Received: 27 October 2017 | Accepted: 19 February 2018
DOI: 10.1111/1365-2745.12960

INTRANSITIVE COMPETITION AND SPECIES COEXISTENCE

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

Cyclic population dynamics and density-dependent intransitivity as pathways to coexistence between co-occurring annual plants

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Funding information
Australian Research Council, Grant/Award Number: DP140100574 and FT140100498; Royal Society Te Apārangi, Grant/Award Number: 16-UOC-008 and RDF-13-UOC-003

Handling Editor: Eric Allan

Abstract

1. Recent studies have brought renewed attention to the importance of complex species interactions—notably intransitive interactions—to patterns of plant community diversity. One underappreciated avenue through which intransitivity can occur is through cyclic population dynamics. Although such cyclic intransitive relationships have been extensively studied in predator–prey systems, evidence of their importance in competitive communities, notably plant communities, is more limited. Most studies of coexistence in plant communities assume fixed-point coexistence even while utilising models that allow for cyclic population dynamics.
2. In this paper, we explore the potential for density-dependent, cyclic population dynamics and intransitivity in a model for annual plants. We then examine how these density-dependent cycles impact mutual invasibility and ultimately stable coexistence between plant species pairs. We do this using data collected from four co-occurring annual plant species living in natural wildflower communities in SW Western Australia. To maximise the number of biologically plausible pathways by which coexistence mediated by density-dependent cyclic intransitivity can occur, we use an annual plant model that allows for competitive direct interactions, facilitative direct interactions and higher-order interactions between species.
3. Results from our empirically parameterised model suggest that monocultures of all four focal species can have cyclic solutions with periodicity <1 under sunny ("open") or shaded field conditions. Cyclic patterns drive variation in annual abundance patterns, with stable solutions for persistent monocultures and invasibility potential (the capacity of one population to invade another) common. Mutual invasibility in the face of cyclic population dynamics was found for just one of six species pairs, only under open environmental conditions. Our results illustrate the potential for cyclic intransitivity to both drive and prevent stable coexistence in environmentally heterogeneous biological communities.
4. *Synthesis*. We provide analytical and empirical evidence that coexistence in competitive communities (annual plants) can be achieved under non-equilibrium circumstances, through density-dependent cyclic intransitivity. Our results suggest

that cyclic population dynamics may be common and important for coexistence dynamics in some types of communities. In such communities, the exploration of stable coexistence should, therefore, include consideration of cyclic as well as fixed-point equilibria for maximal accuracy.

KEYWORDS

annual-plant models, density-dependent intransitivity, environmental heterogeneity, fixed-point equilibria, mutual invasibility, oscillating population dynamics, plant population and community dynamics

1 | INTRODUCTION

Understanding how coexistence among species occurs and results in observed patterns of diversity are long-standing goals in community ecology (Gause, 1934; Levine, Bascompte, Adler, & Allesina, 2017). Although numerous models of coexistence in plant and animal communities have been developed over the years (Chesson, 2000; Hubbell, 2001; Levine et al., 2017; Lotka, 1925; Volterra, 1926), those that have gained the most traction in plant community ecology typically assume stable, fixed-point equilibria, in which population sizes do not fluctuate predictably (cycle) over time (Chesson, 2000; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012). Models that predict cyclic population behaviours—in which the population dynamics of coexisting species exhibit temporally varying abundances—have been used more widely for animal communities, particularly in the context of predator–prey dynamics (Hastings, 2001; Higgins, Hastings, Sarvela, & Botsford, 1997; Huisman & Weissing, 1999). Lotka–Volterra predator–prey models are a classic example; in these models, crashes in prey populations are followed by predator declines, which allow prey populations to rebuild again (Lotka, 1925; Volterra, 1926). Such cyclic food chain dynamics are famously evident in Canadian lynx and hare populations (Elton & Nicholson, 1942; Stenseth, Flack, Bjornsted, & Krebs, 1997).

The idea that coexistence within a competitive system, or within any single trophic guild (such as primary producers), can result in cyclic population dynamics is less well developed than for food chains, but has been known to be theoretically possible for decades (Gilpin, 1975; May & Leonard, 1975). May and Leonard (1975) notably used a restricted Lotka–Volterra competition model to explore this idea for a very narrow set of conditions, specifically a community of three species with symmetric equilibrium points. For this specific type of community, they found that coexistence could occur under very specific conditions, but almost any disturbance to the system would destabilise the population cycles, driving a slow convergence on a single competitively dominant species over time. As a result, they concluded that stable coexistence resulting from cyclic population dynamics of competing species was very unlikely. Using a much less restricted model, in which communities could contain any number of species and symmetric or asymmetric equilibria points, Gilpin (1975) found that stable coexistence among species exhibiting inter-annual population cycles was possible and in fact likely. In this paper, Gilpin shows that intransitive competition dynamics resulting from competition-driven population cycles result in stable coexistence in multispecies communities. Although Gilpin's model showed a more likely pathway to coexistence due to population cycles resulting from competition, his model was still characterised by some major assumptions. Most notably, his model assumed that all species interactions were direct and competitive in nature, thus omitting the possibility that facilitative or nonadditive interactions might contribute to stable population cycles and thus coexistence among species pairs. The importance of different types of interactions in this context have, however, been noted elsewhere (Lewontin, 1968).

There has been mounting evidence in the literature that direct competition between species pairs is neither the only possible nor even the only likely interaction type important for coexistence in plant communities. Increasingly, studies are highlighting the possibility for coexistence to be mediated by more complex interactions between species pairs or among large numbers of species (Allesina & Levine, 2011; Levine et al., 2017; Maynard et al., 2017). In particular, this discussion has focused on two nonadditive types of species interactions: higher-order interactions and intransitive interactions (Godoy, Stouffer, Kraft, & Levine, 2017; Levine et al., 2017; Mayfield & Stouffer, 2017). Higher-order interactions, in this context, refer to the suite of nonadditive effects of interactions between individuals of co-occurring neighbour species on focal individuals and can conceptually be expressed as a density dependence of species' pairwise interaction strengths. These interactions function to mediate direct competitive and facilitative effects and are central to determining the net effect local neighbourhoods have on individual fitness, a key component of coexistence (Mayfield & Stouffer, 2017). Most recently, Mayfield and Stouffer (2017) found strong evidence for higher-order interactions impacting fitness outcomes in diverse natural plant communities.

Broadly speaking, "intransitivity" refers to any relational loop of association. In the modern coexistence literature, intransitivity most often refers to non-hierarchical buffering of the competitive effects one species has on another (or "rock, paper, scissor" competition). Importantly, this definition assumes that all involved species are at steady state equilibria; resulting in the assumption that intransitive loops must involve three or more species (Laird & Schamp, 2006; Rojas-Echenique & Allesina, 2011; Soliveres et al., 2015). By removing the assumption that the populations of each species involved are at a fixed equilibrium, we can broaden the definition of intransitivity to include changes in the competitive hierarchy brought about by cyclic population dynamics for any involved species (including distinct populations or distinct density phases of the same species). This non-equilibrium "density-dependent" definition of intransitivity is not new (Gilpin, 1975). In 1975, Gilpin illustrated the idea of density-dependent intransitivity, in which intransitive dynamics do not occur through a non-hierarchical loop of fixed competitive outcomes but instead via endogenous changes in population densities over time. A key difference between Gilpin's definition of intransitivity, which we refer to here as "density-dependent cycle intransitivity," and the more common "rock, paper, scissor" definition is that density-dependent intransitivity does not assume steady-state equilibria while the standard definition does. By releasing this assumption, density-dependent intransitivity allows for the possibility that population cycles of one or two species can generate intransitive dynamics as easily as fixed-density populations of three or more species (Gilpin, 1975). Relaxing the assumption that only direct, competitive interactions are important for mediating coexistence and including direct facilitation and higher-order interactions further expand the opportunities to observe density-dependent intransitivity. This is because by allowing for more types of species–species interactions in our models, we expand the types of interactions available to drive cyclic population dynamics, intransitivity and ultimately coexistence.

Although conceptually distinct, higher-order interactions and intransitive dynamics are related in that they both add complexity and realism to plant coexistence models based on modern coexistence theory and combined, they can greatly increase the possible pathways to coexistence (Chesson, 2000). Higher-order interactions have been shown to be theoretically and empirically important for improving estimates of species fitness, a key component of coexistence models (Bairey, Kelsic, & Kishony, 2016; Mayfield & Stouffer, 2017; Wootton, 1994). Numerous papers have shown the theoretical importance of intransitivity among sets of species to coexistence (Laird & Schamp, 2006; for example), but efforts to provide empirical evidence of intransitivity using modern coexistence models have been less successful (Godoy et al., 2017). In this study, we use a novel approach with data from natural annual-plant communities to explore the possibility that density-dependent intransitive dynamics can drive coexistence. The approach also allows for higher-order interactions to maximise the types of intra- and interspecific interactions that can result in endogenous density cycles and ultimately mediate coexistence.

Mutual invasibility is a central component of predicting pairwise coexistence between competing species (Chesson, 2000). Conceptually, mutual invasibility can result from nonlinear or cyclic density-dependent population growth (Gilpin, 1975; May, 1973). Fundamentally, this involves the restriction of a resident species' population growth, due to intraspecific competition, allowing a second species to invade with positive growth rates when rare and continued population growth until self-regulation of the invader ultimately allows the resident species to avoid being competitively excluded (Adler, HilleRisLambers, & Levine, 2007; Chesson, 2000). If competitive effects are independent of population densities, mutual invasibility is a sufficient condition for pairwise coexistence in this conceptual framework. In contrast, higher-order interactions can accelerate or occlude the successful establishment of an invader even when they have positive growth rates when rare. This softening of the predictive power of mutual invasibility may become even more pronounced when the invader is entering a resident population that cycles in size between growing seasons since there may only be a subset of abundance values that are compatible with invasion or the establishment of an invader. The combination of cycling population dynamics and higher-order interactions may therefore provide a wide range of pathways by which species can coexist in competitive systems.

The long-term stability of coexisting species likely also depends on the environmental conditions in which populations are found (Hart, Usinowicz, & Levine, 2017). Although density-dependent interactions and/or population growth can theoretically drive population cycles, the carrying capacity of a population, and thus the peak and trough of invasion cycles, logically varies as a function of the environment. We, therefore, expect that the existence of population cycles for a given species will depend on environmental context and will vary across relevant environmental gradients. For the reasons explained above, this environmental context should be quite important for determining when changes in population size will impact on the coexistence of a species pair or group of species.

In this study, we use fitness data from annual-plant communities in southwest Western Australia to test whether density-dependent intransitivity can result in stable coexistence in real plant communities via effects on mutual invasibility. Our aim is not to show that cyclic population dynamics are necessary for coexistence, only that such cycles may offer additional pathways to coexistence that are not evident if population sizes are assumed to be fixed through time. We do this by looking for solutions to a discrete model of annual-plant communities, for which resident populations exhibit annual abundance cycles of periodicities ranging from 1 to 5. A periodicity of 1 represents the typically assumed situation of fixed-point equilibrium. This is where invasion is assumed to occur at a single abundance value regardless of year or condition. Fixed-point equilibria are widely assumed in studies of coexistence in annual-plant communities (Godoy & Levine, 2014; Kraft, Godoy, & Levine, 2015; Levine & HilleRisLambers, 2009). Periodicities of 2–5 indicate cyclic population dynamics with the 2–5 values referring to the number of recurring annual intervals (see Figure 1). This modelling approach is conceptually similar to Gilpin (1975), but with several important differences. First, we use a modified annual-plant population dynamics model (Mayfield & Stouffer, 2017) that allows for species interactions to be competitive or facilitative, direct or higher-order, rather than directly competitive only (the assumption made by Gilpin, 1975). This decision stems from growing evidence that negative direct, positive direct and higher-order interactions between species can be important for determining fitness outcomes in real plant communities (Mayfield & Stouffer, 2017). Second, we parameterise the model directly using field-collected

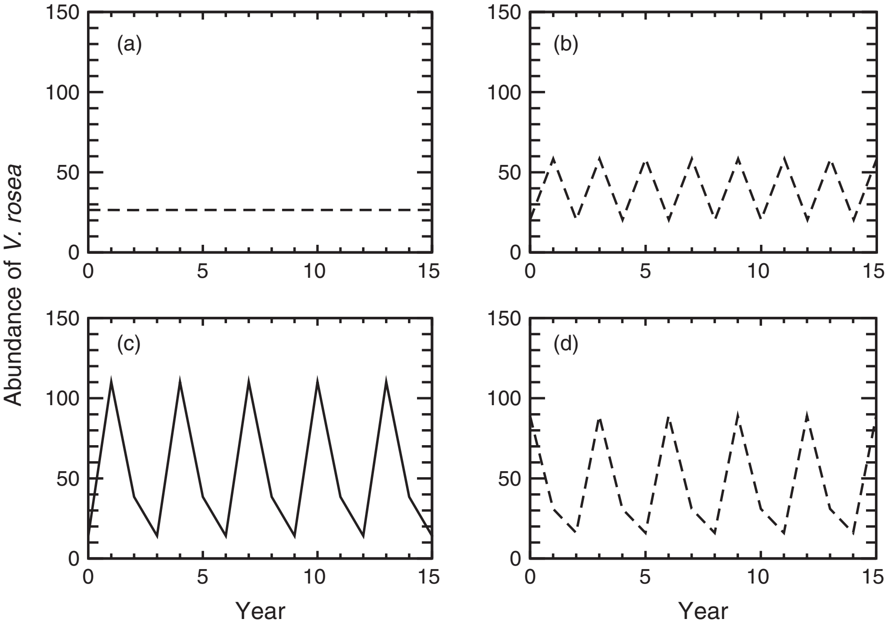

FIGURE 1 Under shade conditions, monocultures of *Velleia rosea* are predicted to exhibit several unstable solutions (dashed black lines) and one stable solution (c, solid black line). (a) *Velleia rosea* shows an unstable fixed-point equilibrium (period-1 solution), (b) an unstable period-2 solution, and (c and d) show two different period-3 solutions, one of which is stable (c, solid line). One unstable solution with periodicity 4 and two unstable solutions with periodicity 5 were also identified but are not shown here

data in order to provide a proof of concept based on real, rather than simulated, annual-plant communities. Third, we also explore how population cycles vary across a strong environmental gradient, in this case shade (previously shown to be important for local patterns of diversity; Dwyer, Hobbs, Wainwright, & Mayfield, 2015), in order to quantify the potential importance of environmental heterogeneity ("context") for how species persist and coexist in real plant communities.

The specific questions we ask are:

1. Can annual plants persist when exhibiting cyclic population growth? And does stable persistence sometimes occur when abundances cycle at periodicities >1?
2. When a resident species exhibits cyclic population growth, can an invader establish? If so, when does establishment occur?
3. How does the abiotic environment modify cyclic persistence and invasion dynamics in annual-plant communities?

2 | MATERIALS AND METHODS

2.1 | Study system

Our study took place in the York gum *Eucalyptus loxophleba* Benth.–jam *Acacia acuminata* Benth. woodland understories in West Perenjori Nature Reserve (29°28′01.3″S, 116°12′21.6″E) in southwest Western Australia. Mean annual rainfall in West Perenjori for 2015 was 330.4 mm and 298.7 mm in 2014 (the year *Arctotheca calendula* supplementary data were collected, see below; BOM 2017, station ID 008013). Southwest Western Australia has a semi-arid Mediterranean climate. Canopies of York gum–jam woodlands are relatively open and are dominated by *E. loxophleba* and *A. acuminata*. Understories are composed of dense annual forb communities with a sparse shrub and perennial grass component (Dwyer et al., 2015; Prober & Wiehl, 2011). Although these understorey communities are often invaded, many are composed of species-rich communities of native and exotic annuals that co-occur over local spatial scales (<0.09 m^2; Lai, Mayfield, Gay-des-combes, Spiegelberger, & Dwyer, 2015).

Field data were collected on four common winter annual-plant species: native forb *Velleia rosea* S. Moore (Goodeniaceae), native forb *Hyalosperma glutinosum* Steetz (Asteraceae), exotic annual grass *Pentameris airoides* Nees (Poaceae) and the exotic forb *A. calendula* (L.) Levyns (Asteraceae). All data for *V. rosea*, *H. gluinosum* and *P. airoides* were collected as part of a shade manipulation study conducted in the winter–spring growing season of 2015. Due to a limited number of *A. calendula* individuals in open sites in 2015, we supplemented data on *A. calendula* from 2015 with data from another study conducted in the same site in 2014 (described below).

2.2 | Field data

In the growing season of 2015 in West Perenjori Reserve (July to November), we collected seed production (fecundity) and neighbourhood composition data for all four of our focal species across a shade manipulation experiment. In this experiment, we recorded the fecundity of 1,213 individual focal plants growing naturally across the reserve. These individuals were divided among our four focal species and one of two shade treatments: "open" (limited canopy cover, full sun) or "shade" (artificially created shade conditions). In addition, focal plants were either located in "natural communities," in which no neighbourhood thinning was conducted or in "thinned communities" in which neighbourhoods were heavily thinned, such that each contained fixed numbers of two of the four focal species only. Below, we provide descriptions of all treatments and community types.

2.2.1 | Shade treatment

To examine the influence of local-scale variation in a key environmental factor in this system, we manipulated shade above half of our study plots. We selected shade because it has previously been identified as having a structuring effect on local patterns of diversity in this system (Dwyer et al., 2015; Wainwright, Dwyer, & Mayfield, 2017). To do this, plots were positioned in locations where the four focal plants were found living. Each plot was then randomly assigned a shade or open treatment. For shaded plots, we draped wide-aperture camouflage netting (CamoSystems) *c*. 0.5 m above the tallest plants in each plot. The netting created a level of canopy cover similar to that found under natural tree canopies in this system (Dwyer, Hobbs, & Mayfield, 2014; Wainwright et al., 2017). The wide aperture of the camouflage netting allowed pollinating insects access to flowers and a natural dappled light effect. Open plots varied in natural level of shade but were significantly less shady on average than shade plots (mean canopy cover [*SE*]: open = 9.30% [1.78], shade = 47.52% [1.63]). The same shade treatment was applied to natural and thinned communities.

2.2.2 | Natural communities

Plots for unthinned or "natural" communities were located in five blocks no greater than 15 m × 15 m in size and separated by at least 50 m from each other across West Perenjori Reserve. Within each block, we established between 12 and 15 30 cm × 30 cm plots containing at least one individual of one or more of our four focal species, each of which we marked with a coloured toothpick. The competitive neighbourhoods around each focal individual within each plot were left unthinned and the abundances of each neighbouring species (including conspecifics) were recorded. Each plot contained two focal individuals, always at least 5 cm apart from each other. To quantify the impact of competition on intrinsic seed production, we also marked "solo" individuals of each focal species immediately adjacent (within 0.5 m to each plot to minimise microenvironmental variation) to natural community plots, removing all neighbours in a 5 cm radius area around each solo plant. At the end of the growing season, we collected all seed produced from all focal individuals in all plots. After accounting for some early focal mortality, we were able to use fecundity data on 93 focal individuals from 54 "natural community" plots along with 95 paired solo plants.

2.2.3 | Thinned communities

In addition to the focal plants grown in natural communities, we also collected fecundity data from focal individuals growing in heavily thinned plots spread across five additional blocks also in West Perenjori Reserve. In these blocks, we marked 282 10 cm × 10 cm plots containing naturally occurring pairs of our four focal species. These plots, however, were assigned one of three manipulated density levels (thinned); low density (one plant of each species – one neighbour per focal plant), medium density (two plants of each species – three neighbours per focal plant) and high density (three plants of each species – five neighbours per focal plant). We obtained these density treatments by thinning all but the desired number of individuals of the relevant species pair. We also cleared a 5 cm buffer around each thinned plot to prevent impacts of the larger more diverse community on these focal plants. Interspersed with thinned plots were >30 solo plants per focal species (128 solo plots divided among the four focal species), for which all neighbouring plants were removed in a 5 cm radius area. Replicates of species pairs and density level combinations were distributed as evenly as possible among the blocks. In total, we were able to collect fecundity data on 1118 focal individuals (including solo plants) from 114 thinned plots.

2.3 | Supplementary field data for *Arctotheca calendula*—open conditions

Due to lower abundances of *A. calendula* in 2015, samples sizes for *A. calendula* as a solo plant and as a competitor in open conditions were lower than other species/treatment combinations. Rather than removing this species/treatment from consideration, we supplemented our dataset for *A. calendula* in open (sunny) conditions with data from another experiment run the previous year in the same West Perenjori site.

These *A. calendula* supplementary data were a subset of data collected for a larger study involving 24 blocks of five 50 cm × 50 cm quadrats across West Perenjori Reserve in winter/spring 2014. Each quadrat contained two or more individuals of four focal species, one of which was *A. calendula*. Given our use of *A. calendula* focal plants only from this field season, data used here from this dataset came from 26 focal *A. calendula* plants from 23 quadrats across 11 blocks.

Each quadrat was divided into four quarters (each 25 cm × 25 cm) and a focal plant close to the centre of two quarters of each quadrat was marked with a coloured toothpick and tracked through the season. Each quadrat (50 cm × 50 cm) was randomly assigned one of five treatments in reference to the focal individuals. These treatments were "control" (no thinning), "native neighbourhood" (all exotic neighbours removed), "exotic neighbourhood" (all native neighbours removed), "monocultures" (all neighbours that were not the focal species removed) and "solo plants" (all neighbours removed in a 25 cm diameter area around focal plants). All quadrats were thinned periodically throughout the season to maintain treatment-assigned neighbourhood compositions. The mean number of neighbours in these plots was 12.85, ranging from 0 (solo plants) to 75. No effect of neighbourhood treatment was found on *A. calendula* fitness; thus, the exotic, native, control and monoculture treatments were not considered as separate treatments in our analyses. At peak biomass, the identity and abundance of all plants within the 25 cm × 25 cm area around each focal plant was recorded. At the end of the growing season, we recorded the number of inflorescences produced by each focal plant and when possible the total seed production of each focal individual. In cases where seeds disperse prior to collection, we extrapolated total seed production per plant based on total plant flower counts.

For a given individual where a dispersed flower head was found, we multiplied the average seed count from flowers collected from that individual and multiplied this average seed count by the number of dispersed flower heads. This number was then added to the collected seed count for an estimate of total seed count per individual. Flower heads eaten prior to seed set were not included in seed estimates.

2.4 | Seed survival rates

For all four focal species, we used laboratory-derived seed viability rates (D. Manietta, J. Dwyer, & M. Mayfield, unpubl. data) as a proxy for seed survival. This approach likely overestimates seed survival rates under field conditions, where seed predators and pathogens are likely present, but we felt that they offered a coarse estimate of each species' reliance on an inter-annual seed bank. Seed viabilities were tested according to standardised methods in the AOSA/SCST Tetrazolium (TZ) handbook (Miller, 2010). Seeds were imbibed overnight and then soaked in a 400 ppm Gibberellic Acid (GA_3) solution to alleviate dormancy and promote germination. Germinated seeds were scored as viable, and ungerminated seed embryos were extracted and placed in a 1% TZ solution for up to 48 hr and scored as viable if they stained. All nonstaining embryos were recorded as non-viable. Seed survival estimates are presented in Table S1.

2.5 | Germination rates

Seed germination rates were also taken from a laboratory study (D. Manietta, J. Dwyer, and M. Mayfield, unpubl. data). Seeds of all focal species were collected from the study site in 2010 and underwent a 2-week dry-after-ripening treatment at 40°C to alleviate dormancy (Hoyle, Daws, Steadman, & Adkins, 2008). Seeds were placed on sterilised germination paper in culture plates exposed to one of three constant temperature: 7°C, 14°C and 25°C. The seeds were wetted with DI water as needed to prevent desiccation throughout the germination trials. Plates were placed in a growth chamber (ThermoFisher Scientific, Adaptis 1000, fluorescent tubes providing *c*. 650 μmol m^{-2} s^{-1} white light) at the University of Queensland for 30 days and the locations of germination plates were randomised daily to account for any environmental differences among shelves. After 30 days, ungerminated seeds were removed from the chamber and exposed to room temperature conditions (*c*. 23°C) for 1 week and any additional germination was scored. For this study, the germination temperature treatment resulting in the highest germination rate was used, with all germination proportions viability adjusted (divided by the proportion of viable seeds). Germination rates used in this study are presented in Table S1.

2.6 | Annual-plant model

Analyses in this paper are based on a well-established model of inter-annual population dynamics for annual plants:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1-g_i)s_i + g_i F_{i,t} \tag{1}$$

where $N_{i,t}$ is the number of seeds of species i in the seedbank in year t, g_i is the germination rate of seeds of species i, s_i is the survival rate in the seedbank of seeds of species i and $F_{i,t}$ is the number of seeds produced by individuals of species i in year t (Godoy & Levine, 2014; Levine & HilleRisLambers, 2009). Fundamentally, this model examines how vital rates (germination and seed survival) and individual seed production (fecundity) impact population dynamics of seeds in the seedbank.

Unlike past studies that have used this or similar annual-plant models, we have modified the fecundity component to allow for different types of species interactions to impact on individual seed production. Namely, most annual-plant models assume that the only important species interactions for modelling co-occurrence or coexistence are competitive. Mayfield and Stouffer (2017) instead used a modified annual-plant model to illustrate that facilitative direct interactions and higher-order interactions are both important for accurately modelling individual fecundity in natural plant communities. To do this, they made two changes to a standard model. First, they used an exponential formulation that allowed direct interactions to be negative or positive without the risk of biologically unrealistic predictions (e.g. negative fecundities). Second, they added an additional model term incorporating information on intra- and interspecific nonadditive interactions among species pairs in neighbourhoods around focal individuals (HOIs; Mayfield & Stouffer, 2017).

In this study, we use the model presented in Mayfield and Stouffer (2017) to predict fecundities in the annual-plant model as quadratic functions of neighbour densities:

$$F_{i,t} = \lambda_i e^{-\left[\sum_j \alpha_{ij} n_{j,t} + \sum_j \beta_{ijj} (n_{j,t})^2 + \sum_{k>j} \beta_{ijk} n_{j,t} n_{k,t}\right]} \tag{2}$$

where λ_i is the intrinsic fecundity of species i (i.e. its per capita seed production in the absence of neighbours), α_{ij} is the direct per capita effect of neighbours of species j on individuals of species i, β_{ijj} captures the effect of intraspecific crowding of neighbours of species j surrounding individuals of species i (intraspecific HOIs), β_{ijk} captures the effect of interspecific crowding of neighbours of species j and k surrounding individuals of i (interspecific HOIs) and all $n_{j,t}$ are the number of germinants/individuals of species j in the community in year t and hence $n_{j,t} = g_j N_{j,t}$. Note that, in all instances, the sums over j include species i. As can be seen in Equation 2, the per capita interaction strengths within F_i vary as a function of the densities of conspecific and heterospecific neighbours. In order to better reflect this density dependence and its potentially "intransitive" behaviour, Equation 2 can be equivalently rewritten as:

$$F_{i,t} = \lambda_i e^{-\sum_j (\alpha_{ij} + \beta_{ijj} n_{j,t} + \frac{1}{2} \sum_{k \neq j} \beta_{ijk} n_{k,t}) n_{j,t}} \tag{3}$$

2.7 | Estimating model parameters

Following Mayfield and Stouffer (2017), we estimated species' intrinsic fecundities (λ_i) and the strength of direct and high order interaction coefficients based on field data using a negative-binomial regression framework, which is mathematically equivalent to Equation 2. Using our field-collected individual seed production, this involved fitting a statistical model with fecundities F_i as the response variables and the sets of neighbour species' abundances—or functions thereof in the case of the β-terms—as the predictors. Since plot sizes varied between the natural communities, thinned plots and 2014 supplementary data, we normalised all neighbour abundances to be on a per-plot-width basis prior to fitting the regression models. Note that per-plot-width is more consistent with the spatial nature of competition than would be per-plot-area since the average distance from any point in a square to the square's centre scales linearly with the width of the square (Bolker & Pacala, 1999; Pacala & Tilman, 1994). Since our later use of the annual-plant model only required interaction coefficients related to our four focal species, we lumped together neighbour abundances of all other species and allowed them to have a single coefficient that captured direct competition only. We note that "other" abundances ranged from 0 to 5.13 per cm (M = 0.79) in the natural plots in our main 2015 dataset. There were no "other" neighbours in the 2015 thinned plots and the abundance range of "other" neighbours in our supplemental data for *A. calendula* (2014) were 0 to 3 per cm (M = 0.32). The abundances of focal species as competitors across these plots ranged from 0 to 3.9 per cm (M = 0.20), 0 to 0.3 per cm (M = 0.08) and 0 to 1.6 per cm (M = 0.05) for the natural, thinned and supplemental data, respectively.

We performed these regressions in R (R Core Team, 2017) using the function *manyglm* from the package *mvabund* (Wang, Neuman, Wright, & Warton, 2012) and fit separate regressions under the open and shaded conditions for each of the four focal species. Prior to using the estimated interaction coefficients within the annual-plant model, we then divided all α's by 25 and all β's by 25^2 so that the abundances predicted by the model would correspond to what we would expect to observe in 25 cm × 25 cm plots.

2.8 | Periodic behaviour of the annual-plant model

In the simplest case, single-species fixed-point dynamics within the annual-plant model correspond to solutions of the equation $N_{i,t+1} = N_{i,t}$. This is equivalent to setting the left-hand side of Equation 1 to 1 and finding the abundance n_i such that $F_{i,t} = (1 - (1 - g_i)\, s_i)/g_i$. If we substitute this relation into Equation 3 and rearrange, this implies finding solutions to:

$$\beta_{iii} n_i^2 + \alpha_{ii} n_i - \ln \eta_i = 0 \tag{4}$$

where $\eta_i = (\lambda_i\, g_i)/(1 - (1 - g_i)\, s_i)$ and captures the annual seed production per seed lost from the seed bank. In order to identify solutions exhibiting periodicity τ, it is necessary to solve the more general equation:

$$\prod_{t=1}^{\tau} \left[(1-g_i)s_i + g_i F_{i,t}\right] = 1 \tag{5}$$

Although no straightforward analytical solution exists for Equation 5 when τ > 1, it is possible to solve this equation numerically, and we do so using the function *uniroot.all* in the R package *rootSolve* (Soetaert, 2009; Soetaert & Herman, 2009). Note that the inclusion of higher-order interactions in $F_{i,t}$ is neither a sufficient nor necessary condition for any solution to exist when τ > 1, and cyclic solutions exist for just under half of the species condition combinations we explored when all β values are set to zero in the parameter estimation (results not shown). HOIs do, however, increase the number of candidate solutions since the order of Equation 5 is 2τ when quadratic HOIs such as ours are included in the expression for density dependence of fecundities.

2.9 | Invasion growth rates

As a first exploration of whether or not pairwise coexistence between species j and species i may be possible given the population dynamics of a resident species i while in monoculture, we calculated the growth rate of j when rare as a function of the abundance of species i. This quantity is given by:

$$r_{ji} = \ln \frac{N_{j,t+1}}{N_{j,t}} = \ln \left[(1-g_j)s_j + g_j \lambda_j e^{-(\alpha_{ji} + \beta_{jii} n_{i,t}) n_{i,t}}\right] \tag{6}$$

Positive values of r_{ji} imply that j can invade i and potentially coexist whereas negative values of r_{ji} imply that i competitively excludes j.

2.10 | Pairwise coexistence

Solutions to Equation 5 can correspond to large variation in the abundances of the resident species i year to year. Therefore, the ability of species j to potentially invade does not in fact guarantee persistence of j in the community. This is because j establishing at a non-trivial abundance is a complex function of both its own abundance dynamics and the varying abundances of the resident. To identify situations in which positive invasion growth rate did, and did not, lead to species persistence, we ran numerical simulations of the short- and long-term dynamics of the annual-plant model given by Equation 1 and for simulated "invasions" of a single seed of j for any resident species and resident abundance with which j had a positive invasion growth rate. We then used the final state of the two-species community to determine whether (1) i and j coexist, (2) i excludes j or (3) j excludes i.

All code and data used in this study are available as Supporting Information files and through Dryad (see Data Accessibility).

3 | RESULTS

3.1 | Parameter estimation

The negative binomial regressions provided strong support for the inclusion of HOIs in the estimation of observed fecundities in both open and shaded environmental conditions (Table 1). Within these regressions, we were able to infer the maximum-likelihood estimates of all parameters necessary to study the single-species dynamics for all four species and pairwise population dynamics for all six pairs of the same; this included intrinsic fecundities, direct interaction coefficients and higher-order interaction coefficients (Table S2).

3.2 | Cyclic behaviour of monocultures

Given the maximum-likelihood parameter estimates for the open plots, the annual-plant model predicts that monocultures of

TABLE 1 Goodness-of-fit estimates by environmental condition (open, shade) for the null, alpha only and full HOI inclusive models. "Treatment" indicates the environmental treatment from which data were used. "Model Form" indicates whether the model was the null model (intrinsic fecundity only and no species interactions), the model including intrinsic fecundity and alphas (direct interactions) or the full HOI inclusive model (full model) specified by Equation 2 in the main text, which included information on intrinsic fecundity, alphas (direct interactions) and betas (higher-order interactions). The best fit model for both open and shade treatments has been bolded

Treatment	Model form	AIC	Deviance explained
Open	Null	7,714.06	0.357
Open	Direct interactions	7,720.35	0.375
Open	**Full model**	**7,709.94**	**0.408**
Shade	Null	7,559.06	0.439
Shade	Direct interactions	7,537.44	0.464
Shade	**Full model**	**7,530.96**	**0.489**

A. calendula are capable of exhibiting fixed-point or two-period behaviours, and the period-2 solution is locally stable (Table 2). Monocultures of *H. glutinosum* and *P. airoides* are predicted to show stable fixed-point dynamics (Table 2), while populations of *V. rosea* are predicted to show unstable, unchecked growth in the absence of interspecific competition (Table 2).

Given the maximum likelihood parameter estimates for the shaded plots, the annual-plant model predicts that monocultures of *A. calendula* are capable of exhibiting fixed-point and two-period behaviours, with a separate four-periodic solution being locally stable (Table 2). Monocultures of *H. glutinosum* are capable of two fixed-point solutions, only one of which is locally stable, while populations of *P. airoides* show unstable, unchecked growth in the absence of interspecific competition (Table 2). Finally, monocultures of *V. rosea* can exhibit fixed-point, two-period and 2 three-period solutions, with one of the period-3 solutions being locally stable (Table 2 and Figure 1).

3.3 | Invasibility

Models predicted that monocultures for all four focal species could potentially be invaded by all other focal species when the resident species is at certain realistic abundances within a 25 cm × 25 cm area (Table 3; Figure 2 for an example). These invasible resident abundances varied depending on shading conditions. Under both open and shade conditions, *V. rosea* was able to invade more readily (under broader ranges of abundances) than the other focal species, while *H. glutinosum* is only likely to invade monocultures of the other focal species when their abundances (within 25 cm × 25 cm areas) are very low (Table 3).

3.4 | Long-term coexistence

Although invasion of one species' population into another was potentially achievable for most species pairs (Table 3), invasion leading to stable coexistence was less common under the invasion

TABLE 2 The number of distinct solutions of periodicity 1, 2, 3, 4 or 5 for each of the four focal species in monoculture. Solutions with greater periodicity may also exist for monocultures of these species, but these were not systematically explored here. The abundance peaks of each stable solution (meaning the number of seeds in the seed bank at a cycle peak) are provided for stable solutions under open and shade field conditions. A period 1 stable solution indicates a fixed state solution; thus for period 1 stable solutions, the abundance of that fixed state is provided in the "Stable Solution" column. For period 2 and 3 stable solutions, the peaks and trough abundances of the inter-annual cycle are provided in the "Stable Solution" column. *Arctotheca calendula* under shade conditions only had a stable solution of periodicity 4. No stable or unstable solution was found for *Velleia rosea* in open conditions or *Pentameris airoides* in shade conditions. The period 1, 2 and 3 solutions for *V. rosea* in shade conditions are plotted in Figure 1 for clarity

Species	Stable solution	Periodicity 1	Periodicity 2	Periodicity 3	Periodicity 4	Periodicity 5
Open conditions						
A. calendula	217.8, 1,054.0	1	1[a]	0	0	0
Hyalosperma glutinosum	10.3	1[a]	0	0	0	0
P. airoides	70.4	1[a]	0	0	0	0
V. rosea	NA	0	0	0	0	0
Shade conditions						
A. calendula	137.1, 1,556.0, 321.4, 444.1	1	1	0	1[a]	0
H. glutinosum	20.5	2[a]	0	0	0	0
P. airoides	NA	0	0	0	0	0
V. rosea	37.6, 14.1, 110.9	1	1	2[a]	1	2

[a] The periodicity of the stable solution (for which details are provided in the "Stable solution" column) for each species under the indicated treatment.

circumstances explored in this study. In fact, among our four focal species, only *P. airoides* and *A. calendula* were able to stably coexist and then only under open conditions (Table 4 and Figure 3). Specifically, *P. airoides* can invade monocultures of *A. calendula* and eventually coexist if introduced at any time point, even though the annual-plant model predicts a year of negative population growth of *P. airoides* if its introduction coincides with the peak of *A. calendula*'s oscillations (Figure 3). *Arctotheca calendula* can invade equilibrium populations of *P. airoides* and eventually establish the same stable coexistence that occurs in the opposite scenario (Figure 3). The resulting two-species community oscillates stably with periodicity 6 (Figure 3).

All other species pairs met some but not all criteria for dynamic mutual invasibility. Which criteria were met by each species pair varied depending on whether they were growing under open or shade conditions (Table 4). Under open conditions, there is no time point at which *H. glutinosum* can invade *A. calendula* and establish despite the latter's stable period-2 oscillations in monoculture. Both *A. calendula* and *P. airoides* can invade *H. glutinosum* in monoculture, but this leads to competitive exclusion of *H. glutinosum* in equilibrium populations. *Velleia rosea* can always invade and competitively exclude monocultures of all other species, though we note that competitive exclusion here is driven in large part by the model predicting net positive intraspecific effects for *V. rosea* even at large abundances.

TABLE 3 Invasibility results under open and shade conditions for stable monocultures (except when noted otherwise[a]). "Resident seedbank abundances" indicate the number of seeds in the seed bank per unit area that are needed for positive invasion growth rates of the indicated invader. "Mean (range) resident germinants" are the mean number of observed germinants (and range of observed germinants) for the indicated resident species. "Mean (range) effective seedbank size" is the mean number of observed germinants divided by the resident species' germination rate, so this number represents the effective mean (and range) number of seeds that produce the number of germinants listed in the previous column ("Mean resident germinants"). Observed numbers of germinants were estimated using data from "natural" 2015 plots and have been corrected to reflect abundances for 25 cm × 25 cm areas. Effective seedbank sizes have been calculated with the laboratory-measured germination rates (Table S1)

Resident species	Invading species	Resident seedbank abundances	Mean (range) resident germinants	Mean (range) effective seedbank size
Open conditions				
Arctotheca calendula	*Hyalosperma glutinosum*	<134	1.26 (0–5.83)	26.23 (0–121.53)
	Pentameris airoides	<519		
	Velleia rosea	Any abundance		
H. glutinosum	*A. calendula*	<962	21.78 (0–85.83)	152.29 (0–600.23)
	P. airoides	<647		
	V. rosea	<476		
P. airoides	*A. calendula*	<131	10.17 (0–26.67)	50.83 (0–133.33)
	H. glutinosum	<28		
	V. rosea	Any abundance		
V. rosea[a]	*A. calendula*	Any abundance	3.45 (0–25)	9.21 (0–67.20)
	H. glutinosum	<16		
	P. airoides	Any abundance		
Shade				
A. calendula	*H. glutinosum*	<65	1.02 (0–4.17)	21.34 (0–86.81)
	P. airoides	<234		
	V. rosea	<138		
H. glutinosum	*A. calendula*	Any abundance	24.29 (0–97.50)	169.80 (0–681.80)
	P. airoides	<1,165		
	V. rosea	Any abundance		
P. airoides[a]	*A. calendula*	Any abundance	18.41 (0–90.83)	92.01 (0–454.17)
	H. glutinosum	Any abundance		
	V. rosea	<153		
V. rosea	*A. calendula*	Any abundance	1.44 (0–8.33)	3.87 (0–22.04)
	H. glutinosum	<31		
	P. airoides	Any abundance		

[a] Monocultures of resident species were not found to be stable and thus abundances compatible with invasion should also be considered unstable for these focal resident species/treatment combinations.

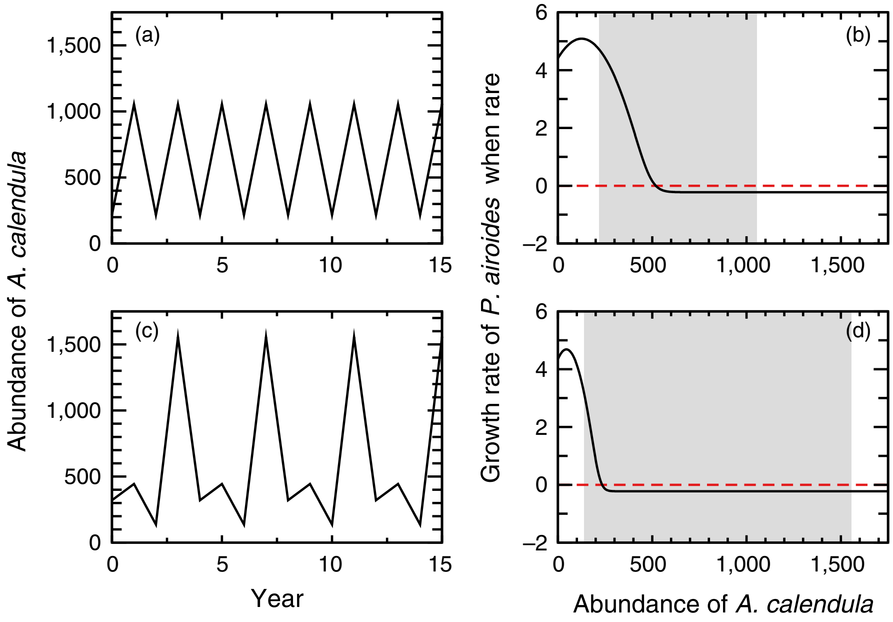

FIGURE 2 (a) Under open conditions, populations of *Arctotheca calendula* are predicted to exhibit stable, oscillatory dynamics of periodicity 2 (i.e. $N_{t+2} = N_t$). (b) The region shaded in grey depicts the range of abundances of *A. calendula* spanned during the cyclical dynamics shown in (a). This single-species community can potentially be invaded by *Pentameris airoides* at low abundances, as indicated by the fact that its growth rate when rare (solid black line) is greater than 0 (red dashed line) at lower abundances. (c) Under artificially shaded conditions, populations of *A. calendula* are predicted to exhibit stable, oscillatory dynamics of periodicity 4. (d) The single-species community shown in (c) can potentially be invaded by *P. airoides* at only the lowest abundance of this cycle [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Outcomes of a simulated invasion by each focal species (columns) into a stable monoculture of each other focal species ("resident"; rows), by environmental condition. Diagonal cells (grey) indicate the stable periodicity of each species in monoculture (row and column). Period 1 is the same as fixed-point equilibrium (no cyclic dynamics) and "none" indicates that no stable solution was found for the indicated species under those environmental conditions. In off-diagonal cells, we indicate the "winner" of the invasion. Except where indicated ([a,b]), invasion results in straightforward competitive exclusion of one species by the other species (surviving species listed) or pairwise coexistence ("both" species survive). For instance, *Arctotheca calendula* competitively excludes *Hyalosperma glutinosum* in open conditions while *Velleia rosea* competitively excludes *A. calendula* in the same open conditions. In open conditions for *V. rosea* and shade conditions for *Pentameris airoides*, there was no stable solution in monoculture, making it biologically unrealistic to calculate the outcomes of invasion by another population; these cases are indicated with "None" in respective cells

	Invader			
	A. calendula	***H. glutinosum***	***P. airoides***	***V. rosea***
Open conditions				
Resident				
A. calendula	Period 2	*A. cal*	Both	*V. ros*[a]
H. glutinosum	*A. cal*	Period 1	*P. air*	*V. ros*[a]
P. airoides	Both	*P. air*	Period 1	*V. ros*[a]
V. rosea	None	None	None	None
Shade conditions				
Resident				
A. calendula	Period 4	*A. cal*[b]	*P. air*[a]	*A. cal*[b]
H. glutinosum	*A. cal*	Period 1	*P. air*[a]	*V. ros*
P. airoides	None	None	None	None
V. rosea	*A. cal*	*V. ros*[b]	*P. air*[a]	Period 3

[a] Exclusion of the resident species is driven by unchecked population growth of the invader.

[b] Invader cannot successfully establish despite the existence of at least one time point (abundance peak or trough) at which it can invade with a positive growth rate.

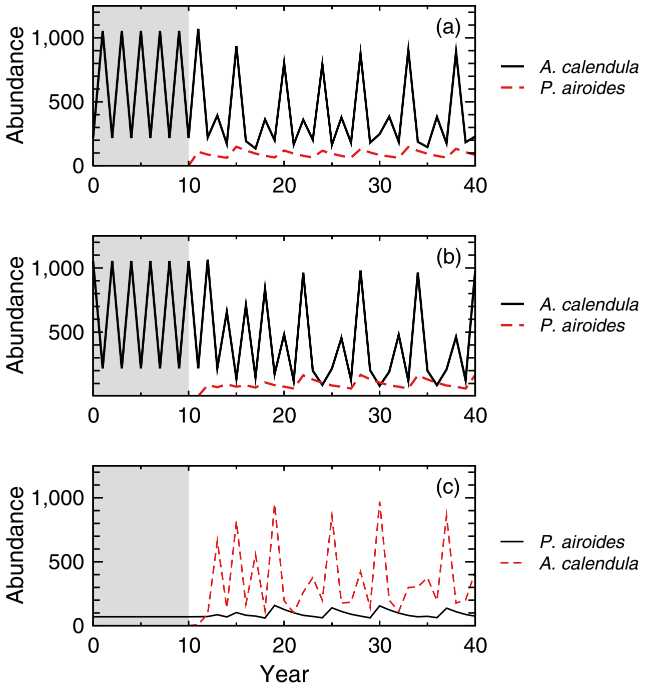

FIGURE 3 Predicted long-term coexistence of *Pentameris airoides* and *Arctotheca calendula* as a result of the invasion of one species by the other under open conditions in West Perenjori Reserve. In each panel, we show the stable abundance values of the "resident" species in monoculture (solid black line) over an initial 10-year period (shaded in grey; stable solutions from Table 2). In (a and b), we see that *A. calendula* is predicted to show a stable period-2 abundance cycle when in monoculture in open environments. (c) *Pentameris airoides* monocultures are predicted to have a stable fixed-point equilibria (period 1). At year 10 in each panel, we simulate the introduction of a single seed of the invader into the resident population and show the invader's population dynamics (red dashed line) and those of the resident for a further 30 years. (a) The outcome of *P. airoides* invading a stable *A. calendula* monoculture when year 10 corresponds to the low point of the resident species' intrinsic oscillation cycle. (b) The predicted outcome when *P. airoides* invades a monoculture of *A. calendula* in a high-abundance year. (c) The outcome of *A. calendula* invading a stable monoculture of *P. airoides*. In all three scenarios, the model predicts that the two species enter into identical period-6 joint abundance cycles that persist indefinitely [Colour figure can be viewed at wileyonlinelibrary.com]

Under shaded conditions, no species pairs were found to coexist stably due to mutual invasibility. Neither *H. glutinosum* nor *V. rosea* can invade *A. calendula* at any time point and establish. This is true although the low point in the latter species' stable period-4 oscillations corresponds to a positive invasibility (growth rate when rare) for *V. rosea* (Tables 2 and 3). Both *A. calendula* and *V. rosea* can invade *H. glutinosum* in monoculture but this leads to competitive exclusion of *H. glutinosum* in equilibrium populations. *Arctotheca calendula* can invade and competitively exclude equilibrium populations of *V. rosea* whereas *H. glutinosum* cannot establish in the long term although the low point in *V. rosea*'s stable period-3 oscillations corresponds to positive invasibility for *H. glutinosum*. *Pentameris airoides* can always invade monocultures of all of the other species but this also always leads to competitive exclusion. The competitive exclusion here is driven in large part by the model predicting net positive intraspecific effects for *P. airoides* even at large abundances, as was the case for *V. rosea* in open conditions.

4 | DISCUSSION

This study highlights the potential for density-dependent cyclic intransitivity to mediate coexistence in real plant communities. Importantly, our study also illustrates that interactions other than direct competition do mediate population cycles. Using data from annual plant communities in southwest Western Australia, we show that intraspecific cyclic population dynamics can impact pairwise invasion outcomes as well as stable coexistence. This scenario is a clear case of density-dependent intransitivity, and it was only possible because we dropped the assumption of stable, fixed-point population equilibria when analysing our model. That said, three species in our study were predicted to have stable fixed-point population equilibria, including one of the species involved in our observed case of stable mutual invasibility. Another three were predicted to cycle with periodicities 2, 3 and 4. Although our sole case of mutual invasibility and coexistence involved a species with cyclic dynamics in monoculture—and resulted in cyclic pairwise dynamics as well—there is no a priori reason for why mutual invasibility would not be possible between two different species exhibiting non-cyclic populations, as would be expected under the standard definition of intransitivity and the standard coexistence framework. As such, our findings highlight the importance of considering cyclic population dynamics as well as, not instead of, the commonly assumed fixed-point equilibria, if we wish to maximise our ability to detect evidence of stable coexistence in natural, diverse communities. Our results also highlight the value of considering a broader definition of intransitive dynamics in efforts to integrate theory on complex species interactions and coexistence. Specifically, we provide a proof-of-principle that coexistence can be driven by endogenous, cyclic population dynamics that lead to density-dependent intransitivity. We do not go so far here as to show specific cases where higher-order interactions were necessary for coexistence nor density-dependent intransitivity; indeed, we saw that endogenous and stable population cycles were possible in models without them. Nevertheless, statistical support for their inclusion in our models points to the potential for these interactions to act as an additional driver of the type of density-dependent intransitivity that allows for coexistence.

In our study system, all four focal species were found to exhibit endogenous inter-annual abundance cycles under either open or shade conditions, with approximately half of these cyclic solutions expected to be stable over time. In cases where abundance cycles with periodicities <1 were stable, invasion by other species was expected to only be possible in years when the resident abundances were below estimated invasibility thresholds (Table 3). Most current studies that use annual-plant models to test for invasibility assume fixed-point equilibria (periodicities of 1). If this test is applied to assess the mutual invasibility of species which have stable abundance cycles (periodicities >1) rather than fixed-point equilibria, there is a strong chance of failing to identify potential opportunities for invasion and ultimately coexistence.

Over the last 5 years, the empirical literature on modern coexistence theory has begun to uncover a range of issues that arise when attempting to operationalise its use to explain real patterns of annual-plant diversity (Godoy, Kraft, & Levine, 2014; Kraft et al., 2015; Mayfield & Stouffer, 2017). Notably, there are a variety of examples where tests of coexistence in annual-plant communities have provided limited evidence of stable coexistence among species pairs despite expectations to the contrary (Godoy et al., 2014, 2017; Kraft et al., 2015). The authors of these studies suggest that few species pairs are found to coexist stably because of issues of scale and lack of consideration of spatial and temporal environmental complexity. Other studies have examined specific reasons why we may find it hard to detect coexistence in natural systems using modern coexistence theory and associated annual-plant models. For instance, Mayfield & Stouffer (2017) showed that modifying the fitness component of annual-plant models to allow for direct positive and higher-order interactions along with negative species interactions can substantially improve the accuracy of the fitness components in these and associated coexistence models. Hart et al. (2017) showed that selecting the correct spatial scale and accounting for environmental heterogeneity are critically important for being able to accurately detect coexistence using this approach. In this study, we have incorporated information on environmental heterogeneity (shade) and positive and higher-order interactions. We found that invasibility and coexistence outcomes were significantly impacted by environmental condition and that model fit was improved by including higher-order interactions (Table 1). Although beyond the scope of our study, an interesting next step would be to examine the importance of different types of species interactions and a broader range of environmental gradients to mutual invasibility and coexistence outcomes.

Another possible explanation for why coexistence has proven difficult to detect in real plant communities is that the stable solutions for many species and species pairs may correspond to cyclical as opposed to fixed-point population dynamics. It remains to be seen whether or not cyclic populations are as common in other annual-plant communities as they appear to be in the subset of Western Australian plants used for this study; if they are, we can improve our ability to detect and predict coexistence by first determining whether species/environment combinations of interest have stable fixed-point or stable cyclic populations. Results of this study, therefore, add to the growing literature on operationalising annual-plant coexistence models and contribute a new tool and perspective to help move us closer to predicting and explaining real-world patterns of natural plant diversity.

4.1 | Population persistence

The first step in determining how cyclic population dynamics could impact stable coexistence was to determine if there was evidence that Western Australian annual-plant species could persist stably in monoculture while exhibiting annual population cycles. We then aimed to determine if changes in a single environmental factor, in this case shade, could substantially change which type of abundance dynamics would be stable. The answer to both questions was clearly yes. Notably, we observed that under open ("not shady") conditions, one of our focal species, *A. calendula*, was predicted to persist stably with its abundance cycling with periodicity 2. When shade was introduced, however, this stable solution became one with periodicity 4; this suggests that we would expect this species to show greater variation in local abundances when in shaded areas, which is consistent with previous observations of this species (Lai et al., 2015).

The native *V. rosea* was the other species, for which we found stable cyclic monoculture abundance dynamics to be possible. For this species, however, there were no stable monoculture solutions of any periodicity, including one—fixed point—in open, unshaded conditions. In the shade, however, seven different solutions were found including those with periodicities ranging from 1 to 5, with a period-3 solution found to be stable. These findings suggest that *V. rosea* cannot persist in monoculture in open sunny positions without interspecific competition to control its population while it can persist in the short and long term in a number of different ways in the shade. These results confirm the importance of shade in mediating this species' population growth, and probably other native species, in this system (Dwyer et al., 2015). Combined, all results for monocultures suggest that a full understanding of how important cyclic abundance dynamics are for coexistence will likely depend heavily on the environmental conditions.

4.2 | Invasibility and coexistence

Detecting coexistence in natural systems is complicated by the fact that there are many pathways to coexistence (Chesson, 2000), and testing for all of them in real communities can be prohibitively difficult (HilleRisLambers et al., 2012). In this project, we have focused on one such pathway, invasibility, and even in this regard have only provided a proof-of-principle that mutual invasibility can occur when resident species have cyclic abundance dynamics. In particular, we identified stable monocultures for all focal species in at least one of the two environmental circumstances (open or shade) which could theoretically be invaded by all other focal species at some abundance threshold. For *A. calendula* in open conditions and *V. rosea* in shade, invasion thresholds corresponded to peak or trough years in persistent cyclic abundance dynamics. Density-dependent cyclic intransitivity, however, only led to stable coexistence for *A. calendula* and *P. airoides*. In this case, our models suggest that *A. calendula* can stably persist in monoculture with a period-2 abundance cycle in open conditions and *P. airoides* can successfully invade when just a single seed is introduced. Once *P. airoides* or *A. calendula* successfully invades and establishes, they enter into a stable period-6 cycle of abundances (Figure 3).

While we explored the possibility of mutual invasibility of all pairs of our four focal species, we note that this examination was not exhaustive and other stable cyclic solutions for the resident monocultures are also possible; these include greater periodicities (>5) and chaotic dynamics, none of which we considered here. We also only tested for stable coexistence resulting from mutual invasion of species pairs noting that density-dependent cyclic intransitivity can lead to scenarios where the presence of multiple resident species can alter invasibility and thus persistence. Although we considered two sets of environmental conditions, open and sun, which had substantial impacts on stable monoculture and two-species solutions, we are also aware that other environmental conditions also likely impact model outcomes (Dwyer et al., 2015; Wainwright et al., 2017). We note that future studies of density-dependent cyclic intransitivity should include more thorough explorations of these dynamics. In our study, we explored a single invasion scenario, one in which a single seed of the "invader" species is introduced in a peak or trough year (or at the fixed-point abundance) of a resident species exhibiting a stable abundance cycle. This was done to explore the situation where invasion occurs when the invading species is very rare, but it is likely that other biologically realistic invasion scenarios, such as the introduction of two, three or four seeds, could also lead to stable coexistence while meeting the rarity criteria of the mutual invasibility principle (Adler et al., 2007; Chesson, 2000). Stochasticity in vital rates is also likely to have impacts on invasibility and coexistence outcomes and worth exploring in detail in future studies.

5 | CONCLUSIONS

This study builds on Gilpin's (1975) theoretical expectations that stable coexistence can occur via density-dependent intransitivity in competitive communities displaying stable cyclic population dynamics. Although not an exhaustive assessment of the commonality of cyclic population dynamics, or their invasibility, our results demonstrate that this phenomenon is indeed possible in real annual-plant systems. Moreover, our simple exploration of this type of density-dependent intransitivity in four Western Australian plants shows that predicting coexistence with annual-plant models that assume fixed-point abundances may be failing to detect coexistence in systems dominated by cyclic competition dynamics and that such dynamics may be both mediated by nonadditive, higher-order interactions and more common than previously thought. Moving forward, it is clear that we need broader tests of more species, combinations of more than two species and more complex cycles to fully assess the commonality of such intransitive dynamics in a variety of systems. As we only had data on four species in this study, there was limited scope to explore the range of possible outcomes or the general likelihood of each outcome. As such, a useful next step in studying density-dependent cyclic intransitivity would be to use a pure modelling approach to quantify which outcomes are more or less prevalent as well as which parameters need to change and in what ways to drive mutual invasibility. In short, our study adds to the growing literature suggesting that complex species interactions and intransitive competition in particular are likely to represent important mechanisms of coexistence in plant systems.

ACKNOWLEDGEMENTS

We would like to thank Hao Ran Lai, Xingwen Loy, Maia Raymundo, Stephanie Creer and Timothy Staples for help with data collection and J. Dwyer, A. Pastore and A. Letten for thoughtful discussions of this paper. This project was made possible by the Australian Research Council (DP140100574 and FT140100498 awarded to MMM) and a Rutherford Discovery Fellowship and the Marsden Fund Council from New Zealand Government funding, both of which are managed by the Royal Society Te Apārangi (RDF-13-UOC-003 and 16-UOC-008 awarded to DBS).

AUTHORS' CONTRIBUTIONS

D.B.S. and M.M.M. developed the idea for this project; C.E.W. and T.F. collected the field data; D.B.S. conducted all analyses and M.M.M. wrote the paper with contributions from all other authors.

DATA ACCESSIBILITY

The full dataset used in this study is included as part of the Supporting Information r code and is also archived on Dryad Digital Repository: https://doi.org/10.5061/dryad.8v13t2q (Stouffer, Wainwright, Flanagan, & Mayfield, 2018).

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How to cite this article: Stouffer DB, Wainwright CE, Flanagan T, Mayfield MM. Cyclic population dynamics and density-dependent intransitivity as pathways to coexistence between co-occurring annual plants. *J Ecol*. 2018;106:838–851. https://doi.org/10.1111/1365-2745.12960