER ESTIMATION

With a model describing population dynamics, and observations of individual performance as a function of the density of interacting species in the community, users can estimate model parameters using the functions *cxr_pm_fit* (for population model optimization) and *cxr_er_fit* (for effect/response model optimization). These functions are highly flexible, as users can choose to estimate all model parameters or only a subset of them (e.g. if one already has independent estimates of λ_i). In addition, the associated standard errors of the optimization procedure can be computed via bootstrapping. This uncertainty estimation substitutes the use of hessian matrices during the optimization process, which does not fit properly when data are not normally distributed. For calculating model parameters, we included 19 numerical optimization procedures with different

combinations of efficiency, speed and robustness (Mullen, 2014). Our fitting functions attempt to minimize the negative log-likelihood of the provided data given the selected model. For this procedure the functions rely, for the most part, on the *OPTIMX* package (Nash, 2014), which provides a unified and robust interface to different numerical optimization algorithms. These procedures are no substitute for statistical methods (as in e.g. Mayfield & Stouffer, 2017), but rather complementary. In particular, fitting model parameters via numerical minimization of objective functions, such as in *cxr*, can be particularly useful when using complex formulations that are not easy to translate to a statistical model, or when parameters need to be constrained to a certain interval. The *cxr* documentation includes a basic vignette on how to estimate parameters from any given underlying model (*Getting started*), as well as more complex examples in the subsequent vignettes.

5 | COEXISTENCE METRICS

Given estimates of per capita pairwise interaction strength (α_{ij}) and intrinsic performance (λ_i), *cxr* provides functions to estimate several metrics related to species coexistence: niche overlap, competitive ability, average fitness differences between pairs of species and species fitness in the absence of niche differences (see Figure 1, Table 3 for a list of parameters that can be obtained and their associated functions and the vignette *Coexistence metrics* in the package documentation for a full example on estimating all available metrics). The package also decomposes fitness differences in two components: demographic differences and competitive response differences (see Godoy & Levine, 2014 for their definition). These two components are important to understand whether a species is on average a superior competitor because it performs better (i.e. higher viable seed or biomass production), because it is not sensitive to reduction in performance due to interactions with others, or a combination of both. Note that niche differences are defined as 1 minus niche overlap and in principle can be both negative and positive. Negative values imply the existence of priority effects, a well-documented phenomenon in the literature (Ke & Letten, 2018), in which the order of species arrival determines the long-term trajectory of the community, usually by pioneering species preventing the establishment of subsequent colonizers.

It is also possible that during the estimation process, pairwise interaction strength values (α_{ij}) obtained would be negative rather than positive. Negative values in Beverton–Holt-like models, and in general in *cxr* model outputs, imply facilitative interactions rather than competition. In these cases, niche overlap or average fitness differences as defined by MCT are not computable (see Chesson, 2013 and eqs. 3 and 4 in Godoy & Levine, 2014). An alternative framework for analysing species coexistence, that does allow for competition and facilitation in interaction coefficients, is the structural approach (Saavedra et al., 2017). This framework provides alternative definitions of structural niche and fitness differences. We have included these as well in the appropriate functions of *cxr*, yet the user should

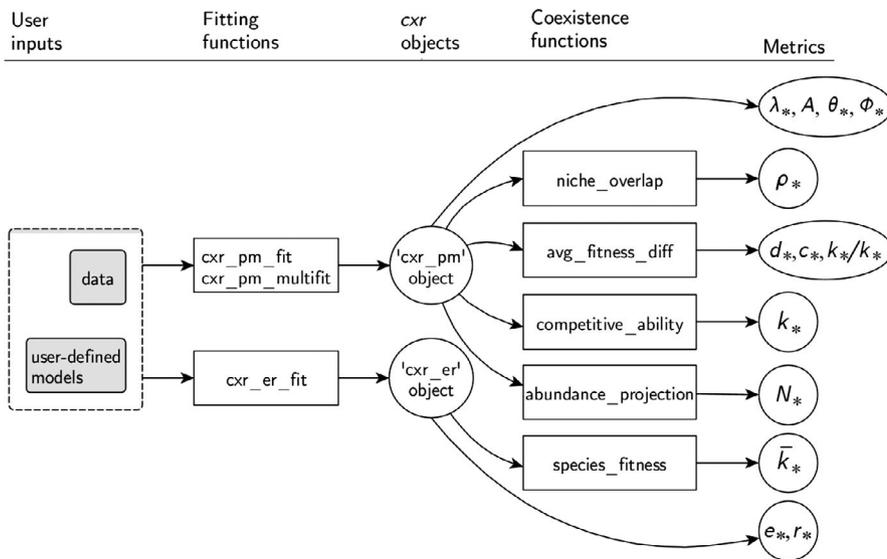


FIGURE 1 Diagram of the functionality included in *cyr*. Grey boxes represent user inputs, rectangles are functions and ellipses are outputs. The different metrics are defined in Table 3

TABLE 3 Parameters that can be calculated with the package, and the function with which they can be obtained

Parameter	Definition	<i>cyr</i> function	References
λ_i	Per capita fecundity of species <i>i</i> in the absence of competition	<i>cyr_pm_fit</i> <i>cyr_pm_multifit</i>	Godoy and Levine (2014)
α_{ij}	Magnitude of interaction effect of species <i>j</i> over species <i>i</i> , elements of matrix <i>A</i>	<i>cyr_pm_fit</i> <i>cyr_pm_multifit</i>	Godoy and Levine (2014)
θ_{ik}	Effect of covariate <i>k</i> on λ_i	<i>cyr_pm_fit</i> <i>cyr_pm_multifit</i>	Lanuzá et al. (2018)
ϕ_{ijk}	Effect of covariate <i>k</i> on α_{ij}	<i>cyr_pm_fit</i> <i>cyr_pm_multifit</i>	Lanuzá et al. (2018)
e_i	Competitive effect of species <i>i</i>	<i>cyr_er_fit</i>	Godoy, Kraft, and Levine (2014)
r_i	Competitive response of species <i>i</i>	<i>cyr_er_fit</i>	Godoy et al. (2014)
ρ_{ij}	Niche overlap between species <i>i</i> and <i>j</i>	<i>niche_overlap</i>	Godoy and Levine (2014)
d_{ij}	Demographic ratio between species <i>i</i> and <i>j</i>	<i>avg_fitness_diff</i>	Godoy and Levine (2014)
c_{ij}	Competitive response ratio between species <i>i</i> and <i>j</i>	<i>avg_fitness_diff</i>	Godoy and Levine (2014)
$\frac{k_i}{k_j}$	Average fitness difference between species <i>i</i> and <i>j</i>	<i>avg_fitness_diff</i>	Godoy and Levine (2014)
k_{ij}	Competitive ability of species <i>i</i> relative to species <i>j</i>	<i>competitive_ability</i>	Hart, Freckleton, and Levine (2018)
\bar{k}_i	Fitness of species <i>i</i> in the absence of niche differences	<i>species_fitness</i>	Godoy et al. (2014)

not expect equal estimations with both approaches (see Saavedra et al., 2017 for methodological differences).

6 | PROJECTION OF ABUNDANCES

An important, but often missed, feature of MCT is that it can be used to predict densities of coexisting species, thus providing a continuous answer to the coexistence problem, rather than a dichotomic (yes/no) outcome. This opens the possibility of verifying to what extent model predictions match field observations, or whether additional factors such as indirect or high-order interactions (HOIs) should be included to better describe population dynamics. With

cyr, we specifically provide functionality for projecting population dynamics based on user-defined models. In particular, the function *abundance_projection* returns the expected densities of a set of species for a given predictive model and values of parameters and covariates. We have implemented predictive counterparts of the five models listed in Table 2, for the four model families included (see vignette *Projecting species abundances* for more details).

7 | A NOTE ON USABILITY

As with any toolbox for estimating metrics based on underlying theories, *cyr* is limited to the same extent MCT is limited. Basically, the

estimation of species' interaction strengths as well as coexistence metrics previously presented is phenomenological. This means that the underlying biological mechanisms driving estimated differences between species cannot be teased apart from the models included in our functions, although the use of covariables can help. This is a task that ultimately depends on the ecological knowledge of the system by the researcher. More generally, expert knowledge should in all cases guide model selection and the interpretation of coexistence metrics.

Modern coexistence theory, despite being so far mostly applied to plant communities, can be potentially useful for studying a broad range of ecological communities. In that sense, *cxr* is best suited to fit interactions in which the fitness of individuals of a focal species is described as a function of the spatial configuration of the neighbour species. This approach brings the first challenge of tracking the fitness per individual of the focal species, which can be reasonably done with either sessile species or with species that locate their offspring in specific sites that can be monitored (e.g. holes, nest). The second challenge is the definition of the extent of the neighbourhood that affects individual fitness, which can range from few centimeters in sessile organisms, to hundreds of metres for e.g. animals that are central place foragers. With these two challenges addressed, *cxr* is a particularly interesting toolbox for applications in which interactions with other guilds (e.g. for plant species, number of floral visitors, numbers of fruits eaten or herbivory rates) and environmental variation modify coexistence relationships among species of a certain trophic guild (e.g. Lanuza et al., 2018).

Another important issue, related to the interpretation of coexistence metrics, is that we present niche and fitness differences as independent metrics, but both definitions are interrelated. This is because density-dependent processes jointly operate in both species differences (see Song, Barabás, & Saavedra, 2019 for a detailed explanation). *cxr* can be useful for users to understand the consequences of such interdependence numerically for their particular dataset. Finally, *cxr* functions estimate species interaction strengths (and niche and fitness differences) at the pairwise level without the default possibility to include multispecies effects such as HOIs (Mayfield & Stouffer, 2017). This, however, does not mean that *cxr* cannot be used to study coexistence within a multispecies context. It is possible to obtain a matrix of $n \times n$ species containing n^2 pairwise interactions, but the estimation of indirect multispecies interactions (e.g. HOIs) will require further effort from users to define their own functions.

8 | CONCLUSIONS

With *cxr*, we provide researchers with a toolbox for obtaining information on the interaction strength between pairs of species from empirical data and user-defined models. With this information, in turn, key components of MCT can be obtained, such as average stabilizing niche differences and average fitness differences. Importantly, we facilitate the study of the influence of external covariates in these species differences, opening the way to test the long-standing issue

of how interaction outcomes, and species coexistence, vary across environmental gradients. In a broader context, the package may be of interest to researchers interested in estimating species competitive abilities as per capita interaction strengths. Estimating the community interaction matrix associated with these pairwise effects is a key step for exploring a wide range of questions related to the structure and stability of multispecies communities. Thus, we hope that this set of tools will, on the one hand, facilitate the use of robust theoretical concepts by empiricists, and on the other hand, help theoreticians evaluate their models and assumptions under the light of empirical data and predictions.

9 | IMPLEMENTATION

The code is available at the developing website (<https://github.com/RadicalCommEcol/cxr>) and is released under the MIT license. *cxr* is under active development, and we welcome contributions and bug reports through the GitHub site. This note describes version 1.0.0 of *cxr*.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the R package and the writing of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

No data were used in this manuscript, however, we have included an example dataset with *cxr*: see the correspondent help files in the package for details. The development version of the package is maintained at GitHub (<https://github.com/RadicalCommEcol/cxr>), and the stable 1.0.0 version of *cxr* described in this manuscript is stored at Zenodo <https://doi.org/10.5281/zenodo.3909328> (García-Callejas, Bartomeus, Lancelot, & Godoy, 2020).

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