

Forum

Inclusive fitness, asymmetric competition and kin selection in plants



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The findings that some plants alter their competitive phenotype in response to genetic relatedness of its conspecific neighbour (and presumed competitor) has spurred an increasing interest in plant kin-interactions. This phenotypic response suggests the ability to assess the genetic relatedness of conspecific competitors, proposing kin selection as a process that can influence plant competitive interactions. Kin selection can favour restrained competitive growth towards kin, if the fitness loss from reducing own growth is compensated by increased fitness in the related neighbour. This may lead to positive frequency dependency among related conspecifics with important ecological consequences for species assemblage and coexistence. However, kin selection in plants is still controversial. First, many studies documenting a plastic response to neighbour relatedness do not estimate fitness consequences of the individual that responds, and when estimated, fitness of individuals grown in competition with kin did not necessarily exceed that of individuals grown in non-kin groups. Although higher fitness in kin groups could be consistent with kin selection, this could also arise from mechanisms like asymmetric competition in the non-kin groups. Here we outline the main challenges for studying kin selection in plants taking genetic variation for competitive ability into account. We emphasize the need to measure inclusive fitness in order to assess whether kin selection occurs, and show under which circumstances kin selected responses can be expected. We also illustrate why direct fitness estimates of a focal plant, and group fitness estimates are not suitable for documenting kin selection. Importantly, natural selection occurs at the individual level and it is the inclusive fitness of an individual plant – not the mean fitness of the group – that can capture if a differential response to neighbour relatedness is favoured by kin selection.

Keywords: coexistence, intraspecific variation, kin competition, plant–plant interactions

Introduction

The processes that govern the outcome of competitive interactions in plants have profound implications for within and between species co-existence. A prevailing framework for understanding species co-existence, the resource partitioning theory, predicts that ecologically equivalent plant species that compete for the same resource,

experience stable coexistence when intraspecific competition is stronger than interspecific competition (Tilman 1982, Chesson 2000). Members of the same species are expected to have more similar resource requirements than members of different species, thereby strengthening intraspecific competition (MacArthur and Levins 1967), giving rise to the theory that species coexistence is mediated by relatively stronger intraspecific than interspecific competition. However, empirical studies comparing the outcome of intra and interspecific plant competition have not conclusively found that intraspecific competition is consistently stronger than interspecific competition (reviewed by Goldberg and Barton 1992, Aguiar et al. 2001, Leger and Espeland 2010). One explanation for this is the finding that fitness differences between species can depend on the interacting genotypes (Fridley et al. 2007, Lankau and Strauss 2007, Fridley and Grime 2010). Intraspecific genetic variation for quantitative traits like plant size, growth rate and growth allocation create variation in competitive ability, which may account for genotype-dependent interaction outcomes. The degree of asymmetry in competitive ability between genotypes thereby influences the competitive outcome both within and between species. Genotype-dependent interactions have been found to explain the coexistence of competing species and competing genotypes via both equalizing (i.e. reducing fitness differences between species/genotypes), and stabilizing (i.e. negative frequency dependency) mechanisms (Laird and Schamp 2006, Ehlers et al. 2016a).

For intraspecific competition, a special type of genotype-dependent interaction may occur when the strength of competition depends on the genetic relatedness of conspecific neighbours, i.e. whether intraspecific competition occurs among related or unrelated individuals. As many plant species show limited dispersal, intraspecific competition does not occur equally frequent among all available genotypes in a population, but more often in locally structured patches among genetically related individuals (i.e. kin). Genetic similarity is expected to reflect similarity in resource use, and the resource-partitioning hypothesis would therefore predict competition between close relatives to be stronger than competition between unrelated conspecifics (Young 1981, Kelly 1996). However, strong competition towards a relative can be detrimental because it reduces their fitness and thereby the inclusive fitness of the competing individual (Hamilton 1964, West et al. 2007). To reduce detrimental effects of kin competition, individuals can evolve the ability to reduce competitive interactions (which can be interpreted as a cooperative trait) towards relatives, or to disperse to reduce direct competition with kin (West et al. 2002, Ronce 2007). Kin selection theory predicts a focal individual to differentiate their competitive response depending on the relatedness of the competitor in a way that reduces competition between close relatives (West et al. 2002, Dudley et al. 2013).

The processes that shape interactions among members of the same species can also influence on interspecific interactions. Positive frequency dependent interactions occurs when

a species creates positive feedback on itself, thereby making local patches of a species more resistant to invasion by other species. Positive frequency dependent interactions can occur by allelopathy (i.e. release of phytochemicals that inhibit growth of heterospecifics) or by positive plant soil feedback mechanisms, where a species enhances presence of its beneficial soil microorganisms creating a self-reinforcing process that maintain its local dominance (Van der Putten et al. 2013). This mechanism may explain range expansion and invasion success of some exotic species (Crandall and Knight 2015). If kin selection results in reduced competition among relatives, this could create local positive frequency dependency among genetically related individuals, which perform better under kin interactions compared to interactions with unrelated conspecifics. Moreover, if kin selection facilitates better performance among related individuals also compared to heterospecific interactions, this has the potential to alter predictions for species co-existence (Fig. 1) (Ehlers et al. 2016b, but see also Molofsky and Bever 2002 for theoretical prediction on positive frequency dependent interactions and species diversity). Reduced competition among kin may thus be an additional mechanism by which a species can exert local positive frequency dependent interactions among genetically related individuals. This is most relevant to plant species where patches of conspecifics consists of related individuals, i.e. species that exhibit a strong spatial population genetic structure at small spatial scale. For example, annual legumes of the genus *Medicago* disperse their seeds in seed pods that often remain attached to the maternal plant after it has completed its lifecycle. Studies of the fine spatial genetic structure of *M. truncatula* showed that when several genotypes co-exist in a population they grow in distinct patches consisting of more or less identical genotypes most likely descendent from the same mother plant (Bonnin et al. 2001, Siol et al. 2007).

Species with reduced seed dispersal or with directed dispersal of entire fruits consisting of seeds that are all genetically related, will also experience conspecific competition among kin, which may incur sufficiently large costs to counter any benefit arising from kin interactions (West et al. 2002). For this reason, the relationship between costs and benefits of kin interactions in species characterized by variation in local kin structure are particularly suitable for gaining insights into kin interaction effects in plants. Furthermore, depending on whether net fitness effect of kin interactions select for increased or decreased kin competition, this will affect predictions for co-existence by altering differences between kin and non-kin intraspecific interactions, and potentially also between intra- and interspecific interactions. With kin facilitation, we expect positive frequency dependent interactions creating patches of kin that are more resistant to invasion of other conspecific genotypes and potentially also of other heterospecifics. In contrast, if related individuals compete stronger with each other than with non-kin, frequent kin interactions may promote species coexistence by enhancing the negative impact of intraspecific competition relative to interspecific competition (Fig. 1).

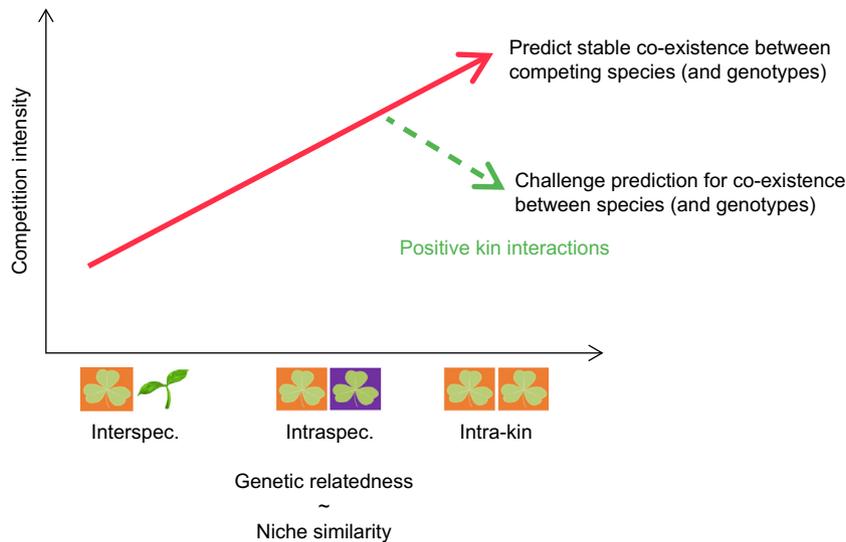


Figure 1. The relationship between genetic similarity and competition intensity. Genetic similarity is expected to predict niche similarity, and under a niche-partitioning hypothesis (red arrow) competition intensity will increase from interaction between species (inter), to interaction within species among unrelated conspecifics (intra) and be highest for intraspecific interactions among kin (intra-kin). With kin selection (green arrow), it is also possible that competition intensity will decrease among kin relative to non-kin. Predictions for species co-existence will depend on whether competition intensity for kin interactions is higher or lower than for interspecific interactions (i.e. how far down the green arrow goes).

Our main objectives here is to: 1) outline the main challenges of studying kin selection in plants and propose a framework that allows to disentangle kin selected responses from those arising from genotype-dependent asymmetry in competitive ability, 2) illustrate why the inclusive fitness framework is necessary for assessing whether kin selection is operating.

Kin interactions in plants: where we stand

It is a relatively recent discovery that plants can alter their competitive phenotype in response to the genetic relatedness of conspecific competitors (Dudley and File 2007). This observation has been interpreted as evidence for kin recognition, and introduces kin selection as a possible process to consider for understanding the outcome of intraspecific competition in plants (Callaway and Mahall 2007). Studies that infer kin recognition rely on the observation of plants displaying a plastic growth response that reduces competition towards a related competitor (kin) relative to an unrelated competitor. Examples include reduced root growth towards kin in *Cakile edentula* (Bhatt et al. 2011), or reduced shading of a related neighbour through altered leaf growth in *Arabidopsis* (Crepy and Casal 2015), both of these responses are effective ways to reduce resource competition with kin for nutrients and light. Plants may also modify their investment in floral display in response to relatedness of its neighbours. Floral display serve to attract pollinators but can be costly to produce. Large floral displays not only benefit pollination of the plant producing it, as plants growing in the same patch may also benefit from increased pollinator visitation.

The Mediterranean Brassicaceae *Moricandia moricandioides* shows a plastic response in its investment in pollinator attraction in response to genetic relatedness of its neighbours and produce larger floral display when growing with kin compared to non-kin, suggesting an indirect fitness advantage of higher investment in floral displays (Torices et al. 2018). Kin recognition in plants is not confined to just a few rare plant species, but is documented in common and widespread species like *Plantago* (Tonsor 1989) and *Trifolium* (Lepik et al. 2012), and also in crop species like Soybean (Murphy et al. 2017) and rice (Yang et al. 2018). The challenge of kin selection studies in plants is: 1) to determine that the plastic responses of reduced competitive growth in the presence of kin translates into higher inclusive fitness for the focal individual, as the cost of reducing competitive ability must be compensated by elevated indirect fitness, and 2) to eliminate alternative explanations. We will develop the argument for why we need to apply an inclusive fitness framework to be able to unequivocally determine whether and how altered growth responses towards kin is shaped by kin selection.

There are several reasons for why kin selection in plants is controversial. Most studies that document plastic responses in response to the relatedness of competitors do not measure the fitness consequences of this behaviour (Dudley and File 2007, Fang et al. 2013). Studies that compared fitness between kin and non-kin in competitive interactions showed that plasticity in response to a neighbours' relatedness did not necessarily result in higher fitness of the individuals grown together (Cheplick and Kane 2004, Milla et al. 2009, Crepy and Casal 2015). Although a higher fitness of all individuals grown together would be compatible with patterns expected under kin selection, this explanation would not be conclusive

because such a pattern can result from other mechanisms than kin selection, for example asymmetry in competitive ability among genotypes. Importantly, for kin selection to operate, it is necessary to document not only kin discrimination (i.e. differential growth response by an individual in response to the relatedness of its competitor), but also that this response results in an increase of the fitness of the relative and thereby inclusive fitness, to compensate the cost of reduced growth by the acting (altruistic) individual (Hamilton 1964, Maynard Smith 1964, Griffin and West 2002). The decisive measure of inclusive fitness of the focal individual is very rarely measured in studies that invoke kin selection.

Kin selection and inclusive fitness

An individual's fitness is comprised of the sum of copies of their own genes plus the genes that they share with their relatives that are propagated to the following generation. Inclusive fitness is therefore determined by both direct reproduction (own offspring and grand-offspring) + indirect reproduction (offspring of relatives, e.g. nephews and nieces and their offspring) (Hamilton 1964, Maynard Smith 1964, West et al. 2007). It follows that the closer related cohabiting individuals are, the higher the contribution of indirect fitness to a focal individual's inclusive fitness is expected to be (see example in Fig. 2). Natural selection acts on heritable traits that confer a fitness advantage, by which the genes underlying these traits are propagated. Kin selection acts on traits that elevate an individual's indirect fitness at the expense of their direct fitness, i.e. increases the production of non-descendant offspring and thereby an individual's inclusive fitness (Hamilton 1964, Maynard Smith 1964, West et al. 2007). In social animals, such as cooperatively breeding birds or mammals or ant colonies with differentiated worker castes, kin-directional altruism at the expense of direct reproductive success has been well documented (reviewed by Boomsma 2013), but in plants, a kin selected trait could be the reduction of competitive growth in direct response to a relative

who thereby gains a reproductive advantage. Kin selected traits are per definition costly because the energy spent to facilitate the performance of kin (reduced uptake of nutrients in the example with the plant) reduces the fitness of the individual that acts altruistically (the focal plant). This cost must be compensated by an indirect fitness gain that increases the focal's inclusive fitness. Hamilton (1964) proved this point mathematically, illustrated in its simplest form with the equation coined Hamilton's rule: $B \times r > C$. C represents the cost (in offspring equivalents) to the focal altruist, B is the fitness benefit (in offspring equivalents) to the receiving individual, and r is the relatedness coefficient, which determines whether there is an indirect benefit to the focal ($r \times B$). If $r=0$ no indirect fitness will be obtained.

Kin selection requires differential responses by an actor towards kin and non-kin respectively. This can happen through the ability to recognize kin from non-kin, and the display of a differential response towards individuals in a way that favours relatives (nepotism). However, individuals that compete for the same resources also experience kin competition (West et al. 2002), which reduces the fitness of related individuals and imposes a loss of indirect fitness. Such negative indirect fitness effects must be included in the net calculation of inclusive fitness, and it should be realized that under some circumstances these negative effects can completely cancel out positive effects of altruism towards kin (Frank 2013). Interactions among relatives can therefore have both positive and negative fitness consequences.

We propose an inclusive fitness framework that relies on the ability to measure inclusive fitness. Although it has been debated whether this can be done accurately, and whether Hamilton's rule holds under various scenarios (van Veelen et al. 2017), there is strong consensus that approximate predictions of kin selection hold and are testable in empirical systems (Abbot et al. 2010, Gardner et al. 2011, van Veelen et al. 2017). The approach proposed here will provide an approximation of inclusive fitness measures that is applicable to empirical studies. However, we acknowledge that population level and demographic processes will affect

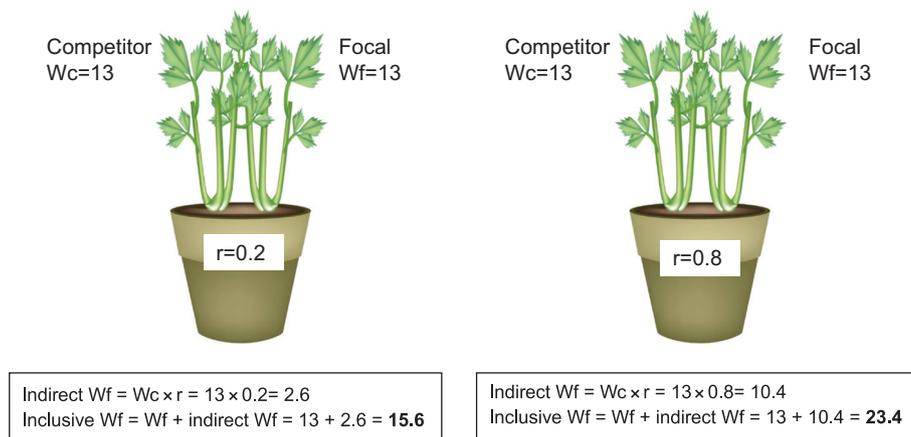


Figure 2. Calculating the inclusive fitness of a focal plant in competition with a neighbour plant that vary in relatedness (r). W_f : seed set of focal, W_c : seeds set of competitor.

any attempt to accurately measure inclusive fitness. The same problem will apply to other proposed approaches (reviewed by File et al. 2012).

Disentangling processes governing intraspecific interactions

Although members of the same species are expected to have similar resource requirements, competition among conspecifics is often asymmetric (Weiner and Thomas 1986). Asymmetric competition is the unequal division of resources among competing plants where some individuals acquire a disproportionately larger amount of resources, which results in size inequality among competing individuals (Weiner and Thomas 1986, Freckelton and Watkinson 2001). Large individuals generally produce more offspring than small individuals (Weiner et al. 2009), and size asymmetry therefore also results in fecundity asymmetry. Differences in competitive abilities between genotypes are common (Cahill et al. 2005, Masclaux et al. 2010, Simonsen et al. 2014). If some genotypes have higher competitive abilities, these will grow larger, capture more of the available resources, and thereby reduce growth and seed production of competing individuals with a less competitive genotype. Competitive asymmetry is highly relevant for designing and interpreting results of competition experiments that compare fitness outcomes of kin and non-kin interactions. Genetically related individuals competing in a similar environment may exhibit a more similar growth rate and hence experience more symmetric competition than what unrelated individuals experience. A lower variance in biomass among plants grown in kin groups relative to non-kin groups is indeed a common observation (Tonsor 1989, Donohue 2003, Simonsen et al. 2014), suggesting more symmetric competition among kin. When competition in non-kin groups results in larger size asymmetry among plants, and when there is a curvilinear saturating relationship between plant size and fitness, this results in a higher mean 'fitness' (biomass or seeds for example) of the kin groups relative to that of non-kin groups (Masclaux et al. 2010, Simonsen et al. 2014) – a pattern consistent with kin selection, but that can also be explained by competitive asymmetry in non-kin groups (Fig. 3).

Importantly, a reduced seed set/performance of a focal plant surrounded by kin relative to its performance when surrounded by non-kin does not necessarily imply that kin selection does not operate. For instance, if reduced seed set in a focal plant occurs because it is compensated for by increased seed set in its related neighbour, the inclusive fitness of the focal plant grown with kin may still be higher than the (direct) fitness of the focal growing with non-kin. Therefore, it is imperative to quantify the fitness of all interacting plants and calculate inclusive fitness to assess kin selected responses. For example, individual plants grown in groups of relatives can obtain a higher mean fitness because of more symmetric growth (Fig. 3). However, individuals grown in non-kin

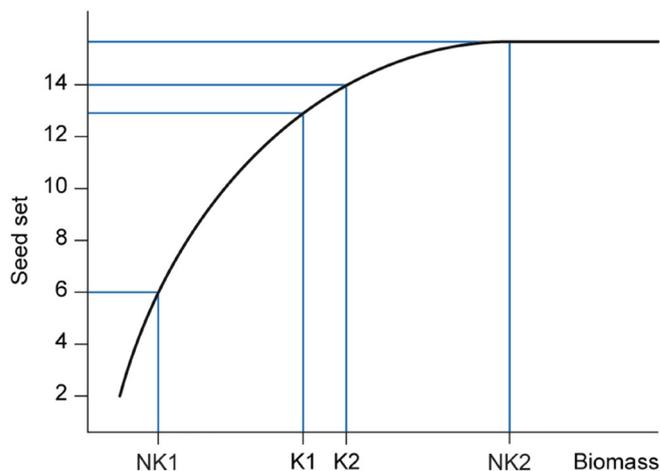


Figure 3. Diagram illustrating how genotypic differences in competitive ability and a curvilinear relation between biomass and seed set can cause pots with related plants to have a higher mean fitness (seed set). NK1 and NK2 are different genotypes and due to differences in competitive ability experience asymmetric competition. K1 and K2 are kin plants and more competitively equivalent. In both types of interactions the total biomass produced by the two plants are the same: total biomass non-kin pot: 2 g (NK1) + 12 g (NK2) = 14 g, total biomass kin pots 6.5 g (K1) + 7.5 g (K2) = 14 g. Due to the curvilinear relationship between biomass and seed set, the mean seed set of the kin pot (K1 (13 seeds) + K2 (14 seeds) = 27 seeds, i.e. an average of 13.5 seeds per plant) is higher than the mean seed set of non-kin pot (NK1 (6 seeds) + NK2 (16 seeds) = 22 seeds, i.e. an average of 11 seeds per plant).

groups with little variation in competitive abilities among genotypes could also compete very equally and obtain a similar result in terms of mean direct fitness. We use the term 'similar kind' for unrelated plants that have identical (or near identical) competitive abilities. In order to disentangle effects of variation in competitive abilities (different versus similar 'kinds') from variation that results from differential growth responses to kin (kin versus non-kin), it is necessary to obtain an approximate measure of inclusive fitness and compare fitness consequences of growing with kin versus non-kin in a design that also control for competitive phenotype (similar 'kinds', see also Fig. 4). In other words, we need to compare fitness outcomes between competitively similar plants that are either related or unrelated. It does appear possible to design experimental setups that can disentangle the effects of kin and kind, to unambiguously assess whether kin selection may have shaped competitive response to neighbour relatedness in plant species that also harbour genetic variation for competitive ability.

The core test for assessing kin selected responses, is to determine under which circumstances it is most beneficial for a plant to restrain its competitive growth (can be interpreted as 'kin cooperation' if it happens between relatives), relative to maximizing its competitive growth towards a neighbour. The inclusive fitness framework allows us to calculate estimates to explore at which degree of relatedness kin selected responses are expected (Fig. 4). We will now develop this further.

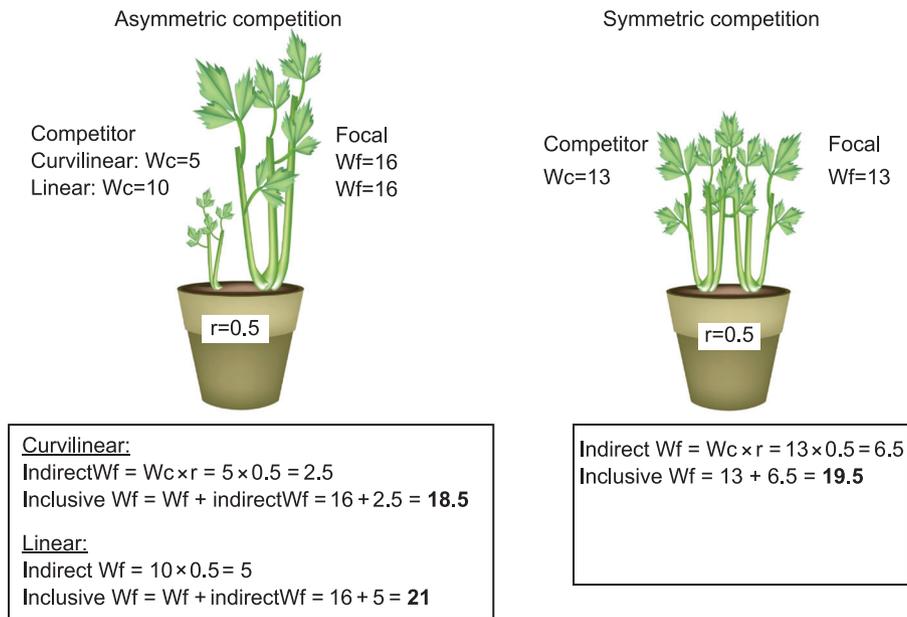


Figure 4. Examples of inclusive fitness estimates for a focal plant under symmetric (similar ‘kind’) and asymmetric (different ‘kinds’) competition. r : the relatedness between the two plants. The estimates of inclusive fitness are given for the examples where the plants have an outcrossing mating system. Note also that with symmetric competition, where plants grow equally large it can be difficult to distinguish if an equal sharing of resources is due to lack of variation in competitive ability, i.e. plants growth rate are equal, or due to below ground partitioning of space (resource partitioning).

Increasing or reducing competition towards your relatives

When should kin selection favour reduced competition towards kin in plants? Another way to approach this question is to ask how related two plants should be before a reduced competition towards a neighbour is beneficial. To illustrate this, we simulated interactions among two conspecific plants grown together in a pot, and calculated the inclusive fitness of a focal plant competing with a neighbour plant of variable relatedness, and under varying levels of asymmetric competition. Our fitness measure is seed set. When competition is symmetric (similar ‘kind’), we assumed that resources are shared evenly among both plants, which obtain more or less the same biomass and thus produce a similar number of seeds. When competition is asymmetric (different ‘kinds’), we assumed that the focal plant acquires more resources than its neighbour, and as a result, produces more seeds. Under asymmetric competition, the ‘loosing’ competitor acquires fewer resources and hence produces less seeds relative to symmetric competition.

Inclusive fitness was calculated under the assumption that the relationship between resources (biomass) acquired and seed production followed either a linear or a curvilinear saturating function (of resources acquired). Under the linear assumption, the number of seeds lost by the smallest competitor was exactly matching the number of seeds gained by the larger competitor. Under the curvilinear saturating relationship, the number of seeds gained by the larger competitor did not outweigh the number of seeds lost by the smaller

competitor (similar to the curvilinear relationship shown in Fig. 3). We performed these simple calculations for plants with a selfing and an outcrossing mating system. Following Bulmer’s (1994) expression for calculating r from inbred and outbred diploid organisms, a plant with a close to 100% selfing mating system is twice as related to the offspring of its related neighbour as a plant with an outcrossed mating system. In other words, if you are related to your neighbour, you are also related to the offspring of your neighbour, and twice as much if your neighbour is selfing compared to if your neighbour is outcrossing. We emphasize that these simulations aimed to illustrate – under a set of pre-specified conditions – how relatedness and mating system can result in reduced competitive growth towards a related neighbour through kin selection. They were not meant to provide a complete dynamic model of all possible combinations of relatedness and degrees of asymmetric competition.

When the number of seeds lost to competition by the ‘loosing’ competitor exactly equals the number of seeds gained by the focal ‘winner’ (linear relationship), the focal plant should always maximize its competition towards its neighbour irrespective of the neighbour’s relatedness (Fig. 5A). However, when the number of seeds lost by one plant is greater than the number of seeds gained by the competitor (curvilinear saturating function), several scenarios occur where kin selection could favour restrained competition towards a neighbouring plant, depending both on the level of relatedness and on the plant mating system (Fig. 5B). For example, if a selfing plant competes with a related neighbour of $r=0.6$, the plant obtains its highest inclusive fitness when competition is

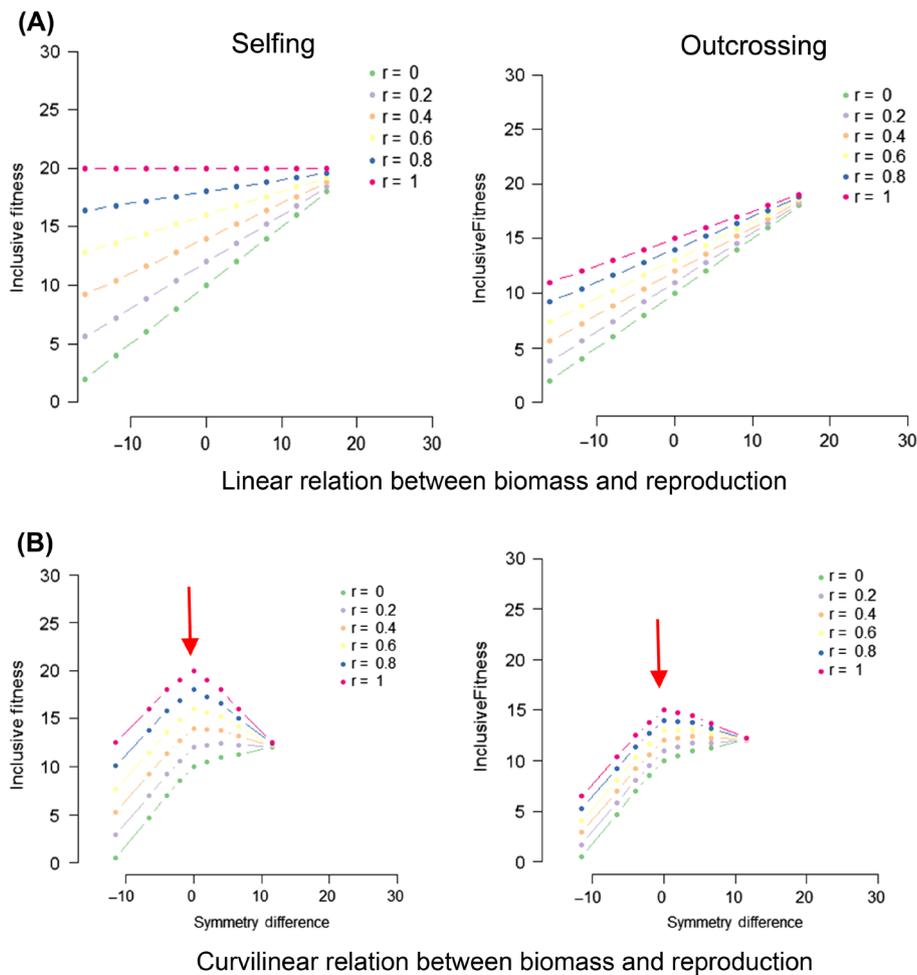


Figure 5. Inclusive fitness of a focal plant growing in competition with a neighbour plant of varying relatedness (r), assuming a selfing (left) or an outcrossed (right) mating system. The number of seeds produced by a plant is directly related to its biomass and follows either a linear (A) or a curvilinear (B) relationship. When symmetry difference = 0, competition is completely symmetric: the two plants share resources equally, and accordingly produce the same number of seeds (direct fitness). In other scenarios competition is asymmetric so that focal plants obtain a smaller or larger biomass than their neighbours. It follows that when r is 0 (or very low) the focal plants obtain the highest inclusive fitness by growing as large as possible. Under the curvilinear scenario, there is a range of r -values for which the highest inclusive fitness of the focal plant is obtained under symmetric competition (red arrow). For these instances, if the focal plant increases its own size at the expense of the size of the related neighbour the indirect fitness loss (from reducing the size of its related neighbour) is higher than the direct fitness gain it obtains from growing larger. The focal plant will thus obtain the highest inclusive fitness if it shares resources equally with its kin. The graph $r = 0$ represents the situation where the two plants are unrelated and hence there is no indirect fitness gain so the inclusive fitness is equal to the direct fitness, i.e. the number of seeds produced by the focal plant.

symmetric (red arrow on Fig. 5B). Under these conditions, if the focal plant increases its own size at the expense of the size of the related neighbour, the indirect fitness loss (from reducing the size of its related neighbour) is higher than the direct fitness gain it obtains from growing larger. The focal plant will thus obtain the highest inclusive fitness if it shares resources equally with its relative. Under our chosen set of conditions, this is true for selfing plants with a relatedness as low as $r = 0.4$. For outcrossing plants, similar scenarios favouring restrained competition can be found but require r values that are higher than those needed for favouring restrained competition in selfers.

The relationship between biomass and reproduction varies among plant species and follow both linear and curvilinear functions (Aarssen and Taylor 1992, Weiner et al. 2009). We arbitrarily chose the slope of the linear, and shape of the curvilinear relationship between biomass (resources acquired) and seeds produced to calculate inclusive fitness under a range of neighbour relatedness coefficients. Importantly, we assumed that interacting plants followed the same function, however if the shape and slope of these relationships are genotype-dependent the expectations for when it is favourable to restrain competitive growth towards related neighbours may change.

Discussion

In studies of how plants perform in competition with relatives, it is common to measure ‘group performance’ in pots with groups of sibling plants or non-sibling plants. The interpretation of these results have been equivocal (reviewed by File et al. 2012), as some studies showed better performance of kin groups than non-kin groups, other studies found the opposite, and yet other studies showed no differences. Our simulations suggest that there are fundamental problems with these types of comparisons, as differences in competitive ability are rarely controlled for, which prevents the ability to disentangle kin selection from other processes. We propose an experimental design that allows to disentangle effects of kin and kind. However, a more conceptual problem is the notion that ‘group fitness’ – the mean performance of all individuals grown in a pot – is assumed to represent the relevant fitness measure (File et al. 2012). We are attempting to assess whether individuals have evolved the ability to respond adaptively to relatedness of competing individuals. Natural selection occurs at the individual level, and the inclusive fitness framework captures this by measuring fitness at the individual level (West et al. 2002, Gardner et al. 2011) (Fig. 2). The term ‘group fitness’ is not meaningful as it invokes the level of selection being on the group, i.e. that group selection should favour evolutionary (inherited) traits of all individuals in the group. The term ‘group fitness’ (for example Stevens et al. 1995) cannot easily be understood in a natural selection framework, which per definition deals with evolved (inherited) traits. The traits to consider under a kin selection framework are individual evolved traits that respond to neighbour identity, and the assessment of whether they have evolved by kin selection should be performed by acquiring an approximation of inclusive fitness of individuals expressing these traits. If we grow plants in pots with kin or non-kin, the inclusive fitness of the focal plant is not determined by the production of the pot (which File et al. 2012 refer to as ‘group fitness’) but by inclusive fitness, i.e. the sum of direct and indirect fitness (Fig. 6). Irrespective of whether an individual is competing with relatives or with unrelated individuals, it is the sum of direct and indirect fitness that constitutes the inclusive fitness of the focal plant. The magnitude of inclusive fitness benefits will then determine whether an individual evolves the ability to modulate its competitive growth in response to the relatedness of a competitor (West et al. 2002, Gardner et al. 2011).

Selection can promote dispersal to reduce kin competition (Ronce 2007), and as a result, inclusive fitness may also be maximized through the avoidance of competition with kin. This implies that we also need to estimate fitness of the related individuals in the other pots (right side of Fig. 6). If kin cooperation results in elevated performance of the focal individual through reduced competition with kin, we expect reduced dispersal and the formation of patches consisting of related individuals (high genetic viscosity, left side of Fig. 6).

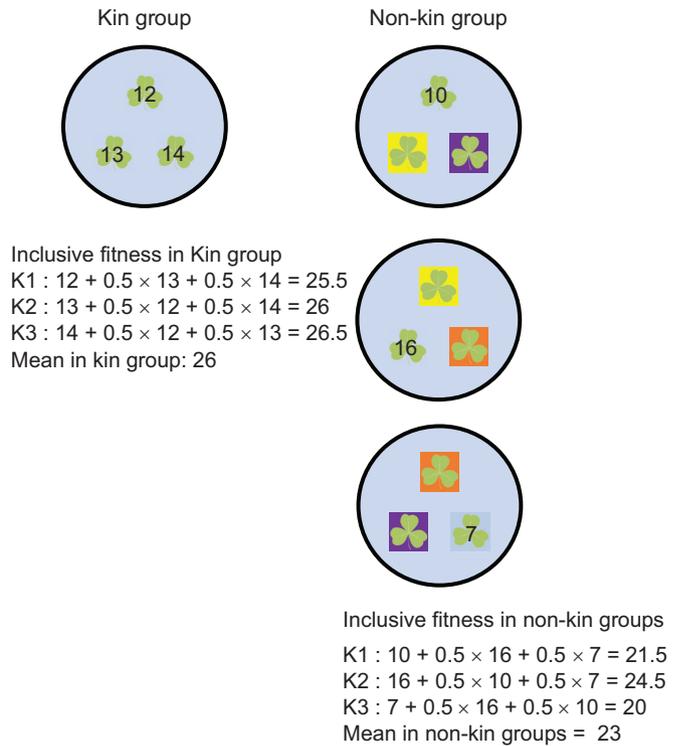


Figure 6. Schematic illustration of inclusive fitness estimates of genotypes (green) represented by three siblings that either do not disperse and hence grow in a kin group, or disperse and therefore grow in groups of unrelated plants. For each of the three individuals the inclusive fitness is calculated when growing with kin and with non-kin. Note, that when growing with non-kin, the fitness of the unrelated neighbour plants is not part of the inclusive fitness of the focal genotype. The mean ‘group’ fitness of kin can therefore be both higher and lower than mean ‘group’ fitness of non-kin groups, which illustrates why mean group fitness is not the relevant composite trait to compare when addressing questions that are about kin selection.

For the reasons outlined above, we argue that the trait-based approach for measuring the outcome of social interactions in plants proposed by File et al. (2012) is not useful for assessing the evolution of kin selected responses. The effect of the neighbour ‘phenotype’ (Fig. 2b in File et al. 2012) is interpreted as a group-selected trait that is proposed to encompass the effect of ‘cooperation by neighbours’ on the focal plants, but this is a composite phenotypic response that does not allow any direct coupling with traits that are inherited. It is a fundamental evolutionary principle that adaptive traits are under individual selection, and therefore selection on whatever trait measured, must also be determined individually. This is why we need individual measures of fitness (inclusive fitness) to be able to identify the selective process underlying the competitive outcome of an interaction between two individuals (Hamilton 1964, West et al. 2002). Inclusive fitness measures are imperative for determining whether individual plants can evolve the ability to respond differentially to relatedness of conspecifics by acquiring

indirect fitness benefits. It is true, that the inclusive fitness framework does not provide information on the mechanism underlying a potential kin selected response, for example whether it results from an above ground or below ground plastic response, but neither does taking a group perspective address such detail (Frank 2013). In our view, it is necessary to first identify the ultimate explanation for an evolutionary response, before attempting to decipher the proximate explanations.

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