Functional niche differentiation in co-occurring congeneric plants

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Abstract

Niche differentiation is argued as one of the mechanisms explaining species coexistence. Despite their sessile nature, similar resource needs and traits to acquire and utilize resources closely related plant species coexist. I hypothesized that i) spatial distribution of congeneric species would be similar because they are closely related with similar traits and resource needs and ii) each species will perform different biological functions (growth vs. reproduction) optimally at different points along a resource gradient and thereby differentiate their functional niche to ensure coexistence by complementary resource use. I collected data on two congeneric wild blueberry species, *Vaccinium angustifolium* and *V. myrtilloides* on occurrence from 13,500 20 x 20 cm quadrates, their growth and reproductive response to light and microhabitat parameters from 360 1 x 1 m quadrates along 90 30 m transects from 5 regions of NW Ontario. I also grew these two species in a common garden experiment (CGE) under a shade gradient to test their response to light in competition-free environment. A chi-square test confirmed that *V. angustifolium* and *V. myrtilloides* are co-occurring species. Variance partitioning analysis revealed that light is the most important microsite variable. Frequency of occurrence showed their abundance gradually increase from low to high light with high niche overlaps. Regression model fitting of cover (indicating growth) and berry yield (indicating reproduction) along the light gradient provided species functional response curves. By rescaling the response curves I obtained comparable functional fitness/performance curves, which showed that for both species optimum performance for growth and reproduction peaked at different light levels in natural habitats and in CGE. But their niche overlaps between growth and reproduction functions were markedly lower in natural habitats than in CGE meaning that these congeneric species differentiate their niche preferences for growth and reproduction. Both species showed conspicuous shift of functional niche in natural habitats from the CGE. Higher growth of one

species was often corresponded with lower growth of the other suggesting a complimentary use of finite growing space. These results suggest that neighbouring plants may reduce their competitive stress by adjusting their biological functions through functional niche differentiation. To my knowledge this is the first study providing clear quantitative evidence of functional niche differentiation in two closely related coexisting plants. One of the mechanisms by which clonal understory woody plants avoid competition for light is through differentiating 'physical space niches' by foraging small resource patches by clonal extension. The results of my study reveal another mechanism of species co-existence, which has evolutionary significance. I show how two congeneric clonal species occupying the same physical niche space can avoid competition by differentiating their functional niche. Further discovery of functional niche differentiation in multiple coexisting species along multiple resource gradients (such as soil nutrients, soil moisture) will make a significant contribution to refining community assembly rules.

Acknowledgement

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Introduction

Competition to occupy a preferred niche leads to exclusion of certain species from a community (Stuble *et al.* 2013; Hardin 1960; Gause 1934). The competitive stress is higher amongst closely related congeneric species than phylogenetically distant ones because of their overlapping niches and common adaptive traits (Harper *et al.* 1961; DeBach 1966). Moreover, due to the sessile nature and limited choice of resources (light, moisture and nutrients), co-occurring plant species are more susceptible to competition than mobile organisms (McKearny 2001, Armstrong 1989). However, species may mediate competition and co-exist by differentiating their niches (Adler *et al.* 2010; Kraft *et al.* 2008; Diamond 1978).

The mechanisms of mediating competition for resources among species show a hierarchical (stepwise/scalar) pattern (Farigone and Tilman 2002). Since timing of life history events and spatial distribution of individuals are not always shared simultaneously, closely related species may limit competition by avoiding concurrent presence in space and time (Barot 2004). However, species do not always segregate their occurrences in space and time due to their similar niche preferences. Concurrently occurring sessile plant species may still make use of smaller scale spatial and temporal heterogeneity (Farigone and Tilman 2002). Such spatial heterogeneity is often vertical, where morphological variation enables a species to use resources (light, soil, water and nutrients) from different vertical profiles. Time difference of phenological events of co-occurring species is another way of using temporal heterogeneity for co-existence. When spatio-temporal heterogeneity does not provide enough scope for co-existence, use of different types of energy from different trophic levels can be another mechanism (Fargione and Tilman 2002; Tilman 1999).

Neutral theory, on the other hand, claims that co-existence is stochastic where simultaneous arrival of two or more species (only dispersal mechanism) can ensure co-

existence (Hubbell 2001). However, neutral theory does not provide any explanation for competition mediation, especially at microsite-scale. At microsite-scale there is a designated safe site for successful seed germination, seedling establishment and growth of a species (Mallik and Kravchenco 2013; Harper 1977). These and safe site conditions differ among species. There are trade-offs between colonization (propagule arrival) and competitive ability (establishment) of a species under a given condition (Farigone and Tilman 2002). This trade-off provides an opportunity for different species to come together at different ontogenic stages. Different species make use of different resources from the same site (McKane *et al.* 2002) over different ontogenic stages and thereby can co-exist. There can be several underlying mechanisms including resource use along horizontal and vertical gradients (Table 1), but none of these mechanisms can fully explain species co-existence alone. It is likely that several mechanisms work simultaneously to ensure species coexistence and diversity within a community (Fargione and Tilman, 2002; Tilman 1982; Janzen 1970; Tilman 1994; Hurtt & Pacala 1995; Pacala, 1997).

The above mechanisms of avoiding similarity in resource utilization (Table 1) are often referred to as niche differentiation (MacArthur and Levins 1967; Schoener 1974). The ecological niche is as an expression of the structural and functional position of a species within an ecosystem (Whittaker 1973) and it encompasses both the physical presence of a species and the roles it plays by participating in various ecological processes (Kearney 2006). The niche concept started as qualitative descriptions of species' roles and requirements in communities (Grinnell 1917; Elton 1927). Hutchinson (1957) later defined niche as a hyperspace in multi-dimensional environmental space in which a species can maintain a viable population. The 'fundamental niche' leaves out biological interactions such as

Table 1. Linking competition mediation mechanisms with niche differentiation and other relevant ecological concepts.

Competition mediation mechanisms	Resource mostly* competed for	Niche based concepts	Other relevant ecological concepts
Avoiding concurrent occurrence	Space (Horizontal)	Habitat niche (occupying different locations)	Spatial heterogeneity, resource partitioning (complementary resource use)
	Time (Diurnality seasonality, annuality etc.)	Fluctuation niche, Phenological niche (utilizing temporal variation)	Temporal heterogeneity
Avoiding structural/ morphological similarity	Space (Vertical), Consumable resources (nutrients, water, CO_2, O_2)	Life history niche (ontogeny phases), Food/Foraging niche (acquiring resources)	Resource allocation trade-off to attain different morphological structure, Ecological drift (by differentiating traits)
Avoiding functional similarity	Physiological resource needs (light, temperature)	Reproductive niche, Regeneration niche (environmental conditioning/ utilizing resources)	Energy (resource) allocation trade-off to perform different biological functions

* The mentioned resources are not exclusive to the competition mediation categories. Many of the mechanisms work simultaneously to mediate competition for resources.

predation and competition, and a 'realized niche' is obtained as a subset when such biological interactions are included in the niche space (Schoener 1989; Chase & Leibold 2003). Schoener (1989) suggested that it is important to perceive niche as a property of the species rather than the surrounding environmental factors and one should also recognize that under similar conditions different species may respond differently due to their varying niche preferences. These differences in niche preference can explain species co-existence at different scales.

In the literature, spatial niche differentiation at the landscape level is widely referred to as habitat, which delineates the preferred occurrence or location of a species. The temporal niche variation is relatively less discussed and is often termed as fluctuation niches (Terrads *et al.* 2009). Spatio-temporal niche differentiation is easily distinguishable in faunal species as they can move away from competitively stressful areas to other areas within its range of habitats (DeBach 1966). Although there are examples of spatial differentiation of niche among plant species, due to sessile nature of floral species niche differentiation patterns are not easy to distinguish (Shmida and Ellner 1984). At the micro-scale, spatial niche differentiation is sometimes facilitated by morphological variations that help to acquire different types of resources or the same resource from different vertical gradients. For plant species, height and crown pattern can be morphological variations indicating variation in light acquisition ability. For faunal species the temporal niche differentiation is also more noticeable as nocturnal and diurnal species may use the same space at two different times of the day-night cycle. For plant species, temporal niches are often mentioned as phenological niches such as difference in timing of leaf flushing, flowering or fruit ripening of different species. There would still be niche conservatism among related species to have similar fundamental and realized niches preferences. Similar resource availability and environmental condition would support such related species to aggregate and form a community at a given

time and space. Hence, in a community spatial and temporal niche differentiation does not sufficiently explain species co-existence. Non-spatially explicit niche conservatism is higher within sessile co-occurring plant species and it is particularly intriguing how closely related plant species with similar evolutionary traits acquire resources or cope with environmental conditions and co-exist (Silvertown *et al.* 2001; Darwin 1859). This leads to the question as to whether niche differentiation can explain the co-existence of closely related plant species. It is reasonable to suggest that niche differentiation in plant species mostly happens at functional levels where competing co-occurring species perform different biological functions (Silvertown 2004; *sensu* Leibold and McPeek 2006).

A species requires different types and levels of resources to perform different biological functions (Grubb 1977). A species at any random locations in a suitable habitat puts its initial efforts toward establishment so that it can survive by acquiring available resources. Once established, individuals concentrate on growth and reproduction (Grubb 1977; Poorter 2007). Based on these key biological activities, one can broadly divide biological functions into two categories: i) growth and ii) reproduction. It is possible that a species will not perform optimally for both of these functions at a similar location and condition. There will be areas where a species can occur but merely survives and areas where growth or reproductive functions would be at optimum. Preferred niche for growth may be a subset of occurrence sites because a species can grow only if it occurs in a site. The same is applicable for reproductive functions. However, the preferred growth and reproductive niches can be different from each other. A niche suitable for growth may not be suitable for producing viable propagules (i.e. reproduction). It is also often evident through plants resource allocation patterns that either growth or reproduction is prioritized under different conditions (Bazzaz *et al.* 1997). Again, under certain conditions, a species can revert to a reproductive mode without attaining (or constrained to attain) preferred growth potential

(Bonser and Aarssen 2009, Aarssen 2008). It is apparent that the niche preferences for different biological functions are different.

In the literature species niche preferences for accomplishing different biological activities are referred to by different names such as food niche, regeneration niche etc. emphasizing particular the biological function(s) in question. Here I use the term 'functional niche' to encompass all biological activity based niches, defined by preferences for accomplishing different biological functions such as resource acquisition, growth, reproduction, migration or dispersion. Earlier Maire *et al.* (2012) referred to 'plant functional niche' as the relative position of a plant functional trait within trait space. I adopted the term in similar notion and defined it based on more classical niche concept. Functional niche preferences are reflected in measured functional trait values and thereby functional niche in trait space and Hutchinsonian niche hyper-volume space is conceptually the same. Functional niche differentiation is not widely reported for plant species, but is important especially for co-occurring congeneric plant species as there is little difference even in their morphological structure. I propose that congeneric species mediate competitive stress by avoiding performance of similar biological functions at a given condition (such as soil moisture), as resource needs would be different for different biological functions such as growth and reproduction. I refer to this phenomenon as functional niche differentiation.

Niche preferences for different biological functions are assumed to be different and as such niche differentiation can be assessed as differences in niche preference (Turnbul 2013). Different environmental variables drive biological functions of a species, and for a particular species its response to each individual variable is different. Even along the gradient of one variable, species may respond differently and niche width of a particular species can be measured either separately on each niche axis or combined for all axes. Furthermore, niche width not only measures a population's range of occurrence on the niche axis but also its

frequency of occurrence along that axis (Maire *et al.* 2012). The occurrence frequency indicates a population's optimal positive response to that particular axis. The combination of niche width along all axes delineates each species' niche preference. This combination of axes gives rise to Hutchinsonian niche space (1957), n-dimensional hyper-volume. The n-dimension comes from n-number of variables driving particular species' performance. These n-dimensions typically include physical conditions (habitat temperature, humidity, soil pH etc.) and resources (e.g. light, nutrient availability). This niche space, in the context of different environmental gradients and other habitat features, can be used to predict survivorship, development, growth, reproduction and ultimately, population dynamics, abundance, distribution and species interactions (Kearney 2006; Holt *et al.* 2009).

One way to assess species interactions for resources is to measure similarity in niche preferences or niche overlaps along a specific resource gradient. Niche overlap measures indicate the degree of ecological similarity and by deducting niche overlap from niche widths of the species in question one can measure niche differentiation of different species along the niche axis (Johnson 1976).

It is naive to perceive that a species preferred niche would be optimum for performing all of its biological functions. This would mean that niche width of species occurrence would be similar for all biological functions of that species. As discussed earlier, biological functions may have differences in niche preference and often would have a different functional niche width for growth or reproduction (Figs. 1 a, b). These functional niches will have a different degree of niche overlaps based on the difference of resource and environmental requirement at a particular niche axis (Fig. 1 c). For phylogenetically closely related species, I would expect to see similar niche width in terms of their occurrence. Their functional niches will be similar as well due to their genetic makeup of evolutionary traits.

However, when they co-occur, I expect to see a shift in functional niches to mediate competition.

In boreal mixedwood forests of northwestern Ontario, wild blueberries are common understory species with two reported congeneric species, lowbush (*Vaccinium angustifolium*) and velvetleaf (*V. myrtilloides*) blueberry. The object of this research is to explore the niche preferences of these two closely related co-occurring species to understand the mechanisms of their co-existence better. The specific objectives of the research are to a) ascertain distribution and co-occurrence of congeneric wild blueberry species at different spatial scale in northwestern Ontario, and b) determine functional niche differentiation of the co-occurring congeneric blueberry species. I hypothesize that

1) Distribution of the two blueberry species would be similar across spatial scales because they are closely related species with similar traits and resource needs.

2) (a) Each of the two blueberry species will perform different biological functions (vegetative growth vs. reproduction) optimally at different points along a resource/environmental gradient (such as light) and (b) thereby the two blueberry species will differentiate their functional niche to ensure coexistence through complementary resource use.

For the first hypothesis, I predict that within suitable habitat range, the two congeneric blueberry species would co-occur across different spatial scales, from regional to microhabitat scale and also along microsite resource gradients. It is important to note that the first hypothesis is a conditional one for hypothesis 2 and if the first hypothesis is not supported, the second hypothesis would become non-testable. If the two species do co-occur spatially, then for the second hypothesis I predict that both the blueberry species will have distinct niche preferences along a niche axis to perform different biological functions

(vegetative and reproductive) and they will exhibit their optimum performance at different points along resource/environment gradient (such as light). Given a non-competitive environment (grown in isolation), then because of their close phylogenetic relationship and similar morphological and functional traits I expect their niche differentiation to be minimum. However, to co-occur in natural habitats in the presence of competition they will show recognizable niche differentiation.
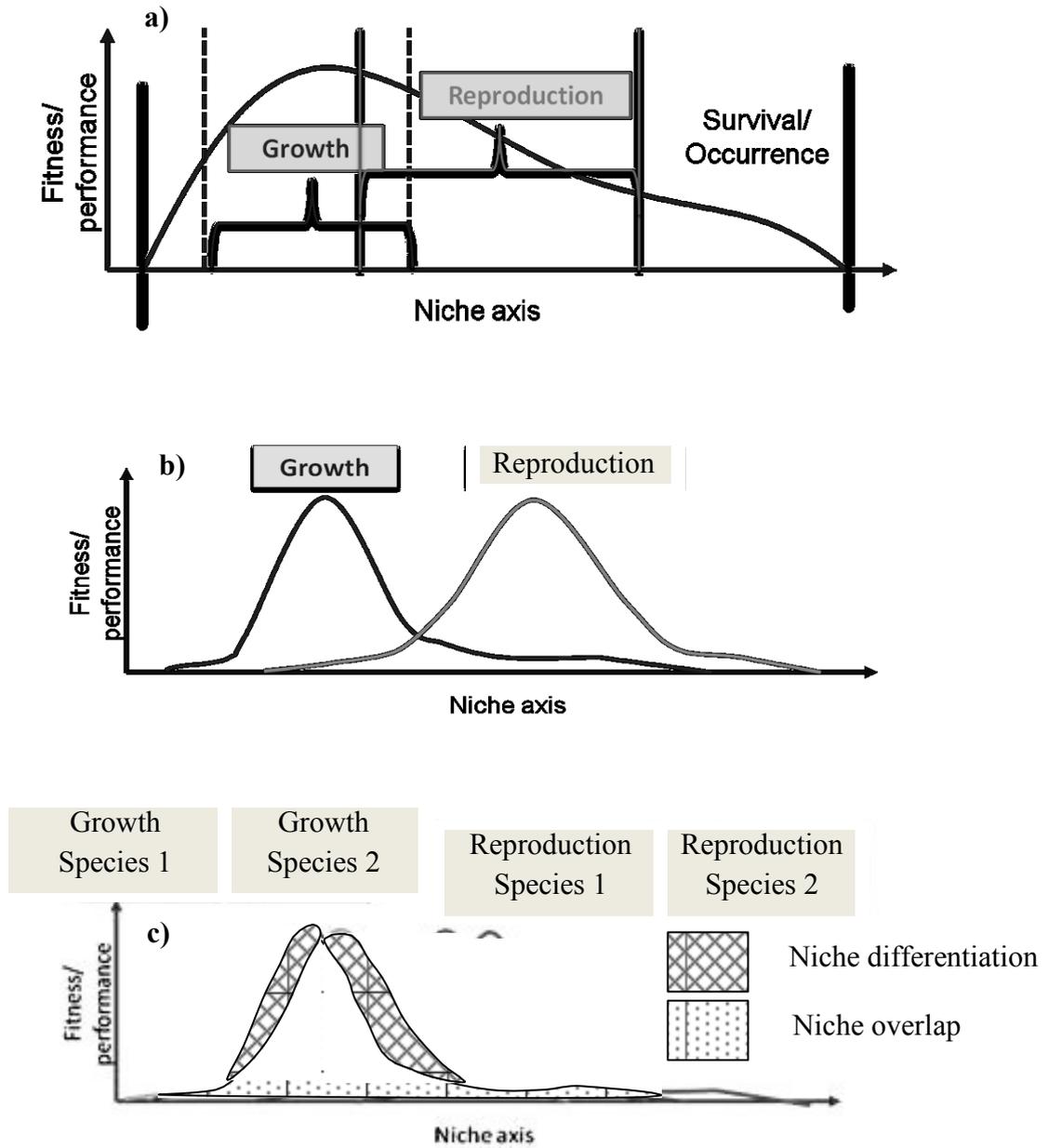
Figure 1. Schematic diagram of niche breadth showing (a) overall niche extent, (b) functional niche subdivisions along a niche axis and (c) niche overlap and niche differentiation showing different functional niches between co-occurring species.

Materials and Methods

Choice of species

The commonly occurring wild lowbush blueberry (*V. angustifolium*) and velvetleaf blueberry (*V. myrtilloides*) species of northwestern Ontario, were selected to test the hypotheses pertaining to niche differentiation for the following reasons: i) phylogenetically they are closely related (Mallik 2011), ii) being congeneric, these two species match the criteria of having similar traits and therefore, expected to have similar distribution, iii) both are perennial understory species and occur in frequently disturbed boreal mixedwood forests iv) natural occurrence of these two species across the eco-district of northwestern Ontario would reflect their niche preference similarity at a macroecological scale, and even at microsite levels the spatial occurrence of these two morphologically similar species would reflect their coexistence within interactive proximity, v) determining the relative spatial occurrence of these two species would be easy because of their small stature and vi) measuring their attributes related to biological functions such as cover for vegetative growth and berry yield for reproductive effort would also be relatively easy.

Both of these species are clonal in nature and resprout from rhizomes in very short time after disturbance. This vegetative spread phenomenon eliminates the concern for having any 'priority effect', i.e. the effect of prior arrival of a particular species on community dynamics of that particular site (Young *et al.* 2001). Regular turnover of shoots also minimizes the concern for the effect of ontogeny on biological functions of these species. Being disturbance tolerant perennials, both species are found along disturbance (clearcut and wildfire) chronosequence. Environmental gradients such as light, soil moisture and nutrients, vary along the chronosequence, hence it was possible to explore the response of these ericaceous species along these gradients. Sensitivity of ericaceous plants to different environmental gradients are widely acknowledged such as varying response of vegetative

spread and reproductive shoot of *Kalmia angustifolia* along a shade gradient (Moola and Mallik 1998; Mallik *et al.* 2012). Moola and Mallik (1998) reported that *V. myrtilloides* occurs in clearcuts to uncut mature forests. Wild blueberries are a good source of income for rural people and they are widely reputed for its health benefits. With efficient management of the wild blueberry species, blueberry production can be increased and its food quality optimized (Mallik 2011). This niche preference study can directly contribute to that endeavor.

Study area: Natural blueberry habitats across northwestern Ontario

The study was conducted in northwestern Ontario, known for different types of wild blueberries including *V. angustifolium* and *V. myrtilloides*. The data were collected in the summer of 2013 from five eco-districts within northwestern Ontario from areas close to Nipigon, Black Sturgeon Lake, Escape Lake, Ignace and Atikokan (Fig. 2). The five eco-districts were selected based on their differences in climatic variables (mean annual temperature and precipitation) and disturbance history (Table 2). Geographical dispersion of sampling areas was also a consideration (Fig. 2).
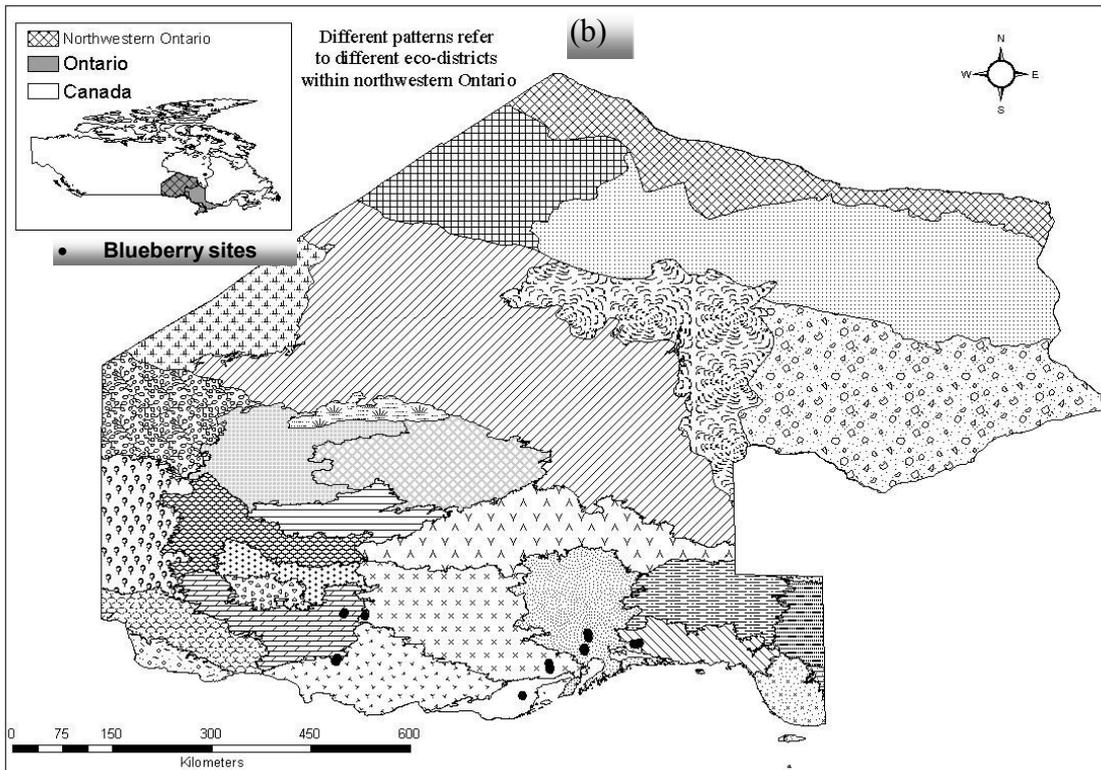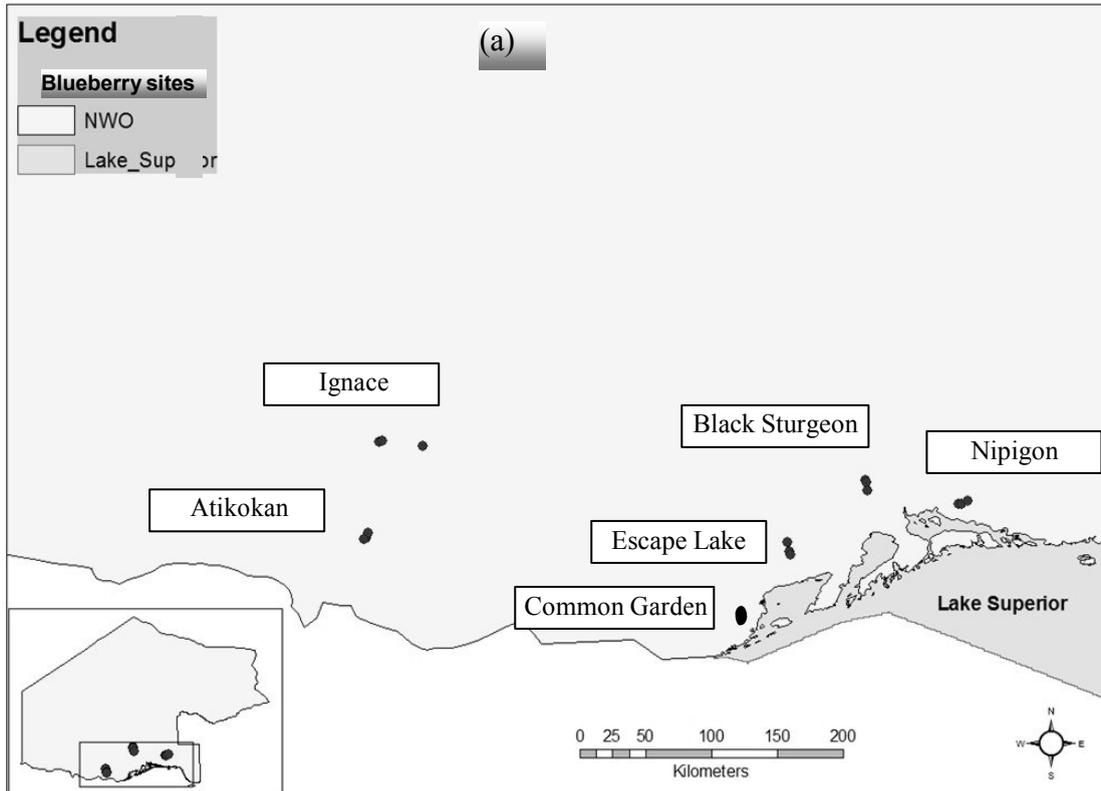
Figure 2. Location of sampling sites and the common garden experiment (Fig 2.a) and eco-districts of northwestern Ontario (Fig 2.b) showing varied ecological profile of sampling sites.

Table 2. Descriptive site attributes of ild blueberry sampling location in northwestern Ontario.

Location	Site ID	Latitude	Longitude	Annual precipitation* (mm)	Mean annual temperature (^{o}C) *	Elevation (m) *	Year of disturbance**	Type of disturbance**
Atikokan	Site 1	48° 48' 14.939" N	91° 56' 34.731" W	689	1.7	414	1995	Clearcut
	Site 2	48° 50' 9.204" N	91° 56' 1.212" W	695	1.7	420	2008	Clearcut
	Site 3	48° 47' 42.900" N	91° 57' 28.728" W	697	1.7	441	2007	Clearcut
Ignace	Site 1	49° 26' 41.533" N	91° 51' 18.613" W	778	1.0	448	2007	Clearcut
	Site 2	49° 27' 20.059" N	91° 49' 55.598" W	784	0.9	470	2007	Clearcut
	Site 3	49° 25' 19.956" N	91° 33' 19.008" W	787	0.9	431	2005	Clearcut
Escape Lake	Site 1	48° 46' 29.190" N	89° 3' 39.420" W	787	0.7	479	2003	Clearcut
	Site 2	48° 42' 41.435" N	89° 2' 43.769" W	787	0.9	472	2002	Clearcut
	Site 3	48° 41' 23.928" N	89° 2' 42.360" W	789	0.9	478	2003	Clearcut
Black Sturgeon	Site 1	49° 11' 17.743" N	88° 31' 48.508" W	782	1.0	327	2006	Fire
	Site 2	49° 10' 24.817" N	88° 31' 20.928" W	783	1.0	332	2006	Fire
	Site 3	49° 7' 18.300" N	88° 30' 55.440" W	777	1.2	301	1999	Fire
Nipigon	Site 1	49° 1' 40.911" N	87° 53' 23.248" W	846	0.4	459	2003	Clearcut
	Site 2	49° 1' 39.151" N	87° 52' 20.537" W	846	0.4	463	2003	Clearcut
	Site 3	49° 3' 6.984" N	87° 49' 49.656" W	844	0.4	456	2004	Clearcut

* Hijman *et al.* (2005); ** OMNR (2013). NB: More data on some other climatic parameter are included in appendix 1.

Data collection on blueberry microhabitats, cover and berry yield

A multistage sampling approach was adopted to collect vegetative and reproductive data for both *V. angustifolium* and *V. myrtilloides* species. A long list of possible sites within each of the selected five eco-districts was created by examining forest harvest and silvicultural databases of the Centre for Northern Forest Ecosystem Research (CNFER), Ontario Ministry of Natural Resources (OMNR), Thunder Bay and also by consulting the forest companies operating in the area. A two-stage randomization procedure was followed, where within each eco-district three sites were randomly selected from the long list of possible sites mentioned above. For ensuring representation from closed canopy mature forest sites, three such sites were randomly selected in the Black Sturgeon area. In total, 18 study sites were selected, and five reference points were selected through random point generator within each of the selected sites. These five reference points were the initial points to lay out five transects in each site. A range of understory light condition was taken into account in selecting sites to ensure representation across a resource (light) gradient. Transects were laid in random direction across any other readily observable gradients such as slope.. It was reasonable to assume that multiple random transects of 30 m would capture the large and small clones and their surrounding microhabitat conditions. Along each transect presence absence data were collected for the two blueberry species within 20 x 20 cm quadrats along the entire length of the transect to assess their co-existence within interactive proximity (Fig. 3). For functional performance of the species, cover was considered as an indicator of vegetative growth and berry yield an indicator of reproduction and data on cover and yield were collected from four 1 x 1 m quadrats laid systematically 9 m apart along each of the 30 m transects. The center of the first and last 1 x 1 m quadrats were placed at the start and end of the transect (Fig. 3). In total, 13500 20 x 20 cm quadrats were sampled for coexistence (presence-absence) and 360 1 x 1 m quadrats (18 sites x 5 transects x 4 quadrats) were

sampled for vegetative growth (cover) and reproductive (berry yield) performance, across the five eco-districts. All blueberries within each of the selected quadrats were collected, divided and labeled according to species to determine berry yield per ha. Abundance of each blueberry species was recorded as % cover within each plot. Microsite (habitat) parameters such as soil pH (using Bluelab soil pH meter, Model 3.2), soil moisture (HH2 soil moisture meter with 2.0 combined WET sensor from Delta Corporation), organic matter depth (from soil profile) and light above blueberry bushes (using densiometer) were measured for each of the selected quadrats. Percent cover data for all the species present within 1 x 1 m quadrats were also recorded to keep track of presence of neighboring plants and their potential effect on blueberry species response under study. Data were collected in the first two weeks of August during blueberry ripening time in the region. Vegetative cover (%) data were collected in early July after all leaves had fully flushed.

Common garden experiment (CGE)

The purpose of conducting a CGE was to determine how niche differentiation in these two species occurs along a light gradient under competition free conditions. Earlier studies (Moola and Mallik 1998, Hoefs and Shay 1981) and initial data exploration revealed that light availability was the most influential factor in regulating biological functions of wild blueberry species. However, under natural conditions these two species may occur separately, together and with other co-occurring species along a range of canopy light conditions. To distinguish the niche preferences of these two congeneric blueberry species in relation to inherent genetic characteristics, phenotypic plasticity and competition, biological and environmental data were collected under field conditions.

Planting materials for CGE

The CGE was installed as a part of a larger study in 2010 to determine phenology, ecophysiology, berry productivity and horticultural suitability of three commonly occurring wild blueberry genotypes (*V. angustifolium* Ait*, V. angustifolium* var. *nigrum* (Wood) Dole and *V. myrtilloides* Michx. of northwestern Ontario (Mallik 2011). Clones of the three blueberry genotypes were collected from three locations, Nipigon, Escape Lake and Black Sturgeon (Fig. 2) in late October 2010 when the plants became dormant. Individual transplants were collected with soil by cutting approximately 30 x 30 x 15 cm deep blocks with a straight edged shovel. All clones were transplanted on the same day, as they were collected from the wild to maintain soil moisture. Each transplanted bush was irrigated with 7.5 l of water immediately after planting. Transplanting was done in the fall because during this period plants are in dormancy. Blueberry grows optimally at a soil pH range of 4.2 - 5.2 (Hall *et al.* 1964). Since the soil of the common garden experimental plot had neutral acidity (pH 7) local peaty topsoil was mixed with commercially available peat-vermiculite mixture (Premier® Sphagnum peat moss, Premier Horticulture Inc., Quakertown, PA, USA) in a 50:50 ratio and obtained a pH of 4.8. This material was used to fill up eight 50 m long, 60 cm wide and 30 cm deep trenches created by a tractor. The low pH peat moss in the experimental plots created a growing medium pH 5.5 comparable to that of natural forests.

The collected plant materials were of similar age and selected ramets had similar height and cover but it was difficult to have all plant materials of the same dimension. After transplanting an initial measurement of the dimension (width, breath and number of shoots) was recorded to normalize the subsequent changes under the experimental condition. Two years after transplanting when they were fully stabilized, six different shade treatments (no shade control, 30, 40, 60, 80, and 95% shade) were applied that allowed respectively 100, 80, 70, 60, 40, 20 and 5% light. Shade clothes made of propylene (VRE Systems, Grasse,

Ontario, model # FAFLS/B/O, FAFLS80; FAFLS60, FAFLS40, FAFLS30 were used. The shade structures were erected on May 28, 2013 as dome shapes with dimension of 3.8 m x 1.8 m and 1 m height . A digital Plant Canopy Imager (CI-110) was used to measure photosynthetically active radiation (PAR) to correlate bioavailability of light under these shades. The experimental design of the CGE was a randomized block design with 4 replicates of each light condition i.e., 24 blocks (4 replicate x 6 light level) under which both species and three provenances combinations were present. In total, 144 sample plants (24 blocks x 6 treatments) were used for the current study. Since I was interested in comparing the performance of two species of blueberry, *V. angustifolium* and *V. myrtilloides* under natural and competition free condition I did not consider any likely variation in their response due to provenance.
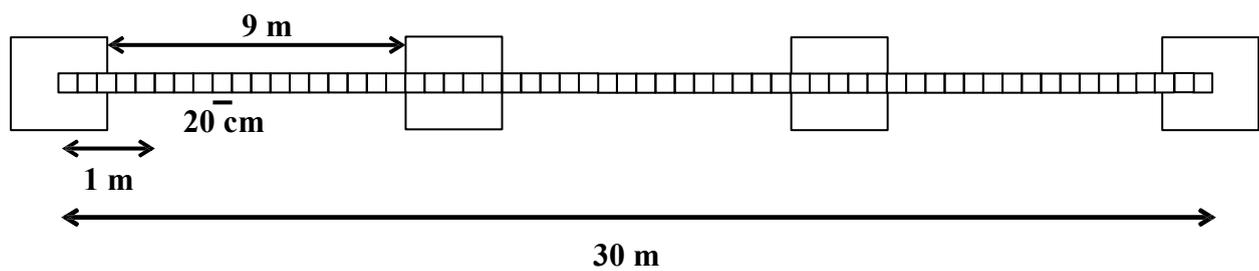
Fig 3. Arrangement of 20 x 20cm and 1 x 1 m plots along 30 m transects (not in scale). Each transects had 150 smaller consecutive quadrates for asessing co-ocurrence (presence-absence) of *V. angustifolium* and *V. myrtilloides*. There were four 1 x 1 m quadrats, each 9 m apart, were used for collecting data on functional performances such as % cover and berry yield as well as associated microsite variables such as canopy density, soil moisture, soil pH and organic matter depth.

Figure 4. Common garden experiment designed as completely randomized blocks with both *V. angustifolium* and *V. myrtilloides* transplants from 3 different eco-districts replicated within each of block with 4 replicates of 5 different light availability (5%, 20%, 40%, 60% and 70% light) treatments using shade clothes. Open blocks allowed 100% light and were used as controls (in total, 24 blocks).

Data analysis

Normality of data distribution was tested using the Shapiro test (Patrick 1982). The variables in the dataset were not normally distributed, therefore, Levene's test for homogeneity of variances was conducted since this particular test does not assume a normal distribution (Brown and Forsythe 1974). Multivariate power transformation of data was carried out to achieve greater normality (Box and Cox 1964). Normality of the transformed response variables were checked using quantile or qq-plot method (Fox 2008) using package car in R (Appendix 2; R codes). The transformed data were used for statistical analyses.

The cause of statistical non-normality of the compiled dataset most likely lies in the large size of the sample itself. With increase in sample size, small deviations become statistically significant. However, in general attributes of biological origin tend to follow normal distribution. Here species % cover and berry yield are biological features. Moreover, data transformation improved on the normality of the data as checked with qq-Plots (Appendix 3). With large sample sizes, the robustness of the parametric tests were also capable of adjusting some deviation from normal distribution. Hence I used parametric tests for the following statistical analyses.

To check for variation among species or variables, a series of ANOVA (with $\alpha = 0.05$) were carried out (Hand and Taylor 1987). For identified significant differences in each independent variable, Tukey's HSD (with $\alpha = 0.05$) was used as post hoc analysis (Box *et al.* 1978) where applicable. The key variables contributing to berry yield or cover of specific species or blueberry in general, were detected by variance partitioning using vegan package in R. To explore microsite (quadrate) level effect of site variables on blueberry cover and yield, a Canonical Correspondence Analysis (CCA) was carried out (ter Braak 1986). For the ordination analysis, cover and berry yield of each of the species were considered instead of

occurrence or variables were checked for co-linearity through multivariate correlation analysis.

All data were stored in MS Excel and analyses were conducted using MS Excel (v. 2007) and various R packages (package Vegan for CCA ordination, package Hmisc for multivariate co-linearity, package party for model based recursive partitioning, package car for data transformation, package pwr for power analysis etc.). The R codes for calculations and detailed outputs can be found in Appendix 2.

Calculating niche breadth and niche overlap

Niche breadth

Hurlbert (1978) developed a niche width calculation procedure that allows for the fact that some resources are very abundant and common, and other are uncommon or rare. The resource usage should be scaled to availability. Since addition of a measure of the proportional abundance of each resource state is more logical, I used the following measure of niche breadth:

$$\overline{\rule{2.5cm}{0pt}}$$

Where, = niche breadth (Hurlbert's)

 = proportion of individuals found in or using resource j

 = proportion of the total available resources consisting of resource j

Standardizing calculated niche breadth

The Hurlbert's niche breadth calculation still remains species specific and cannot be readily compared because the B' can take on values from 1/n to 1.0. Hence it should be standardized for easier comprehension. To standardize Hurlbert's niche breadth to a scale of 0-1, I used the following equation:

$$\overline{\qquad}$$

Where, $\qquad$ = Hurlbert's standardized niche breadth

$\qquad$ = Hurlbert's niche breadth

a_{min} = smallest observed proportion of all the resources (minimum aj)

Niche overlap

Niche widths do not readily provide us with a measure of similarity or dissimilarity of niche breadths. Pianka (1973) developed a niche overlap index, which is standardized within itself and readily comparable for co-occurring species in a community guild. This measure of overlap ranges from 0 (no resources used in common) to 1.0 (complete overlap) (Turnbul 2013). This is a symmetric measure of overlap so that overlap between species A and species B is identical to overlap between species B and species A. Based on these advantages, I used Pianka's niche overlap index for comparing niche preferences of co-occurring blueberry species.

$$\overline{\overline{\qquad}}$$

Where, $\qquad$ = Pianka's measure of niche overlap between species j and species k

$\qquad$ = Proportion resource i is of the total resources used by species j

$\qquad$ = Proportion resource i is of the total resources used by species k

n = Total number of resources states

Niche preference analysis with species response curve

Blueberry vegetative cover and yield as response variables were regressed over micro site parameters through a simple linear model. Here the site parameters were random factors in the regression model. The variables co-linearity was assessed using Spearman's correlation statistics (Myers and Well 2003). Since species response to environmental gradient is widely accepted to be largely unimodal, species responses along different variables were assessed by various non-linear regression models including polynomial (with different degrees), exponential, logarithmic etc.

For selecting the degree of polynomials, I initially used model based recursive partitioning (package party in R; Hothorn *et al.* 2006, Zeileis *et al.* 2008) to identify significant variation in slopes along each gradient. This was used as only an exploratory approach to find possible degree of polynomial for the given dataset and this was not used as a firm selection criterion. Fitted candidate models were cross-checked with ANOVA to ensure significance difference among them and   I adopted smaller Akaike's Information Criterion (AIC) based selection approach to select models, which have fewer variables without compromising much explanatory power in terms of explanatory power of the model or R^2 (Sakamoto *et al.* 1986). Since AIC does not assess the model quality, only plausible candidate models which make ecological sense were compared using Δ AIC, hence ecological reasoning had the priority over statistical model fits in model selection process (Austin 2002; Austin 2007).

Transforming response curves to species functional performance curves

The selected models were based on different scales and levels of transformed data. However, although the fitted response curves were useful for understanding species performance trends, their niche preferences were not readily comparable for among species

and biological functions. To make these comparable, I re-scaled the biological performances of each species. To this end the modeled values were calculated for each resource levels (from 0 to 100% light). I considered the maximum value (peak of the fitted response curve) as the optimum condition for that particular biological function equaling 1 in the performance scale. I rescaled all other values relative to the peak value providing us a scale of 0 (least performance) to 1 (optimum performance). When these rescaled values were plotted against resource levels (% light), the response curves were translated into comparable fitness/performance curves for each species and biological functions. These curves were used as basis for explaining functional niche differentiation among congeneric blueberry species.

I constructed error bars on optimum performance level (Appendix 8) for making the comparison more statistically meaningful. First I fitted lines for response curves with predicted upper values at 95%confidence interval level. The line crosses the optimum level (maximum value 1) at two points while going upslope and down slope. These two points were considered to be the interval between which the optimum level can be found.

I also carried out series of t-tests to compare fitted models based on the predicted values to test whether the visual similarities/differences of fitness/performance curves were statistically significant. I used paired t-test for models fitness curves on natural habitats since the data points had coupled observation from each quadrat. However, I used two sample t-tests with unequal variances for comparing fitness/performance curves under common garden experiment and also when comparing across natural habitats and common garden considering the data points to be independent of each other. Effect sizes of the t-test were calculated based on Wilson (2001) and subsequent power analysis were carried out through package pwr in R.

Trade-off curve analysis

To examine the complementary use of resources in co-occurring blueberry species in relation to performing particular biological functions, several trade-off curves were constructed by plotting *V. myrtilloides'* performance (cover or berry yield) over *V. angustifolium'*s same performance. A negative slope of trade-off curve would indicate that one species' higher performance corresponds with other species lower performance. A flat curve would represent neutral relationship and a positive slope would represent a condition where both species performance would increase simultaneously either referring to facilitation or, at least, absence of competition.

A summary of the data analysis process is summarized in Table 3.

Table 3. Summary of data analyses for comparing spatial occurrence and functional niche preferences of congeneric wild blueberry species of northwestern Ontario

	Objective	Data requirement	Data collection	Data Analysis
1.	Species distribution pattern analysis	At regional and microsite level	Species occurrence	Field survey of sample location across five eco-districts, presence-absence data in 20 x 20 cm plots along 30 m transects	• Descriptive statistics for distribution pattern, • chi-square test
2.	Niche preference analysis	Identify key microsite variable	Species wise cover and berry yield	• Field data from 1 x 1 m quadrats	• Descriptive statistics, • ANOVA with Tukey's post-hoc
			Organic matter depth, Canopy density (light), Soil moisture, Soil pH	• Field data from 1 x 1 m quadrats	• Canonical correspondence analysis • Variance partitioning,
		Conforming co-occurrence along resource gradient	Species occurrence		• Calculating occurrence niche overlaps • t-test (paired and two sample)
		Produce species response curves and fitness/ performance curves		• Data from common garden experiment	• fitting linear/non-linear regression lines through model selection based on AIC
3.	Functional niche differentiation analysis	Compare functional niche preferences			• Calculating functional niche overlaps, comparing optimum performance/fitness level with 95% confidence interval • t-test t-test (paired and two sample)
		Complementary use of resources			Trade-off analysis between performances of the two species for growing space and reproductive effort

Results

Co-occurrence of wild blueberry species in natural habitats

In natural habitats, both *V. angustifolium* and *V. myrtilloides* were abundant across all the five eco-districts of northwestern Ontario. However, *V. angustifolium* occurred more frequently than *V. myrtilloides*. The two species were found together more often (54.24% of the time than either of them occurring alone based on 13,500 20 x 20 cm quadrats. The co-occurrence of *V. angustifolium* and *V. myrtilloides* was also evident in 1 x 1 m plots across the eco-districts, where in 71.94% cases both species were found together based on 360 samples. A chi-square test confirmed that *V. angustifolium* and *V. myrtilloides* are co-occurring species ($\chi^2_{(1,\ N\ =\ 13500)}$ = 0.69; p = 0.405). Details of the chi-square analysis can be consulted at appendix 4.

Identification of influential niche parameter

Canonical correspondence analysis (CCA, Fig. 5) incorporating all the sampled microsite varibles showed that canopy density (light gradient) is the most defining micro-site niche preference varible. Axis 1 of CCA, representing the highest variance within data, was highly significantly correlated with canopy density (CD). Analysis of variance (ANOVA) for constituting regression model of CCA also confirmed that CD was the only significant (p <0.01) variable (Appendix 5; 5.3). Correlation analyses among the microscale niche parameters (soil pH, soil moisture, organic matter depth and canopy density) revealed that of the four parameters only soil moisture and organic matter depth was significantly correlated (Apeendix 5.4). Variance partioning analysis further confirmed that among all the microsite variables CD had the highest relative explanatory power (> 64%) (Appendix 5.5). These analyses revealed that light is the most influential niche parameter and therefore, further niche preference analyses were conducted along the light gradient.
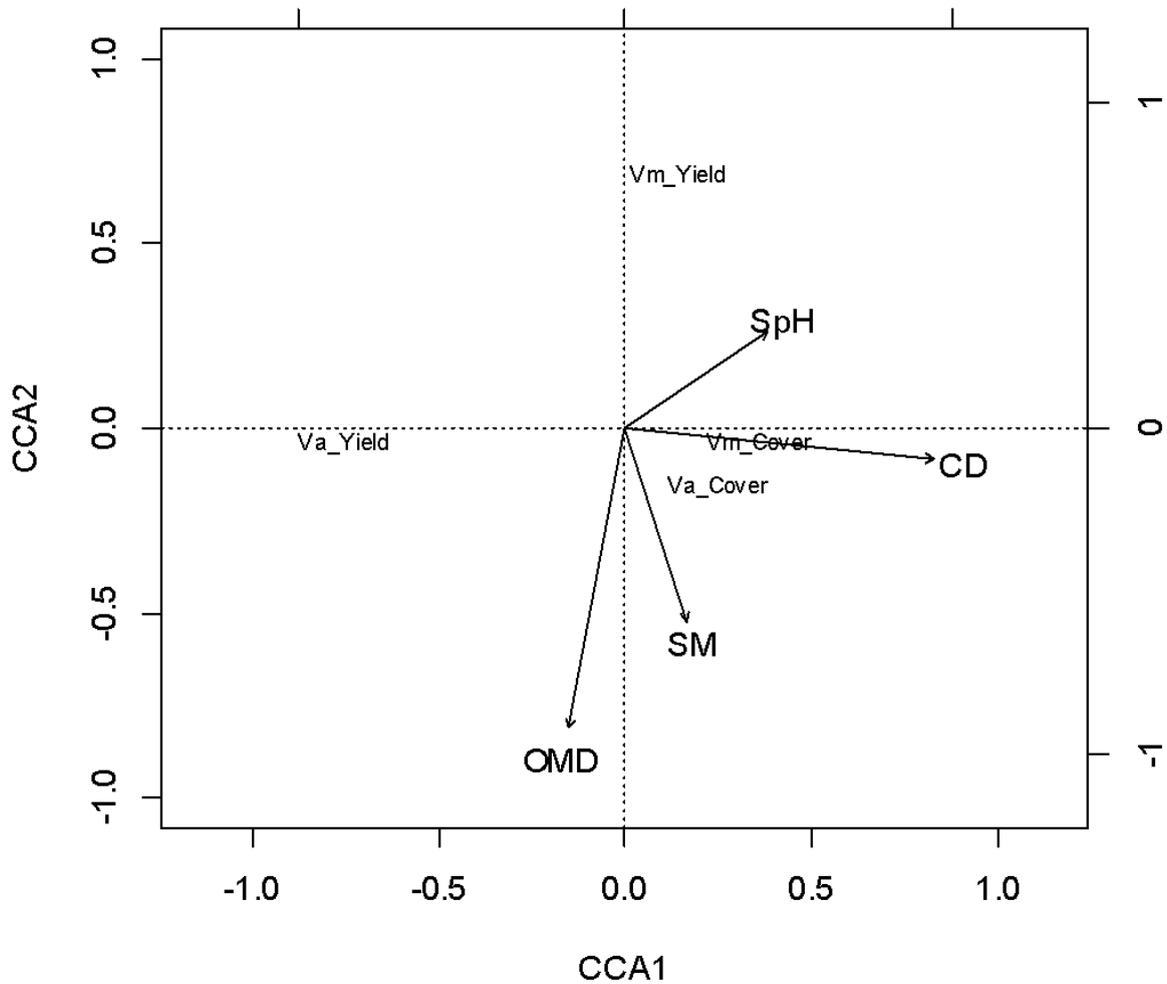
Figure 5. Canonical correspondence analysis (CCA) showing relative positions of the biological functions of the two blueberry species in relation to the microsite parameters converted into the ordination space. Among the microsite parameters, light gradient measured by canopy density (CD) was correlated with axis 1 (CCA1). Cover and berry yield of *V. myrtilloides* (Vm), and cover of *V. angustifolium* (Va) were also correlated with axis 1. SpH refers to soil pH, SM is soil moisture and OMD is organic matter depth.

Co-occurrence of blueberry species along niche axis (occurrence niche breadth)

The frequency of occurrence of congeneric blueberry species was compared along different levels of understory light (shade gradient) in natural habitats where both species co-occur (Fig. 6). Both *V. angustifolium* and *V. myrtilloides* occurred along the light gradient from open (100% light) to heavily shaded (< 5% light) (Fig. 6a). The fitted occurrence response curve (fitted regression line) was transformed into a occurrence fitness/performance curve by dividing the fitted values with maximum predicted value against light gradient. The occurrence pattern of these species was similar along the light gradient, with optimum occurrence of both species in open condition and gradually decreasing with decreasing light i.e., increasing shade level (Fig. 6b). The occurrence pattern of these two congeneric species along light gradient was not significantly different from each other (two-sample t $_{(n = 58)}$ = 1.1397, p-value = 0.257, effect size, Cohen's d= 0.299, power = 0.84). For fitness/performance curves were also not significantly different either (two-sample t $_{(n = 101)}$ = 1.8925, p-value = 0.0598, effect size, Cohen's d= 0.3766, power = 0.78).

In natural habitats, the occurrence niche breadths of *V. angustifolium* and *V. myrilloides* were respectively 0.389 and 0.404. The overall occurrence niche overlap of these two blueberry species was found to be 0.977.

Functional niche breadth and niche overlaps of congeneric blueberry species

For both blueberry species niche breadths were different for different functions. Niche breadth for growth (measured by cover) was higher than reproduction (measured by berry yield) for both species (Table 4). The differences in functional niche breadths were higher in natural habitats (in presence of competition) than in common garden experiment (in absence of competition) (Table 4). Functional niche overlaps for individual species were very high in common garden experiment (> 0.91) for both species, but much
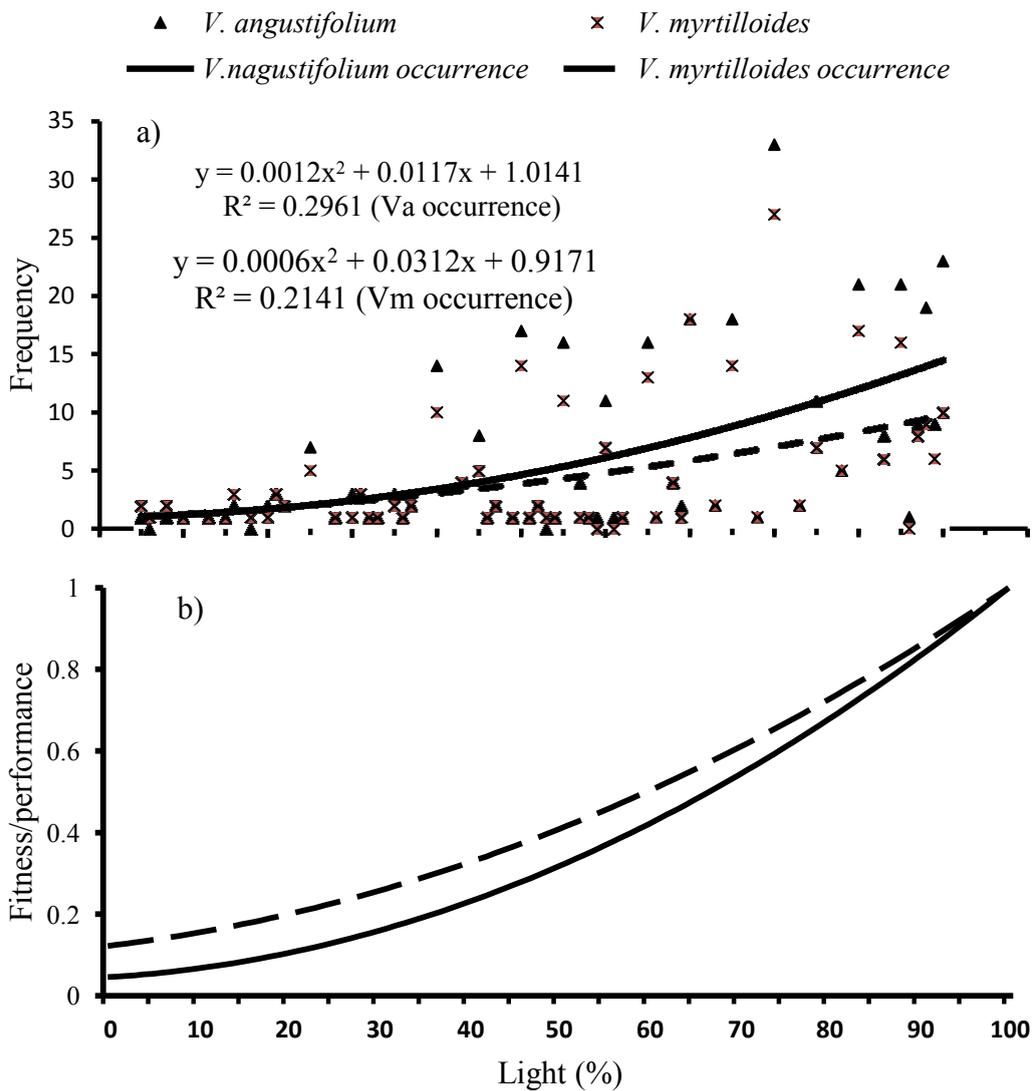
Figure 6. Niche breadth similarity between *V. angustifolium* and *V. myrtilloides* along a light gradient. Both species occurred across a light gradient showing similarity in frequency of occurrence (Fig. 5a) and occurrence fitness/performance (Fig. 5b).

lower in natural habitats, 0.53 for *V. Angustifolium* and 0.62 for *V. myrtilloides* (Table 5).

Growth niche (expressed by cover) and reproductive niche (berry yield) of both the species were almost identical in common garden (niche overlap of 0.99 and 0.94 respectively).. However, niche overlaps for both functions were much lower in natural habitats with niche overlap reduced to 0.79 for growth (lower by 0.20 than in common garden) and 0.58 for reproduction (lower by 0.35 than in common garden) (Table 5).

In common garden, the niche overlap between *V. angustifolium* growth and *V. myrtilloides* yield was 0.94 and that between *V. angustifolium* yield and *V. myrtilloides* growth was 0.90 indicating very high similarity of their niche preferences in absence of competition. However, functional niche overlaps between the two species was much lower in natural habitats. Niche overlap of *V. angustifolium* growth vs *V. myrtilloides* yield was 0.62 (lower by 0.22 than common garden) and *V. angustifolium* yield vs *V. myrtilloides* growth was 0.60 (lower by 0.31 than common garden) (Table 5).

Table 4. Functional niche overlaps between V. angustifolium and V. myrtilloides in natural habitats and common garden experiment.

Functions	Species	Natural habitats	Common garden
Niche breadth			
Growth	*V. angustifolium*	0.819	0.839
	V. myrtilloides	0.737	0.842
Reproduction	*V. angustifolium*	0.389	0.729
	V. myrtilloides	0.372	0.653
Niche overlaps			
Growth	*V. angustifolium* and *V. myrtilloides*	0.787*	0.994
Reproduction	*V. angustifolium* and *V. myrtilloides*	0.584	0.939
Growth and reproduction	within *V. angustifolium*	0.529	0.574
	within *V. myrtilloides*	0.615	0.684
	V. angustifolium growth and *V. myrtilloides* yield	0.616	0..870
	V. angustifolium yield and *V. myrtilloides* growth	0.599	0.921

* Niche overlap is measured in a scale of 0 to 1. 1 refers to complete overlap and no niche differentiation. Lower value of niche overlap indicates higher niche differentiation.

Species functional response curves along light gradient

To obtain species functional response curves for each species and function, regression models were fitted along light gradient. Linear models were found to be sufficient indicated by reasonable fit for berry yield of both species under common garden condition (Fig. 8 b). Model based recursive partitioning of canopy density, representing light gradient (with other microsite parameters as co-variables) found that regression line for growth of *V. angustifolium* and *V. myrtilloides* had three significant slope changes ($p < 0.05$, Appendix 6) indicating that a third degree polynomial was a reasonable criterion for fitting this responses along a light gradient both under natural condition (Fig. 7a, b) and in common garden experiment (Fig. 8a,b). All these polynomial regression models were compared based on AIC values with other candidate model fits and model with loweer AIC were chosen (Table 5 and 6; Appendix 7).

Converting response curves to fitness/performance curve

Since parameters (cover and berry yield) had different scales (Figs. 7 a, b & 8 a, b), the response curves were not readily comparable. I normalized each response curves by dividing with each curves' peak value converted them to fitness/performance curves as described in methods. This normalization makes all the performance/fitness curves rescaled between 0 and 1, with 1 being the optimum performance represented by the peaks of the curves. The resultant fitness/performance curves were comparable irrespective of function or species and they represented functional niche for growth and reproduction in natural habitats (Fig. 7c) and common garden (Fig. 8c).

Table 5. Statistical criteria for selection of regression model as response curves in relation to light gradient for *V. angustifolium* and *V. myrtilloides* growth (cover) and reproduction (berry yield) in natural habitats

SL	Model type	R squared	p-value	AIC	Δ AIC
Natural habitats					
V. angustifolium cover					
1	Linear model	0.131	0.367	1550.40	
2	2nd degree polynomial	0.176	0.6461	1552.33	-1.93
3	3rd degree polynomial	0.434	8.192e-05	1533.38	18.94
4	4th degree polynomial	0.463	2.355e-05	1530.15	3.24
5	5th degree polynomial	0.503	2.668e-05	1530.00	0.15
V. angustifolium yield					
6	Linear model	0.263	0.001877	-6.14	
7	2nd degree polynomial	0.377	0.0001435	-12.29	6.15
8	3rd degree polynomial	0.384	0.0002769	-11.62	-0.67
9	4th degree polynomial	0.432	0.000604	-10.28	-1.34
10	5th degree polynomial	0.445	0.001475	-8.35	-1.92
V. myrtilloides cover					
11	Linear model	0.061	0.2604	759.37	
12	2nd degree polynomial	0.198	2.875e-08	727.50	31.87
13	3rd degree polynomial	0.242	8.302e-08	728.35	-0.85
14	4th degree polynomial	0.249	2.985e-07	730.13	-1.77
15	5th degree polynomial	0.250	5.188e-07	730.65	-0.52
V. myrtilloides yield					
16	Linear model	0.052	0.00299	36.86	
17	2nd degree polynomial	0.079	0.01001	38.45	-1.58
18	3rd degree polynomial	0.085	0.02597	40.37	-1.92
19	4th degree polynomial	0.099	0.03893	41.51	-1.14
20	5th degree polynomial	0.099	0.04813	42.39	-0.88

Table 6. Statistical criteria for selection of regression model as response curves in relation to light gradient for *V. angustifolium* and *V. myrtilloides* growth (cover) and reproduction (berry yield) in common garden experiment

SL	Model type	R squared	p-value	AIC	Δ AIC
Common garden					
V. angustifolium cover					
1	Linear model	0.019	0.248	615.12	
2	2nd degree polynomial	0.306	3.351e-06	592.19	22.9263
3	3rd degree polynomial	0.454	5.115e-09	576.87	15.3331
4	4th degree polynomial	0.471	9.427e-09	576.73	0.1348
5	5th degree polynomial	0.494	9.421e-09	575.45	1.2778
V. angustifolium yield					
6	Linear model	0.111	0.0042	716.59	
7	2nd degree polynomial	0.143	0.0048	715.96	0.62
8	3rd degree polynomial	0.143	0.0142	717.95	-1.99
9	4th degree polynomial	0.143	0.0321	719.92	-1.96
10	5th degree polynomial	0.145	0.0603	721.79	-1.87
V. myrtilloides cover					
11	Linear model	0.081	0.0154	599.99	
12	2nd degree polynomial	0.312	2.438e-06	581.11	18.89
13	3rd degree polynomial	0.447	7.732e-09	567.33	13.78
14	4th degree polynomial	0.518	4.366e-10	559.50	7.82
15	5th degree polynomial	0.530	8.934e-10	559.67	-0.16
V. myrtilloides yield					
16	Linear model	0.082	0.0145	697.11	
17	2nd degree polynomial	0.164	0.0020	692.35	4.761
18	3rd degree polynomial	0.170	0.0051	693.85	-1.50
19	4th degree polynomial	0.170	0.0128	695.85	-1.20
20	5th degree polynomial	0.206	0.0082	694.68	1.165

a) $\times$ Va_Cover $\blacksquare$ Vm_Cover —— *V. angustifolium cover* —— *V. myrtilloides cover*

$y = 0.0005x^3 - 0.0908x^2 + 4.5583x - 24.558$
$R^2 = 0.434$ (Va cover)

$y = -0.0002x^3 + 0.0193x^2 - 0.3053x + 11.215$
$R^2 = 0.2417$ (Vm cover)

b) Va_Yield $\times$ Vm_Yield —— *V. angustifolium yield* —— *V. myrtilloides yield*

$y = -0.0001x^3 + 0.0205x^2 - 0.638x + 7.5765$
$R^2 = 0.3842$ (*V. angustifolium yield*)

$y = -6E-05x^3 + 0.0062x^2 + 0.0173x + 2.5436$
$R^2 = 0.0849$ (*V. myrtilloides yield*)

c) —— *V. angustifolium cover* — · *V. myrtilloides cover*
— — *V. angustifolium yield* — · *V. myrtilloides yield*

Figure 7. Response curves of different biological functions of blueberry species in natural habitats along a light gradient. Curved lines in Figs. 6a,b represent respectively growth and reproduction of *V. angustifolium* (Va) and *V. myrtilloides* (Vm). Equations represent their fitted regression model. Fig. 6c shows the rescaled response curves of comparable functional fitness/performances.
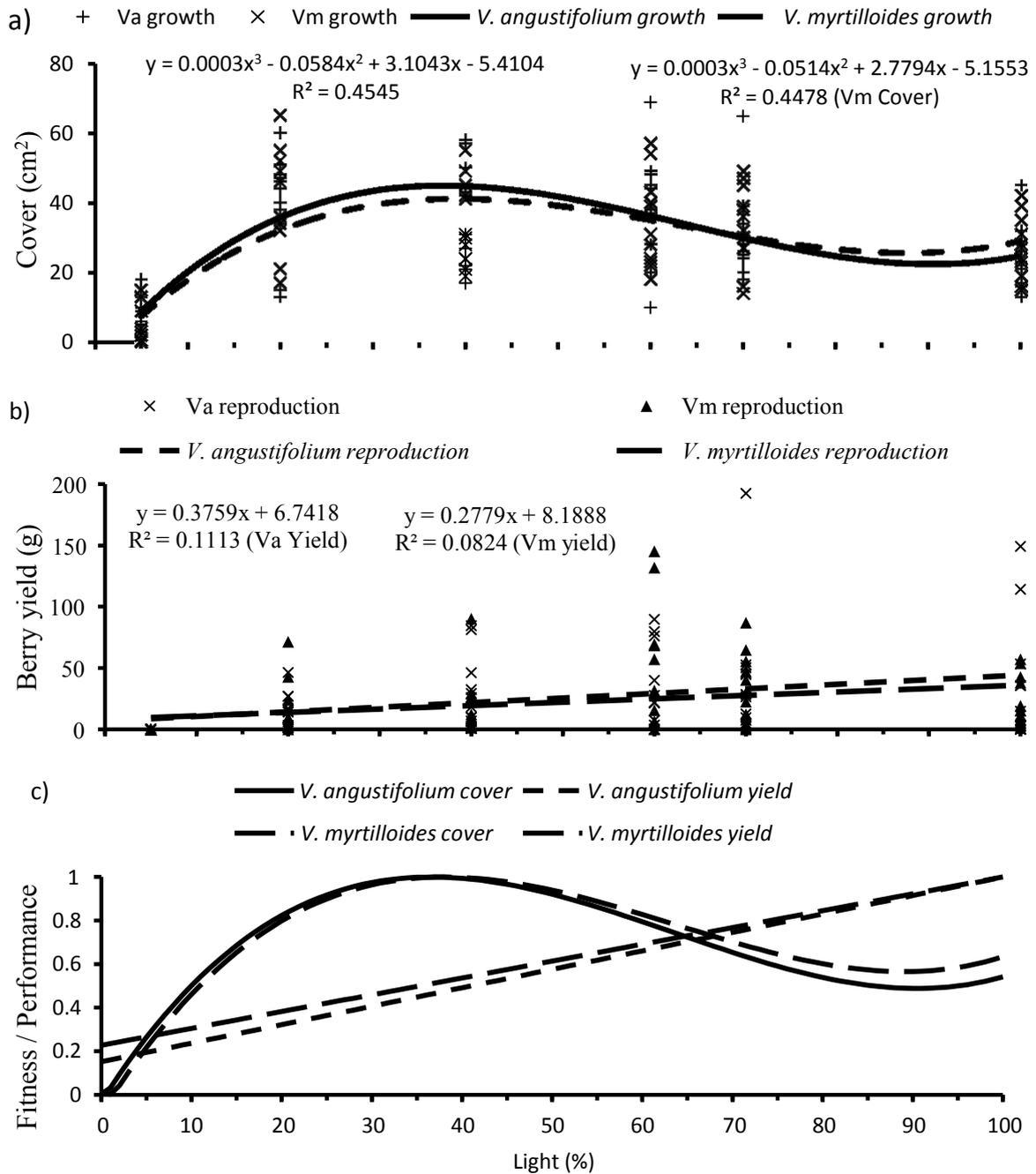
Figure 8. Response curves of different biological functions of wild blueberry species along a light gradient under competition free condition. Lines in Figs. 7 a represent cover (growth) and 7 b represent yield (reproduction) response of *V. angustifolium* (Va) and *V. myrtilloides* (Vm). Equations represent their fitted regression model. Fig. 7c shows the rescaled curves of comparable fitness/performance.

Comparing functional niche of individual species

Comparison of niche preference for different functions using fitness/performance curves makes it clear that both species have contrasting optimum for different functional niches and t-test values confirmed the visual interpretation with high power (Table 7) that both *V. angustifolium* and *V. myrtilloides* had distinct functional niche preference in terms of growth and reproduction under both natural habitat and common garden experiment. For *V. angustifolium* growing in natural habitats and common garden experiment reproduction function peaks at high light while the vegetative growth (measured by cover) had high values in high light followed by a dip at around 75 - 80% light, then rising again with the peak performance around 30-35% light (Fig. 9a). Reproductive fitness of *V. angustifolium* gradually increased with increasing light with peak performance at 100% light. *V. angustifolium* in common garden shows similar trend in functional niche preference between growth and reproduction (Fig. 9d).

Fitness/performance curves of *V. myrtilloides* exhibit significantly contrasting patterns between natural habitats and in common garden (Figs. 10 & 11, Table 8). In common garden, the fitness/performance curves were similar to *V. angustifolium* with growth peaking in lower light (35%) while optimum yield in high light (100%). However, in natural habitats, both growth and reproductive performance followed similar patterns peaking in partial shade (Fig. 8 b). The reproductive function (yield) still favored conditions with relatively more light. Its optimum reproduction (berry yield) was at around 82% light while the vegetative growth performance peaked around 70% light (Fig. 11).
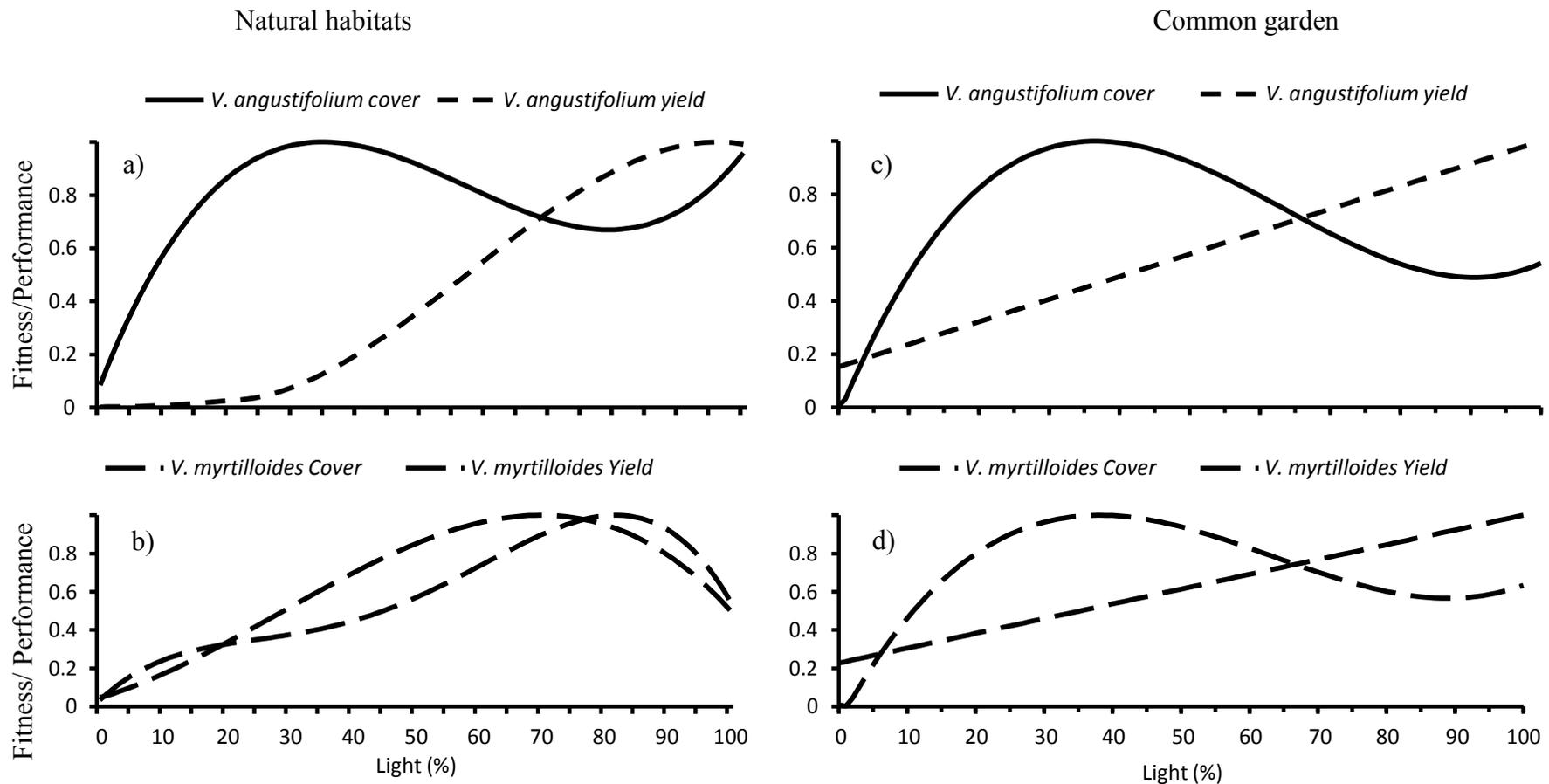
Figure 9. Species-wise fitness/performance curves of growth (cover) and reproduction (berry yield) of *V. angustifolium* and *V. myrtilloides* in natural habitats under competition (9 a, b) and in common garden without competition (Fig. 9 c,d). For both species, optimum condition for performing different biological functions (growth and reproduction) differs in natural habitats in presence of competition and in common garden experiment without competition.
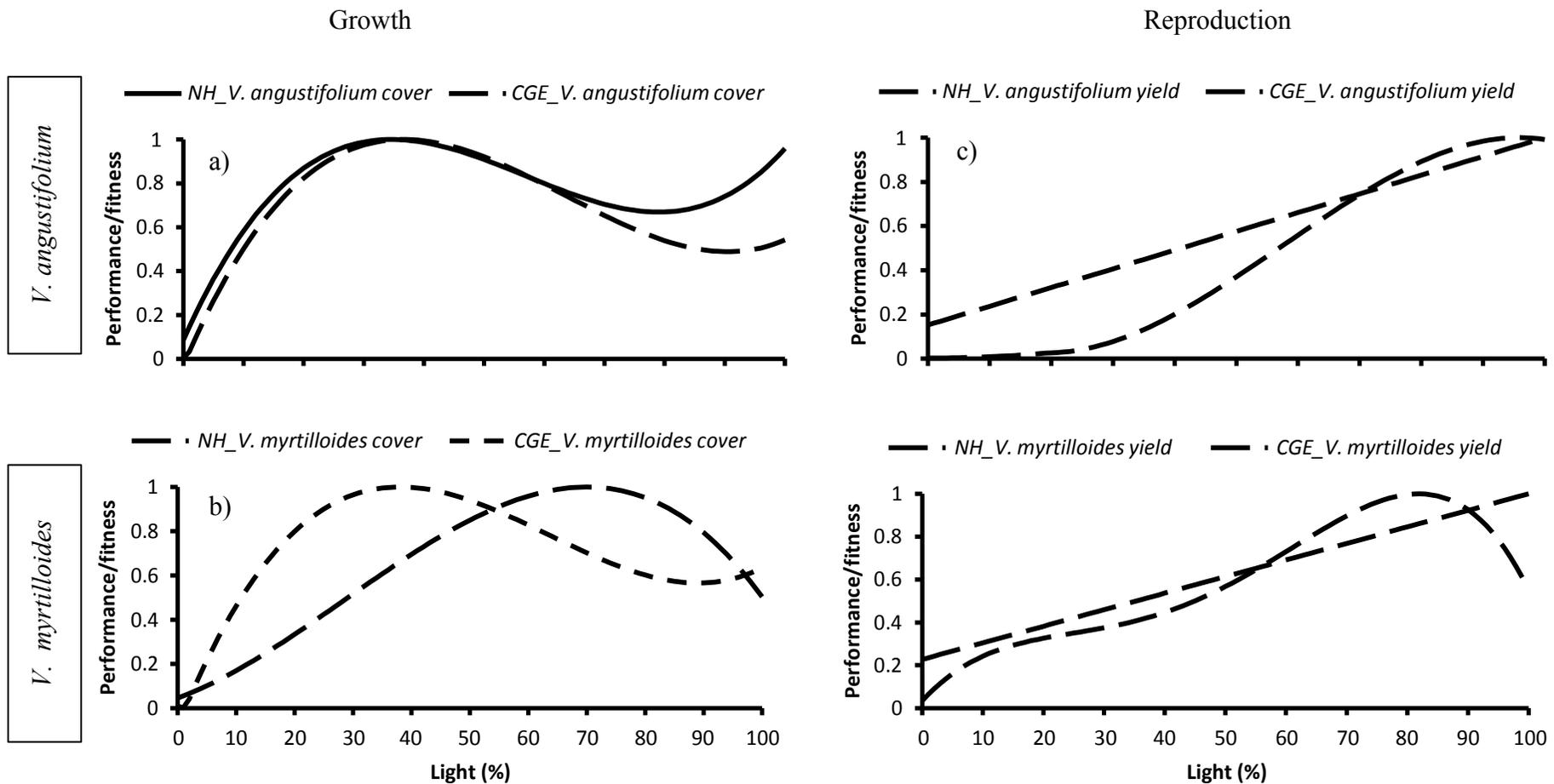
Figure 10. Comparison of fitness/performance curves of growth (cover) (Fig 10 a, b) and reproduction (berry yield) (Fig. 10 c, d) of *V. angustifolium* and *V. myrtilloides* in natural habitats (NH) under competition and in common garden (CGE) without competition. Growth response of *V. angustifolium* to light (%) in natural habitats and in common garden experiment was very similar. But growth response of *V. myrtilloides* differed in natural habitat and common garden.
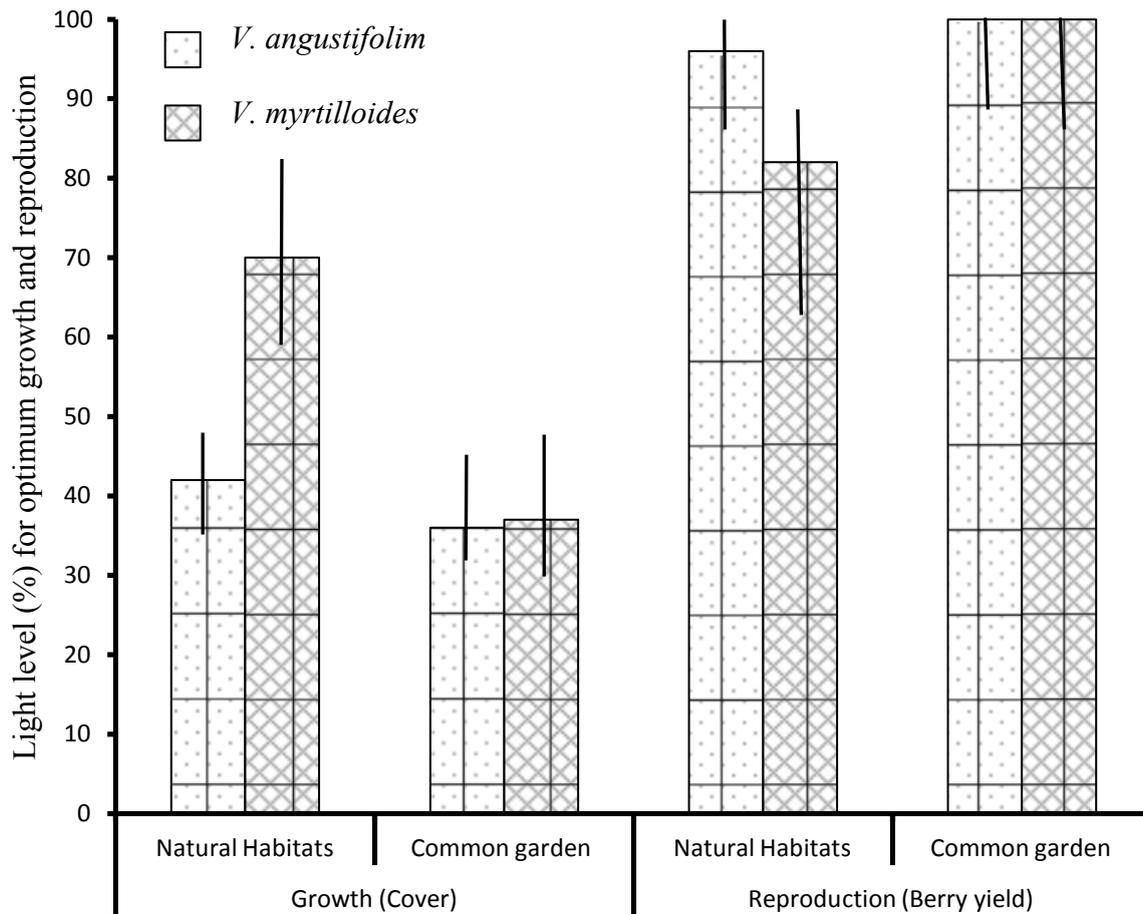
Figure 11. Light levels exhibiting optimum growth and reproduction of *V. angustifolium* and *V. myrtilloides* in natural habitats and in common garden. In natural habitats, both species showed difference in preferred light level for optimum performance. Growth of *V. angustifolium* was optimum at 35% light while *V. myrtilloides* had growth optimum at 70% light. For reproduction, *V. angustifolium*'s optimum was at 96% light and that for *V. myrtilloides* was at 82% light. In common garden, both species had optimum growth at around 25% light and optimum reproduction at 100% light (completely open). Error bars are at 95% confidence interval.

Table 7. Comparing functionl niche preferences of *V. angustifolium* and *V. myrtilloides* through t-test based on predicted values of modeled response curves.

	tstatistics	p-value	Effect size	Power
Natural habitat				
V. angustifolium cover vs. yield	8.0892	1.461e-12	1.6098	0.999
V. myrtilloides cover vs. yield	4.9284	3.293e-06	0.9808	0.983
V. angustifolium cover vs. *V. myrtilloides* cover	4.1573	6.808e-05	0.8273	0.962
V. angustifolium yield vs. *V. myrtilloides* yield	9.3621	2.478e-15	1.8631	0.999
Common garden				
V. angustifolium cover vs. yield	3.4608	0.0006	0.6887	0.921
V. myrtilloides cover vs. yield	3.0841	0.002	0.6138	0.897
V. angustifolium cover vs. *V. myrtilloides* cover	0.5814	0.562	0.1157	0.676
V. angustifolium yield vs. *V. myrtilloides* yield	1.1293	0.2602	0.2247	0.683
Natural habitat vs. Common garden				
V. myrtilloides cover	3.0984	0.002	0.6166	0.899
V. angustifolium yield	0.8197	0.413	0.1631	0.657
V. myrtilloides yield	2.6793	0.008	0.5332	0.865

Comparing functional niches of co-occurring species

Congeneric blueberry species demonstrated different functional niche preferences. In natural habitats, preferred niches for growth and reproduction of *V. angustifolium* and *V. myrtilloides* exhibited contrasts (Fig. 12 a, b) but in common garden, the functional niches of the two species were strikingly similar (Fig. 12 c, d). *V. angustifolium* preferred high light for growth. However its optimal growth was at partial shade (around 70% light). On the other hand, growth of *V. myrtilloides* peaked at high shade (around 30% light) and at this light intensity growth of *V. angustifolium* showed a dip. In other words, as growth of *V. angustifolium* starts to increase with increasing light that of *V. myrtilloides* starts decrease and vice versa.

In natural conditions, the reproductive performance of the two species peaked at two different points along the light gradient. Peak reproduction of *V. angustifolium* was at > 95% light while *V. myrtilloides'* reproduction was highest at around 82 % light (Figs. 10 & 11). However, both species showed a gradual decreasing trend in berry production with increasing shade after the light optima. Berry reproduction of *V. angustifolium* diminished around 20% light while *V. myrtilloides* continued berry production until canopy light was 10% indicating that these two co-occurring species have different functional niche preferences in performing growth and reproduction.

Trade-off for growth and reproduction between congeneric blueberry species

Analyses of cover data of *V. angustifolium* and *V. myrtilloides* from 1 x 1 m plots demonstrate that these two co-occurring species exhibit growth trade-off (Fig. 13). The trade-off line further confirms that growth of *V. angustifolium* and *V. myrtilloides* is inversely related.
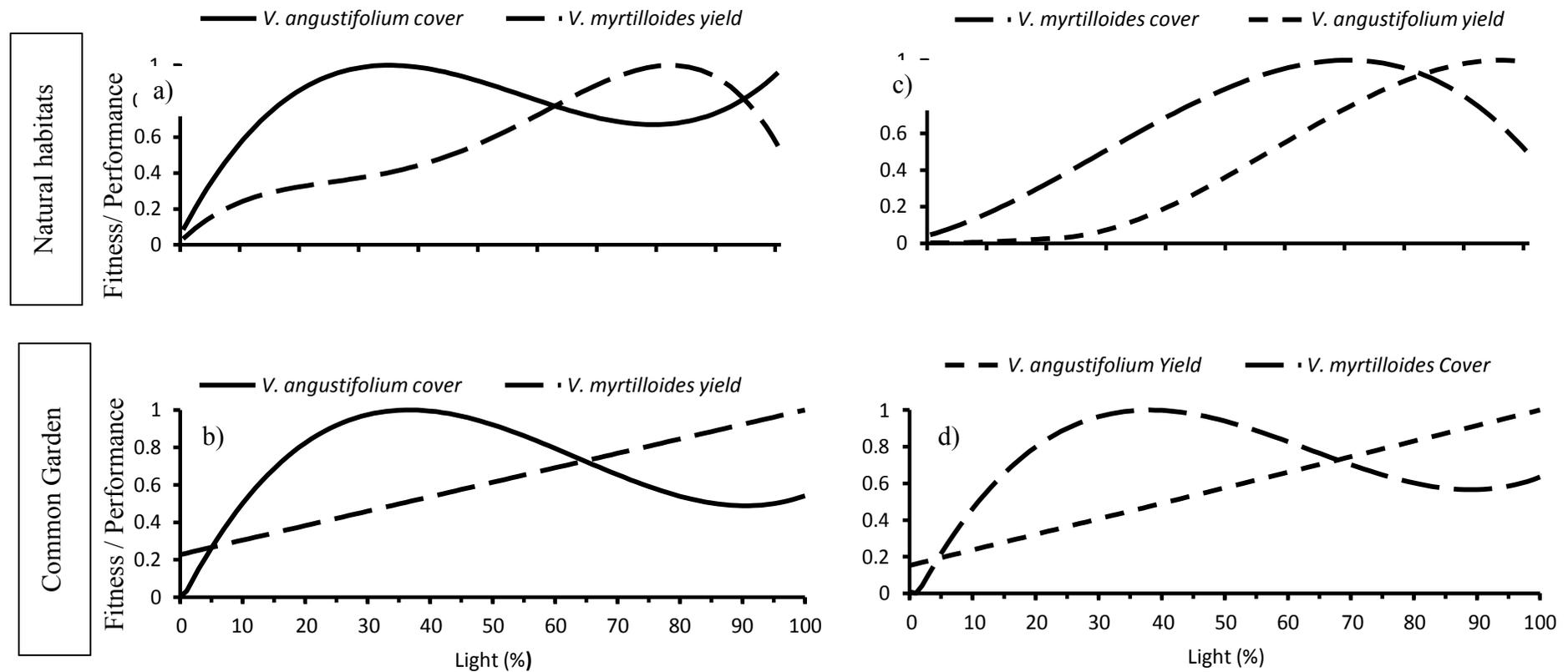
Figure 12. Fitness/performance curves to compare niche preferences for growth and reproduction between *V. angustifolium* and *V. myrtilloides*. In natural habitats growth (cover) and reproduction (yield) had contrasting optima; *V. angustifolium*'s high growth in open (100% light) and again in lower light (30%) correspond with lower yield of *V. myrtilloides* (Fig. 10 a, b). Growth increase of *V. myrtilloides* corresponds with the growth decline of *V. angustifolium* between 75 and 80% canopy light. Optimum reproduction (berry yield) *V. angustifolium* was at open (100%) light while that of *V. myrtilloides* was at 82% light (Fig. 10 a, b). In common garden (10 b, d), the growth niches of the two species are very similar. The similarity is also evident for reproductive niche (10 b, d) with both *V. angustifolium* and *V. myrtilloides* preferring open condition with berry yield gradually increasing with increasing light availability.

The overall tradeoff curve shows that there was a negative relationship between growth of *V. angustifolium* and *V. myrtilloides* i.e., increasing growth of one species corresponded with decreasing growth of the other. However, as the growth responses of these two species are non-linear along light gradient in natural habitats (Fig. 7c), the degree and direction of the relationship varied at different light level (Fig. 13). At low lights, where the overall growth potential is low and thereby less possibility of competition for growing space, the two species showed a positive correlation in terms of growth (curves at 10% and 25% light level; Fig. 13, Table 8). This also corresponded with response curves of these two species (Fig. 7c) where both species' showed an increasing trend in growth under low light. However, as both the species reached their increased growth potential (around 50% light availability) competition increases and trade-off for space become evident from the negative slopes of trade-off curves (curves at 50%, 75% and 100% light; Fig. 13). At 70-80% light *V. myrtilloides* had higher growth than *V. angustifolium* (Fig. 7c) before regaining its growth at 100% light. Nonetheless, higher growth of one species at moderate to low light caused lower growth of the other resulting in a negative slope of their trade-off curves.

The trade-off pattern for reproductive effort between the two blueberry species in natural habitats was not as distinct as the growth trade-offs are (Fig 14), the trade off curves for reproductive effort were not statistically significant either (Table 8). The reproductive trade-off was negative at moderate (46-50% light) with limited overall berry yield. The berry yield for both species increased under higher light, but the trade-off became flatter than those in of moderate light.
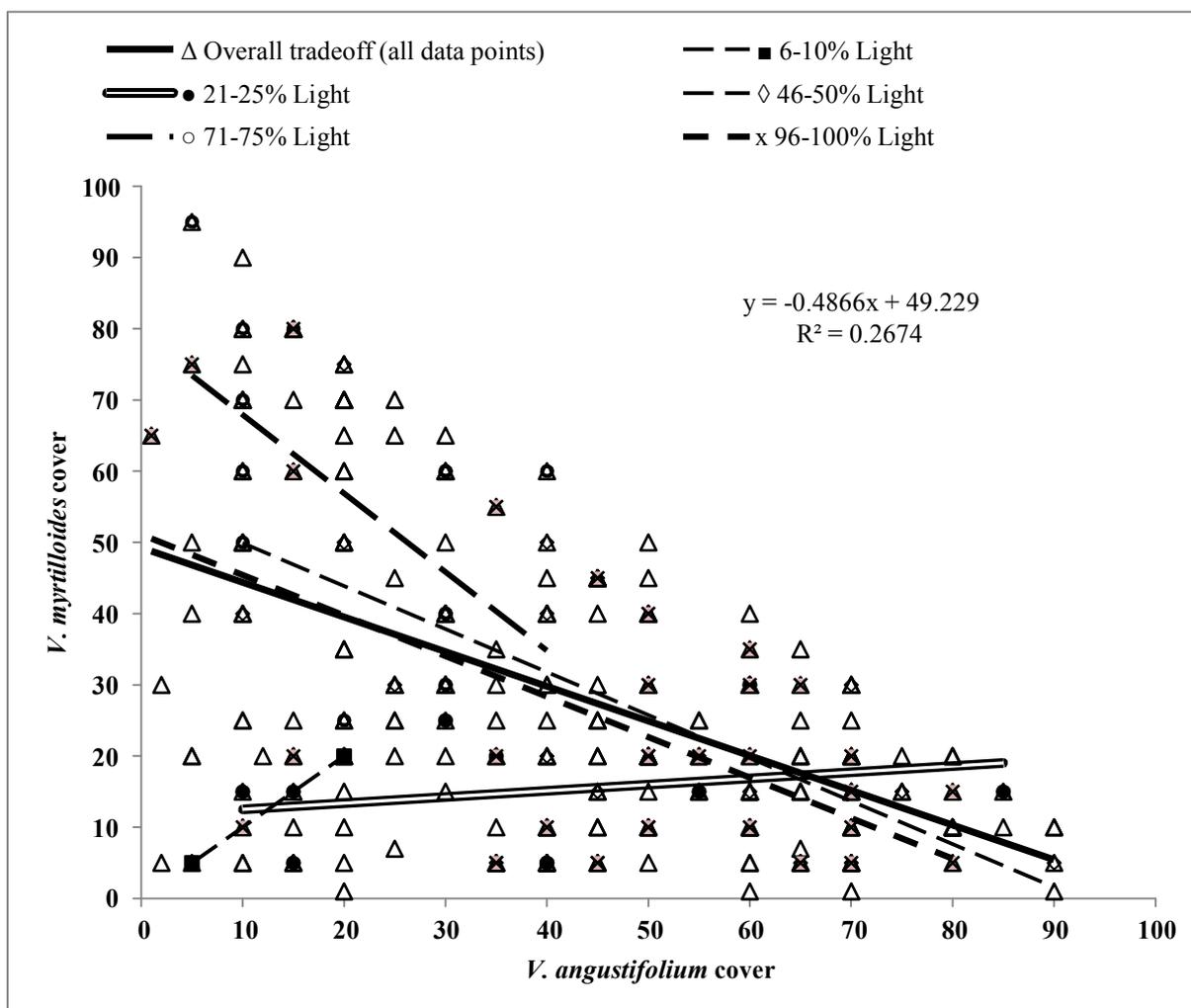
Figure 13. Growth trade-offs between co-occurring *V. angustifolium* and *V. myrtilloides* in response to light within 1 x 1 m plots in natural habitats. The straight lines demonstrate growth trade-off curves between the two co-occurring blueberry species at 10, 25, 50, 75 and 100% light and overall trade-off pattern. Note that from very low light to gradually increasing light level the trade-offs shifts from positive (6-10% light)to almost neutral (21-25% light) to negative (from 50% upto 100% light).
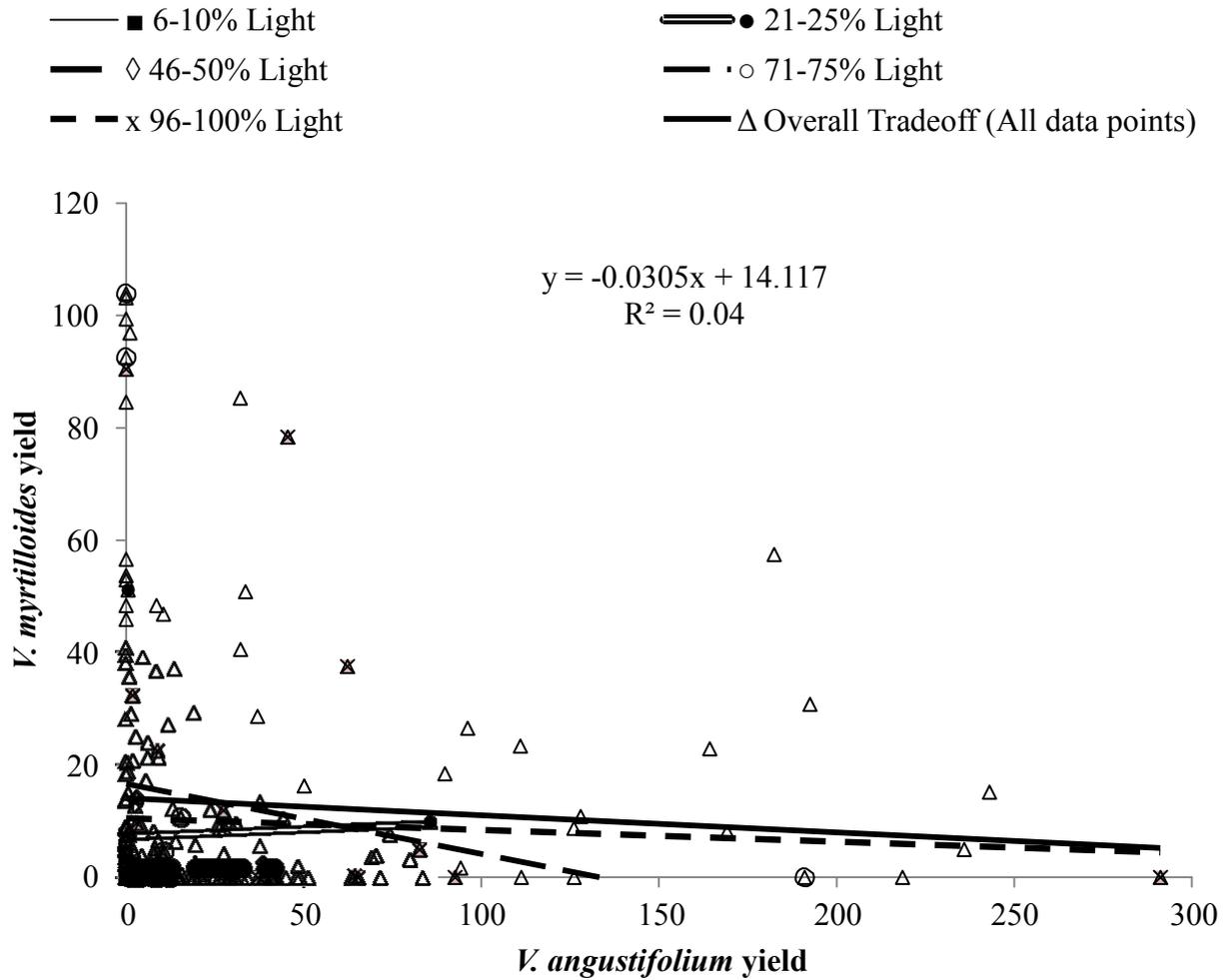
Figure 14. Trade-offs in reproductive effort between co-occurring *V. angustifolium* and *V. myrtilloides* in response to light within 1 x 1 m plots in natural habitats. The lines demonstrates growth trade-off curves between the two co-occurring blueberry species at 6-10, 21-25, 46-50, 71-75 and 96-100% light and the solid straight line represents overall trade-off pattern. Note that overall reproductive trade-off is almost neutral. Reproductive trade-off is strongly negative at 46-50% and 71-75% light.

Table 8. Explanatory power (R^2) and statistical significance (p-value) of trade off curves between *V. angustifolium* and *V. myrtilloides*

Trade-off curves	R^2 Value	P value
Trade-off for growing space		
Cover 6-10% light	0.099	0.976
Cover 21-25% light	0.0567	0.507729
Cover 46-50% light	0.4404	0.003679
Cover 71-75% light	0.3417	0.022106
Cover 96-100% light	0.3265	5.14E-04
Overall cover	0.2674	1.44E-18
Trade-off for reproductive resources		
Yield 6-10% light	0.012	0.886685
Yield 21-25% light	0.002	0.901468
Yield 46-50% light	0.0839	0.25937
Yield 71-75% light	0.0304	0.534055
Yield 96-100% light	0.0138	0.514276
Overall yield	0.002	0.477065

Discussion

The results support my hypotheses that (i) phylogenetically close species are similar in their spatial distribution across scales, (ii) each species has different niche (light) preferences to perform their different biological functions and (iii) in natural habitats with competition, these closely related species differentiate their functional niches. When they co-occur in their natural habitats the two blueberry species exhibited distinct niche differentiation in response to canopy light. The functional niche overlaps between the two species (Table 4) and their fitness/performance comparison curves (Figs. 7-9) and peak performance levels (Fig. 11), provide further evidence in support of the hypothesis that co-occurring congeneric species differentiate their functional niches. My results also showed that these two congeneric species exhibited almost identical niche with respect to growth (cover) and reproduction (berry yield) along a light gradient in competition free common garden experiment confirming their genetic similarity to respond to environmental conditioning. The common garden plants were grown as isolated clumps and weeded regularly to remove the competitive neighboring plants. These results are significant because to my knowledge this is the first study that clearly demonstrated the nature of niche differentiation in closely related co-occurring plant species in natural habitats and in a competition-free common garden experiment. Here I show how congeneric clonal species can co-exist in the same physical niche space by employing functional niche differentiation. In natural community there are large overlaps in functional niche breadths of the two blueberry species. However, they do not employ functional niche differentiation if they are in competition-free environment. For both species the differences in functional niche breadths were higher in natural habitats (in presence of competition) than in common garden experiment (in absence of competition). These results have evolutionary significance because it shows that these coexisting species use the mechanism of functional niche differentiation when needed.

Spatial distribution of closely related species is similar

Research on ecological niche has been advancing in two directions based on i) Grinnellian niche concept by assessing spatial niche to estimate geographic range of species occurrence and ii) Eltonian concept of niche by quantifying niche to understand potential biological interactions among similar species at the micro scale (Krebs 2013). My study spans both these niche concepts and starts with assessing similarity of spatial niche distribution of closely related blueberry species. For seed dispersed species, there is strong evidence that related species occur in similar habitats across large regional landscapes for both terrestrial (Bourret *et al.* 2012) and aquatic species. Within similar habitat competition for food can contribute to the segregation of sympatry across vertical water profiles as reported for adult cutthroat trout (*Salmo clarki*) and dolly varden (*Salvelinus malma*) (Andrusak & Northcote, 1970). For plant species the co-existence of related species is mostly reported from tropical ecosystems and they are mostly seed regenerating species (Silvertown 2004). In my study at regional scale, both blueberry species were found in all the study eco-districts of northwestern Ontario.

Generally speaking phylogenetically closely related and ecologically similar species differ in very few niche dimensions and thereby are more likely to occur together in similar habitats (Burns and Strauss 2011) where micro-scale heterogeneity might help their persistence. Silvertown and Wilkin (1983) experimentally demonstrated that spatial heterogeneity of microhabitats play a role in the co-existence of congeneric plants. My study showed that as the spatial scale becomes larger, the evidence of co-existence of the two blueberry species increases. In 20 x 20 cm plots, the congeneric blueberry species occurred together in 54% of the cases while the frequency of co-occurrence in 1 x 1 m plots was over 69%. At 30 m transect level, both species were found at every transect making the frequency of co-existence 100% at this spatial scale.

Plant species can coexist by habitat differentiation in different successional stages, often referred to as 'successional niche' (Whittaker 1969). Patch dynamics is a recognized factor in species co-existence in regional plant communities (Whittaker and Levin 1977). However, patch-dynamics mechanism is understood as 'non-equilibrium' coexistence (Pickett 1980). Connell (1979) noted that species are only non-equilibrium at the local level of individual patches or sites, but equilibrium at regional scales. However, regional co-existence does not confirm co-occurrence at micro-site level where biotic interactions such as competition play direct role. In this study since both blueberry species were found across a chronosequence of secondary succession after natural and anthropogenic disturbance in boreal mixed-wood forests, patchy habitat differentiation mechanism is not applicable to these congeneric species. In fact the two species in question were found in close proximity to each other under very similar microsite condition, indicating that their coexistence mechanism is not limited only to sorting themselves spatially in relation to favorable micro-scale heterogeneity. They adopt functional differentiation while co-occurring in close proximity.

The clonal nature of these two species is another interesting phenomenon. Their ability to regenerate from belowground rhizomes immediately after disturbance as early colonizers eliminates the concern for temporal variation of immigration or occurrence along succession chronosequence. Clonal propagation ability also reduces the effect of the dispersal factor often argued as one of the major explanatory mechanism of co-existence, especially by neutral theory (Hubbell 2001). Clonal propagation also allows both species to emerge in close proximity and thus provides a unique opportunity to study co-existence mechanism of spatially non-explicit congeneric species. This sort of co-existence mechanism has not been reported in the literature.

Phylogenetically closely related species co-occur at the microhabitat-scale

Congeneric *V. angustifolium* and *V. myrtilloides* were found to be co-occurring at both macro and microhabitat levels. Results on functional niche differentiation of this study exemplify the existence of this phenomenon of species co-existence. Phylogenetically related species tend to be ecologically similar (Burns and Strauss, 2011) and their closeness in evolutionary traits influences the structure of a community (Tan *et al.* 2012). Silvertown *et al.* (2001) reported that congeneric species in natural habitats are more abundant than expected in randomly assembled communities. Williams (1947) also showed that species–genus ratios in several plant and insect communities were higher than expected. This implies that relevant traits have evolved differences so that congeneric species are able to coexist. Silvertown *et al.* (2001) found that community structure was the cumulative result of niche segregation arising at different levels of phylogenetic links and hence niche differences are an accumulation through the evolutionary history of constituent species. Phylogenetically closely related species' coexistence in several plant communities suggests that the ecological traits affecting the similarity of habitat 'choice' between congeners evolve at the level of genus and above. Since stable coexistence requires some ecological differences between species the traits that determine the ability of closely related species to coexist have evolved later than their speciation and towards the tips of the phylogenetic tree (Silvertown *et al.* 2001). This is because to trigger proactive differentiation, the two species has to be sufficiently similar (sensu Chesson 2000).

My study found that these two species demonstrate ability to utilize similar micro site condition to perform a different function which not only enable them to mediate competition, but also help them adopt alternate strategies to persist in the community mix. When one species enhances growth, other ensures reproductive effort to sustain them over time. These alternate life strategies also help them switch efforts across succession chronosequence

without switching their spatial location. Along disturbance chronosequence with increasing time since disturbance, vigor of taller shrubs and trees restricts availability of light to lower plants. The ability of these species to adapt to the varying light condition helps them to remain functional in one way or another over the temporal scale.

Intra and inter species functional niche differentiation

Intra-species functional niche differentiation between growth and reproduction is evident under both common garden experiment and in natural habitats (Figs. 10 & 11). Niche differentiation is mostly described as a mechanism of interspecies coexistence (Farigone and Tilman, 2002). However, resource utilization is mediated within species as well (Lepik *et al.* 2012). Functional niche concept can explain this complementary resource use within same species as well. My study found that the same species perform different biological functions at different levels of the same resource (Figs. 7-8, 10). This means that same species can partition niche even along one particular resource gradient (such as light) by doing different function at different level of resource availability. This ensures maximum utilization of available resources in stressful condition and also helpful for survival and functional role of a particular species along dynamic resource gradient.

Earlier experimental studies with shade treatments also revealed that biomass and berry production for in *V. angustifolium* decreases under shade (Hoefs and Shay 1981). Shade, provided by two layers of cheesecloth, significantly reduced the number of flower buds compared to full sunlight (Hall and Ludwig 1961). Hall *et al.* (1972) showed that light intensity alters the rate of photosynthesis in *V. angustifolium* like most other temperate species. Although *V. myrtilloides* was able to persist in both open and closed canopy boreal mixedwood forests (Moola and Mallik 1998; Kloet and Hall 1981), its reproductive performance was greatest under partial shades associated with shelterwood cutting. In heavy shade *V. myrtilloides* showed significant morphological and biomass allocation plasticity

(Moola and Mallik 1998). Other authors also noted different shade response among blueberry species (Smith 1962) and provenances of New Brunswick and Manitoba (Hoefs and Shay 1981). My findings are in corollary with all these studies regarding occurrence and reproductive response to a light gradient. However, earlier studies did not compare the functional aspects (growth and reproductiom) between or among species and did not explicitly focus on distinguishing growth and reproductive responses of the two species. This study brought further insights with respect to variation of functions (growth and reproduction) of these two species along a light gradient in natural habitats and in common garden experiment.

The growth function of both species in natural habitats responded with higher vegetative cover at open (100%) light condition and also under low light particularly for *V. myrtilloides* (Figs. 7 & 8). This bi-modal response can be explained by two different mechanisms. In the open (100%) light condition, cover (%) increase as the plants would tend to produce more vegetative shoots with individual shoots facing apical growth inhibition due to high light. On the other hand, the increase in cover (%) under higher shade is most likely due to biomass allocation for resource acquisition (more investment to gain more photosynthates) as vitally important light resource starts to diminish. Although in the common garden experiment, both species showed this resource acquisition strategy, *V. myrtilloides* does not show such growth increase in low light in natural habitats (Figs. 9 & 11). In the competitive environment, *V. myrtilloides* probably would allocate more resources to maintenance of acquired body mass (as a resource allocation strategy of limiting expenditure to remain within curtailed energy budget) and likely to enhance a facilitative resource sharing mode from nearby ramets as stress from resource limitation increases. Resource sharing by clonal plants is a common phenomenon also called 'parental care subsidy' to achieve tolerance to shade (Aarssen 2008). However, I found that reproductive

allocation is always higher in both blueberry species with higher resource (light) availability in open condition. The shift of optimum reproductive performance of *V. myrtilloides* (Figs. 9 & 11) towards slightly lower light (82%) in natural habitats (Fig. 11) is most likely due to an adjustment to ensure coexistence in the community through complementary preference for functional niche. Aarssen (2008) suggests reproductive economy of clonal plants (here referring to individual rooted units) is a driving force in their success in understory community by avoiding the cost of sexual reproduction. Therefore, both species have drastically reduced berry production under shaded environment.

Co-occurring congeneric species coexist through functional niche differentiation

Functional niche differentiation between these two species is almost non-existent in the common garden where they were grown in separation, but was very distinct in natural habitats where they co-occurred (Figs. 10 & 12). Both species showed a shift in their optimal growth and reproductive preference with respect to light availability in the natural habitats. This is a significant finding as it explains a fundamental mechanism of congeneric species co-existence under competitive environment. For *V. angustifolium,* the shift in niche preferences in terms of vegetative and reproduction optima were nominal, but for *V. myrtilloides* the shifts were conspicuous. Whittaker (1960) reported that more niche overlap would mean more complete intermixing of species and less niche differentiation. In this study, both species' functional niches had almost complete overlap in the common garden while their overlaps were significantly reduced in natural habitats where they co-occurred (Table 5). This supports my hypothesis that functional niche differentiation contributes to congeneric species coexistence.

Species coexistence is favored by functional trait dissimilarity to avoid competitive exclusion (MacArthur and Levins 1967; Pacala and Tilman 1994). The difference in life history traits or functional traits representing growth and reproduction are often an indicator

of functional niche differentiation in co-occurring species. Niche differentiation, whereby co-occurring species differ in their resource acquisition and utilization traits, decreases the intensity of inter-specific competition (Gross *et al.* 2007) and promotes the complementary resource use in space and time (Silvertown 2004; Carroll *et al.* 2011; Maire *et al.* 2012). Modeling species with similar niches, Shmida and Ellner (1985) reported an unexpected property of the model when two trophically equivalent species can coexist stably in a single patch of identical microsite, in an unchanging environment. The mathematical conditions for this mode of coexistence could be explained as the species pair adopting alternative 'strategies' for utilizing the patch, one emphasizing adult survivorship and the other emphasizing fecundity. They found that at some point, species 1 is the better 'space claimer', while species 2 is the better 'space holder' with higher fecundity and in other cases the roles are reversed. They reported this possibility as alternate life-history strategy for co-existence. However, no empirical evidence has yet been documented from plant communities supporting this modeled solution. The congeneric blueberry species of the present study is the first example reporting co-existing plant species with such alternate life-history strategy supported by functional niche differentiation (Figs. 10 & 12).

Shmida and Ellner (1985) mentioned that the alternate life history strategy is necessary for coexistence. They assumed both species to be seed dispersed and argued that non-uniform seed dispersal by at least one of the species would be necessary. Non-uniform seed dispersal would generate a clumped seedling distribution in each species reducing inter-specific competition to a level where stable coexistence is possible. The clonal nature of the blueberry species of the present study takes out the dispersal argument and can facilitate coexistence of uniformly distributed clumps through resource sharing within nearby neighbours by parental care subsidy (Aarssen 2008) and by functional niche differentiation.

Distinguishing functional niche differentiation from phenotypic plasticity

Variation in plants' response to resource gradients does not always refer exclusively to niche differentiation. Phenotypic plasticity, the ability of a species to respond to environmental changes with variation in phenotype, may also account for such response (Laurans *et al.* 2012). Phenotypic plasticity is not in complete contrast with niche differentiation. Phenotypic plasticity would facilitate niche differentiation in many cases and species with ability to respond with plasticity would be much more adaptive under biotic interaction (competition). Recently several authors have shown that plant species can exhibit plastic response in nutrient uptake under various degrees of competitor proximity (Schiffers *et al.* 2011; Ashton *et al.* 2010; Valladers *et al.* 2000). Involvement of biotic interaction makes this plasticity in root length phenotype, a form of niche differentiation. Similarly in this study, the functional flexibility shown by the two blueberry species in relation to light cannot be perceived only as phenotypic plasticity, as the response in natural habitat involves neighborhood biotic interaction. Evidence of niche shift from common garden experiment to natural habitats with biotic interaction affirms these responses of biological functions as functional niche differentiation.

Mediating competition for resources through functional niche differentiation

Complementary use of space

Competition for space, a finite resource, is thought to determine the structure of most plant and sessile animal communities. Hence trade-off for space is vital and congeneric blueberry species exhibits this tradeoff for horizontal space in their cover within quadrates where they co-exist. Under the competitive environment of natural habitats, higher growth of *V. angustifolium* corresponded with lower growth of *V. myrtilloides* and vice versa demonstrating clear niche differentiation.

Only those species that can win over some growing space can ensure its presence in the community mix. These species can be abundant or rare. Usually there is a trade-off between species abundance and their reproductive effort (Van Duren 2012; Aarssen 2008), allowing them to persist in the community. If any species falls behind in stable abundance, it can regain its status either through quick vegetative growth or higher reproduction (Aarssen 2008). For example, coexistence can occur whenever a superior competitor is also the slower colonizer (space occupier) and when the level of mortality is within allowable limits to maintain a viable population (Armstrong 1976). The result of space competition is also strongly affected by the number of available propagules. With periodic disturbance, a replacement series of species from the most rapid colonizer to the competitive dominant (progressive succession) is predicted between disturbance events (Levin and Paine 1974; Maguire and Porter 1977). If such disturbances are localized, coexistence at a large spatial scale can result through successional niches (Sebens 1982), but at local microhabitat level with species of similar morphological stature, competition for space is mediated through complementary use of this finite resource, even in three-dimensional scale. Only those species that can manage within the growing space through niche differentiation can coexist.

Aarssen (2008) demonstrated that species with lower stature (size) usually have better reproductive economy and they maintain their presence in the community via rapid and larger amount of viable propagules. Aarssen (2008) also showed that under stressful condition most plants would adapt themselves to the competitive suppression and survive by maintaining a lower body mass (size). In my study, I find that the two small sized wild blueberry plant species adopts both of these strategies, but under different resource availability. Strategy to maintain a lower body mass was adopted by *V. myrtilloides* under restricted light availability but the same species adopted higher reproductive allocation under greater light availability. This sort of flexibility to remain functionally active under different environmental

conditioning is certainly helpful in maintaining population across heterogeneous landscapes and also important for evolutionary success since the capability to adjust functional niche preference would provide more opportunity to adapt and survive.

Efficient use of resources required for reproduction

Between species, the trade-off for reproduction (berry yield) was much less distinct than growth, as evident in the trade-off curve analysis. Resources required for reproduction is not always as restrictive (finite) as growing space is. Moisture and nutrients, key resources in reproductive effort, can often be abundant for all individuals within vicinity. For blueberry species that prefer well-drained habitats, soil moisture may be less important than frequency of precipitation during the growing season to provide sufficient moisture required for reproductive effort.. Diurnal temperature fluctuation, late frost during flowering time may also account for some variation in berry yield.

For both the blueberry species, ability to capture enhanced level of nutrients through mycorrhizal association needs be considered. This ability to acquire nutrients reduces competitive stress from limiting soil resources (nutrients and moisture) in low nutrient habitats. However, it is evident that in terms of light resource, higher light availability is generally associated with higher reproductive effort (berry yield) of both species, with *V. myrtilloides* preferring slightly more shaded environment than *V. angustifolium*.

Records of phenological events in common garden experiment and observation in natural habitats suggest a temporal shift in reproductive function between these two species. Berry maturity for *V. angustifolium* was 7-10 days earlier than *V. myrtilloides* (Mallik 2011). This may also reduce direct competitive trade-off for consumable resources at a given time.

Functional niche differentiation in understanding microsite community assembly

In theory, it is perceived that one niche axis can predominantly explain existence and

performance of one particular species (Farigone and Tilman 2002). Using the concept of the functional niche, one niche axis can explain the functional behaviors of many species. Functional niche preference at different levels along the same niche axis opens up the possibility to explain assembly rule of highly diverse communities. In a diverse plant community, many species coexist in competitive proximity and yet remain functionally active. In my study I found switching function of two related species. It is reasonable to perceive that each of the species in a community mix would also have distinguishable functional niches for its growth and reproduction. The differences in functional niche preferences would be important in maintaining coexistence in the microsite communities across heterogeneous landscapes. However, these functional niches may not always be on same niche (resource) axis. A functional niche preference that is undistinguishable along one axis should be distinguishable along another niche axis and only a complete analysis would reveal all the functional niche preferences.

Functional trait analysis can be a vehicle to explore the functional niche concept at community level (sensu Maire *et al.* 2012). Carefully selected response and effect traits can be linked to functional niche preferences of species and trait based quantitative analysis can be used as a surrogate for niche preference. For example, one can adopt height as an indicator for growth and level of resource gradient at which a species attains maximum height can be designated as preferred functional niche for growth. Since height as an effect trait is also an indicator of progressive plant community succession, functional niche analysis would be able to predict community dynamics as long as associated environmental gradients are known. Even if key (possible dominant) plant species are studied in terms of their functional niches, one can predict under which condition one species would grow and under which condition it would switch to either maintenance or reproduction. With this understanding, only presence of a potential dominant in the community mix would not bias the prediction of its dominance

over time, unless favorable functional niche prevails. Empirical studies involving functionally active species in a community guild and their response to multiple niche axes can elucidate this process.

This first empirical evidence of functional niche differentiation between two congeneric co-occurring clonal species will contribute to the mechanistic understanding of species coexistence in a community. The evidence can be strengthened further by assessing functional niche responses of both species grown in common garden experiment within interacting proximity and with varying degree of density dependence (as an indicator of competition) under different light levels and also along other resource axes.

Conclusion

The following conclusions can be made from my study that i) Spatial distribution of congeneric wild blueberry species was similar and these species also coexist along a resource gradient (in this case light) at a microsite level, ii) To maintain coexistence at a microsite level, these clonal species utilize their ability to differentiate functional niches to mediate competition for light. This is a significant finding in evolutionary sense because it explains how congeneric clonal species can coexist under competitive stress occupying the same physical niche by adjusting the performance of different biological functions. Under non-competitive condition there is little functional niche differentiation, meaning that the species employ this functional trait when needed, iii) Functional niche differentiation is not equal between two co-occurring congeneric species. I found *V. myrtilloides* to be more amenable to functional niche differentiation than *V. angustifolium* when co-occurring under different light conditions, iv) Vegetative trait (growth) is more responsive than sexual reproductive (berry yield) to functional niche differentiation in the two blueberry species. These new findings of functional niche differentiation in congeneric blueberry species of northwestern Ontario will

make a significant contribution to explaining the coexistence of closely related species. Up-scaling the functional niche analyses by considering multiple niche axes such as soil nutrients, soil moisture, elevation and near ground growing season temperature for key species in a boreal community can offer an effective tool to quantify and predict community assembly.

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Appendices

Appendix 1. **Climatic parameters of sampling sites**

Parameters	Atikokan			Ignace			Escape Lake			Black Sturgeon			Nipigon		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
BIO1	17	17	17	9	8	10	7	9	9	10	10	12	15	14	15
BIO2	124	124	124	112	112	114	120	120	119	119	119	118	118	118	118
BIO3	25	25	25	23	22	23	25	25	25	24	24	24	25	25	25
BIO4	12325	12287	12293	12580	12578	12624	11668	11584	11559	11781	11748	11659	11470	11508	11555
BIO5	247	245	246	236	235	238	234	233	233	238	237	237	236	236	237
BIO6	-245	-246	-245	-250	-252	-252	-240	-236	-235	-240	-240	-236	-231	-232	-232
BIO7	492	491	491	486	487	490	474	469	468	478	477	473	467	468	469
BIO8	165	164	164	161	160	162	137	138	138	142	142	143	144	144	145
BIO9	-132	-132	-132	-143	-144	-143	-153	-150	-149	-73	-73	-70	-67	-68	-67
BIO10	165	164	164	161	160	162	149	149	149	153	152	153	153	153	154
BIO11	-154	-154	-154	-164	-165	-164	-153	-150	-149	-151	-151	-148	-143	-144	-144
BIO12	690	695	695	781	788	784	787	787	789	781	783	777	754	758	756
BIO13	95	95	95	98	98	98	90	90	91	89	89	89	88	88	88
BIO14	24	25	24	36	37	37	34	34	34	33	33	33	31	32	31
BIO15	41	40	41	32	31	31	29	29	29	30	30	30	31	30	31
BIO16	269	269	271	281	282	277	264	264	265	263	263	262	256	257	257
BIO17	91	94	93	123	124	123	128	129	129	119	119	118	115	116	115
BIO18	269	269	271	281	282	277	263	262	263	261	261	259	252	254	253
BIO19	93	95	93	128	130	129	128	129	129	133	133	132	126	127	126

BIO1 = Annual Mean Temperature*.01 (degree celcius)
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))*.01
BIO3 = Isothermality (BIO2/BIO7) (* 100)
BIO4 = Temperature Seasonality (standard deviation *100)
BIO5 = Max Temperature of Warmest Month*.01
BIO6 = Min Temperature of Coldest Month*.01
BIO7 = Temperature Annual Range (BIO5-BIO6) *.01

BIO8 = Mean Temperature of Wettest Quarter*.01
BIO9 = Mean Temperature of Driest Quarter*.01
BIO10 = Mean Temperature of Warmest Quarter*.01
BIO11 = Mean Temperature of Coldest Quarter*.01
BIO12 = Annual Precipitation (mm)
BIO13 = Precipitation of Wettest Month
BIO14 = Precipitation of Driest Month
BIO15 = Precipitation Seasonality (Coefficient of Variation)

BIO16 = Precipitation of Wettest Quarter
BIO17 = Precipitation of Driest Quarter
BIO18 = Precipitation of Warmest Quarter
BIO19 = Precipitation of Coldest Quarte
Data extracted with arcGIS 9.3 from world climatic dataset from
www.worldclim.com (Hijman *et al.* 2005)

Appendix 2. R code for calculation

#Data input

```
setwd("C:/Users/Saif/Desktop/MscThesis/data")

bb_13<-read.csv ("bb_13.csv")
```

 # Test of normalcy

```
library(mvShapiroTest)

bb_13_var<-as.matrix(cbind(subset(bb_13, select = SpH:VmY_Nr)))

mvShapiro.Test(bb_13_var)
```

 # Data transformation

```
library(car)

bb.var.scale.df<-data.frame(bb.var.scale)

 bb_13t_pwr<-powerTransform(cbind(SpH+1,SM+1,CD+1, OMD+1, CD+1,  Va_Cover+1, Va_Yield+1,
Vm_Cover+1, Vm_Yield+1)~1,bb_13,family="bcPower")

summary(bb_13t_pwr)

qqPlot((bb$Va_Cover+1)^-0.43)

qqPlot((bb$Va_Yield+1)^-0.57)

qqPlot((bb$Vm_Cover+1)^-0.47)

qqPlot((bb$Vm_Yield+1)^-.061)


bb.transformed<-data.frame(cbind(as.character(bb_13$Area),as.character(bb_13$Site),
as.character(bb_13$Quadrate), , (bb_13$Va_Cover+1)^-0.43, (bb_13$Va_Yield+1)^-0.57,
(bb_13$Vm_Cover+1)^-0.47, (bb_13$Vm_Yield+1)^-.061))

colnames(bb.transformed)[c(1,2,3,4,5,6,7,8,9,10)] <- c("Area", "Site", "Quadrate", "SpH", "SM",
"OMD", "CD",  "Va_Cover", "Va_Yield", "Vm_Cover", "Vm_Yield")

bb.transformed$Yield<-as.numeric(as.character(bb.transformed$Yield))


leveneTest(bb.transformed$Yield, bb.transformed$Species,center =median)

leveneTest(bb.transformed$Quality, bb.transformed$Species,center =median)
```

Checking for variation in species and area in terms of growth and berry yield

anova.SY<-aov(Yield~Species,bb)

Tukey.SY <- glht(anova.SY, linfct = mcp(Species = "Tukey"))

cld(Tukey.SY)

anova.AY<-aov(Yield~Area,bb)

Tukey.AY <- glht(anova.AY, linfct = mcp(Area = "Tukey"))

cld(Tukey.AY)

anova.SQ<-aov(Quality~Species,bb)

Tukey.SQ <- glht(anova.SQ, linfct = mcp(Species = "Tukey"))

cld(Tukey.SQ)

bb.site<-aggregate(cbind(Yield) ~ Site, data = bb_13, mean)

bb.site$Area<-c(rep("Atikokan", each = 15), rep("Black sturgeon",each = 15),rep("Escape",each = 15),rep("Ignace",each = 15),rep("Nipigon",each = 15))

Checking site level climatic data variability

bb.sites<-read.csv("bb15.csv")

area.temp.aov<-aov(Temp~LOCATION, bb.sites)

Tukey.area.temp <- glht(area.temp.aov, linfct = mcp(LOCATION = "Tukey"))

cld(Tukey.area.temp)

area.prec.aov<-aov(Prec~LOCATION, bb.sites)

Tukey.area.prec <- glht(area.prec.aov, linfct = mcp(LOCATION = "Tukey"))

cld(Tukey.area.prec)

aggregate(Prec~LOCATION,bb.sites,mean)

aggregate(Temp~LOCATION,bb.sites,mean)

```
# Multivariate correlation

library(Hmisc)

rcorr(as.matrix(bb.tr.var), type="spearman")


# Ordination

bb.env.ord$Site<- paste( as.character(bb.yield$Site),  as.character(bb.yield$Quadrate), sep ="")

bb.spe.ord$Site<- paste( as.character(bb.yield$Site),  as.character(bb.yield$Quadrate), sep ="")

###########


detach("package:ade4")

bb.spe.ord.cca<-bb.spe.ord.df[rowSums(bb.spe.ord.df)>0,]

bb.env.ord.cca<-bb.env.ord.df[-c(27,33,35,90,92,115,125,131,178,207),]


 bb.spe.ord.df1<-as.data.frame(bb.spe.ord.cca)

bb.env.ord.df1<-as.data.frame(bb.env.ord.cca)

rcorr(as.matrix (bb.env.ord.df1), type=c("spearman"))


 bb.spe.cca1<-cca(bb.spe.ord.df1 ~ CD + pH + SM + OMD, bb.env.ord.df1)

plot(bb.spe.cca1,scaling = 3,  display = c("species", "bp"), type="t", ylim= c(-.5,2.3), xlim= c(-3.5,2.2))


cca.cor<-cbind(bb.spe.cca1$CCA$u.eig,bb.env.ord.df1)

rcorr(as.matrix(cca.cor), type=c("spearman"))
```

Producing and comparing models for response curve selection

```
bb_13tb$Va_Cover<-as.numeric(as.character(bb_13tb$Va_Cover))

bb_13tb$Vm_Cover<-as.numeric(as.character(bb_13tb$Vm_Cover))

bb_13tb$Vm_Yield<-as.numeric(as.character(bb_13tb$Vm_Yield))

bb_13tb$Va_Yield<-as.numeric(as.character(bb_13tb$Va_Yield))
```

```
bb_13tb$Light<-as.numeric(as.character(bb_13tb$Light))

bb_13tb$SM<-as.numeric(as.character(bb_13tb$SM))

bb_13tb$OMD<-as.numeric(as.character(bb_13tb$OMD))

bb_13tb$SpH<-as.numeric(as.character(bb_13tb$SpH))


# VA Cover

vac_lm<-lm(Va_Cover~Light, data=bb_13_tb)

vac_nl2<-lm(Va_Cover~poly(Light,2), data=bb_13_tb)

vac_nl3<-lm(Va_Cover~poly(Light,3), data=bb_13_tb)

vac_nl4<-lm(Va_Cover~poly(Light,4), data=bb_13_tb)

vac_nl5<-lm(Va_Cover~poly(Light,5), data=bb_13_tb)


#VA Yield

vay_lm<-lm(Va_Yield~Light, data=bb_13_tb)

vay_nl2<-lm(Va_Yield~poly(Light,2), data=bb_13_tb)

vay_nl3<-lm(Va_Yield~poly(Light,3), data=bb_13_tb)

vay_nl4<-lm(Va_Yield~poly(Light,4), data=bb_13_tb)

vay_nl5<-lm(Va_Yield~poly(Light,5), data=bb_13_tb)


# Vm Cover

vmc_lm<-lm(Vm_Cover~Light, data=bb_13_tb)

vmc_nl2<-lm(Vm_Cover~poly(Light,2), data=bb_13_tb)

vmc_nl3<-lm(Vm_Cover~poly(Light,3), data=bb_13_tb)

vmc_nl4<-lm(Vm_Cover~poly(Light,4), data=bb_13_tb)

vmc_nl5<-lm(Vm_Cover~poly(Light,5), data=bb_13_tb)
```

#Vm Yield

vmy_lm<-lm(Vm_Yield~Light, data=bb_13_tb)

vmy_nl2<-lm(Vm_Yield~poly(Light,2), data=bb_13_tb)

vmy_nl3<-lm(Vm_Yield~poly(Light,3), data=bb_13_tb)

vmy_nl4<-lm(Vm_Yield~poly(Light,4), data=bb_13_tb)

vmy_nl5<-lm(Vm_Yield~poly(Light,5), data=bb_13_tb)

Model comparison for natural habitat

anova(vac_lm,vac_nl2, vac_nl3, vac_nl4, vac_nl5)

AIC(vac_lm,vac_nl2, vac_nl3, vac_nl4, vac_nl5)

anova(vay_lm,vay_nl2, vay_nl3, vay_nl4, vay_nl5)

AIC(vay_lm,vay_nl2, vay_nl3, vay_nl4, vay_nl5)

anova(vmc_lm,vmc_nl2, vmc_nl3, vmc_nl4, vmc_nl5)

AIC(vmc_lm,vmc_nl2, vmc_nl3, vmc_nl4, vmc_nl5)

anova(vmy_lm,vmy_nl2, vmy_nl3, vmy_nl4, vmy_nl5)

AIC(vmy_lm,vmy_nl2, vmy_nl3, vmy_nl4, vmy_nl5)

Organizing data from Common garden

mff_13<-read.csv("C:/Users/Saif/Desktop/MSc Thesis/Data/MFF_13.csv")

mff_13_fc<-read.csv("C:/Users/Saif/Desktop/MSc Thesis/Data/MFF_13_fc.csv")

mff_13$Va.Cover<-as.numeric(as.character(mff_13$Va.Cover))

mff_13$Vm.Cover<-as.numeric(as.character(mff_13$Vm.Cover))

mff_13$Vm.Yield<-as.numeric(as.character(mff_13$Vm.Yield))

mff_13$Va.Yield<-as.numeric(as.character(mff_13$Va.Yield))

```r
mff_13$Light<-as.numeric(as.character(mff_13$Light))

colnames(mff_13)[c(1,2,3,4,5)] <- c("Light","Va_Cover", "Va_Yield", "Vm_Cover", "Vm_Yield")

mff_13_fc$VA_Cover<-as.numeric(as.character(mff_13_fc$VA_Cover))

mff_13_fc$VM_Cover<-as.numeric(as.character(mff_13_fc$VM_Cover))

mff_13_fc$VM_Yield<-as.numeric(as.character(mff_13_fc$VM_Yield))

mff_13_fc$VA_Yield<-as.numeric(as.character(mff_13_fc$VM_Yield))

mff_13_fc$Light<-as.numeric(as.character(mff_13_fc$Light))
```

Response curve generation through model selection
```r
# VA Cover

mff_vac_lm<-lm(Va_Cover~Light, data=mff_13)

mff_vac_nl2<-lm(Va_Cover~poly(Light,2), data=mff_13)

mff_vac_nl3<-lm(Va_Cover~poly(Light,3), data=mff_13)

mff_vac_nl4<-lm(Va_Cover~poly(Light,4), data=mff_13)

mff_vac_nl5<-lm(Va_Cover~poly(Light,5), data=mff_13)


#VA Yield

mff_vay_lm<-lm(Va_Yield~Light, data=mff_13)

mff_vay_nl2<-lm(Va_Yield~poly(Light,2), data=mff_13)

mff_vay_nl3<-lm(Va_Yield~poly(Light,3), data=mff_13)

mff_vay_nl4<-lm(Va_Yield~poly(Light,4), data=mff_13)

mff_vay_nl5<-lm(Va_Yield~poly(Light,5), data=mff_13)


# Vm Cover

mff_vmc_lm<-lm(Vm_Cover~Light, data=mff_13)

mff_vmc_nl2<-lm(Vm_Cover~poly(Light,2), data=mff_13)

mff_vmc_nl3<-lm(Vm_Cover~poly(Light,3), data=mff_13)

mff_vmc_nl4<-lm(Vm_Cover~poly(Light,4), data=mff_13)
```

```
mff_vmc_nl5<-lm(Vm_Cover~poly(Light,5), data=mff_13)
```

#Vm Yield

```
mff_vmy_lm<-lm(Vm_Yield~Light, data=mff_13)

mff_vmy_nl2<-lm(Vm_Yield~poly(Light,2), data=mff_13)

mff_vmy_nl3<-lm(Vm_Yield~poly(Light,3), data=mff_13)

mff_vmy_nl4<-lm(Vm_Yield~poly(Light,4), data=mff_13)

mff_vmy_nl5<-lm(Vm_Yield~poly(Light,5), data=mff_13)
```

Model comparison for common garden

```
anova(mff_vac_lm,mff_vac_nl2, mff_vac_nl3, mff_vac_nl4, mff_vac_nl5)

AIC(mff_vac_lm,mff_vac_nl2, mff_vac_nl3, mff_vac_nl4, mff_vac_nl5)


anova(mff_vay_lm,mff_vay_nl2, mff_vay_nl3, mff_vay_nl4, mff_vay_nl5)

AIC(mff_vay_lm,mff_vay_nl2, mff_vay_nl3, mff_vay_nl4, mff_vay_nl5)


anova(mff_vmc_lm,mff_vmc_nl2, mff_vmc_nl3, mff_vmc_nl4, mff_vmc_nl5)

AIC(mff_vmc_lm,mff_vmc_nl2, mff_vmc_nl3, mff_vmc_nl4, mff_vmc_nl5)


anova(mff_vmy_lm,mff_vmy_nl2, mff_vmy_nl3, mff_vmy_nl4, mff_vmy_nl5)

AIC(mff_vmy_lm,mff_vmy_nl2, mff_vmy_nl3, mff_vmy_nl4, mff_vmy_nl5)
```

CI of models and producing error bars on optimum level

#Va_Cover

```
nh_vac_nls <- lm(Va_Cover ~ poly(Light, 3), data = bb_13tb)

nh_vac_nls_a <- predict(nh_vac_nls, interval="confidence")
```

```
nh_vac_nls_a1<-nh_vac_nls_a/max(nh_vac_nls_a[,1])

plot(Va_Cover/max(Va_Cover)~Light, data=bb_13tb)

lines(bb_13tb$Light, nh_vac_nls_a[,3], lty=2)

abline(1,0)


nh_vmc_nls <- lm(Vm_Cover ~ poly(Light, 3), data = bb_13tb)

nh_vmc_nls_a <- predict(nh_vmc_nls, interval="confidence", level=0.95)

nh_vmc_nls_a1<-nh_vmc_nls_a/max(nh_vmc_nls_a[,1])

plot(Vm_Cover/max(Vm_Cover)~Light, data=bb_13tb)

lines(bb_13tb$Light, nh_vmc_nls_a1[,3], lty=2)

abline(1,0)

nh_vmy_nls <- lm(Vm_Yield ~ poly(Light, 3), data = bb_13tb)

nh_vmy_nls_a <- predict(nh_vmy_nls, interval="confidence", level=0.95)

nh_vmy_nls_a1<-nh_vmy_nls_a/max(nh_vmy_nls_a[,1])

plot(Vm_Yield/max(Vm_Yield)~Light, data=bb_13tb)

lines(bb_13tb$Light, nh_vmy_nls_a1[,3], lty=2)

abline(1,0)

nh_vay_nls <- lm(Va_Yield ~ poly(Light, 3), data = bb_13tb)

nh_vay_nls_a <- predict(nh_vay_nls, interval="confidence", level=0.95)

nh_vay_nls_a1<-nh_vay_nls_a/max(nh_vay_nls_a[,1])

plot(Va_Yield/max(Va_Yield)~Light, data=bb_13tb)

lines(bb_13tb$Light, nh_vay_nls_a1[,3], lty=2)

abline(1,0)
```

Appendix 3.1. qq Plots of response variables from natural habitats
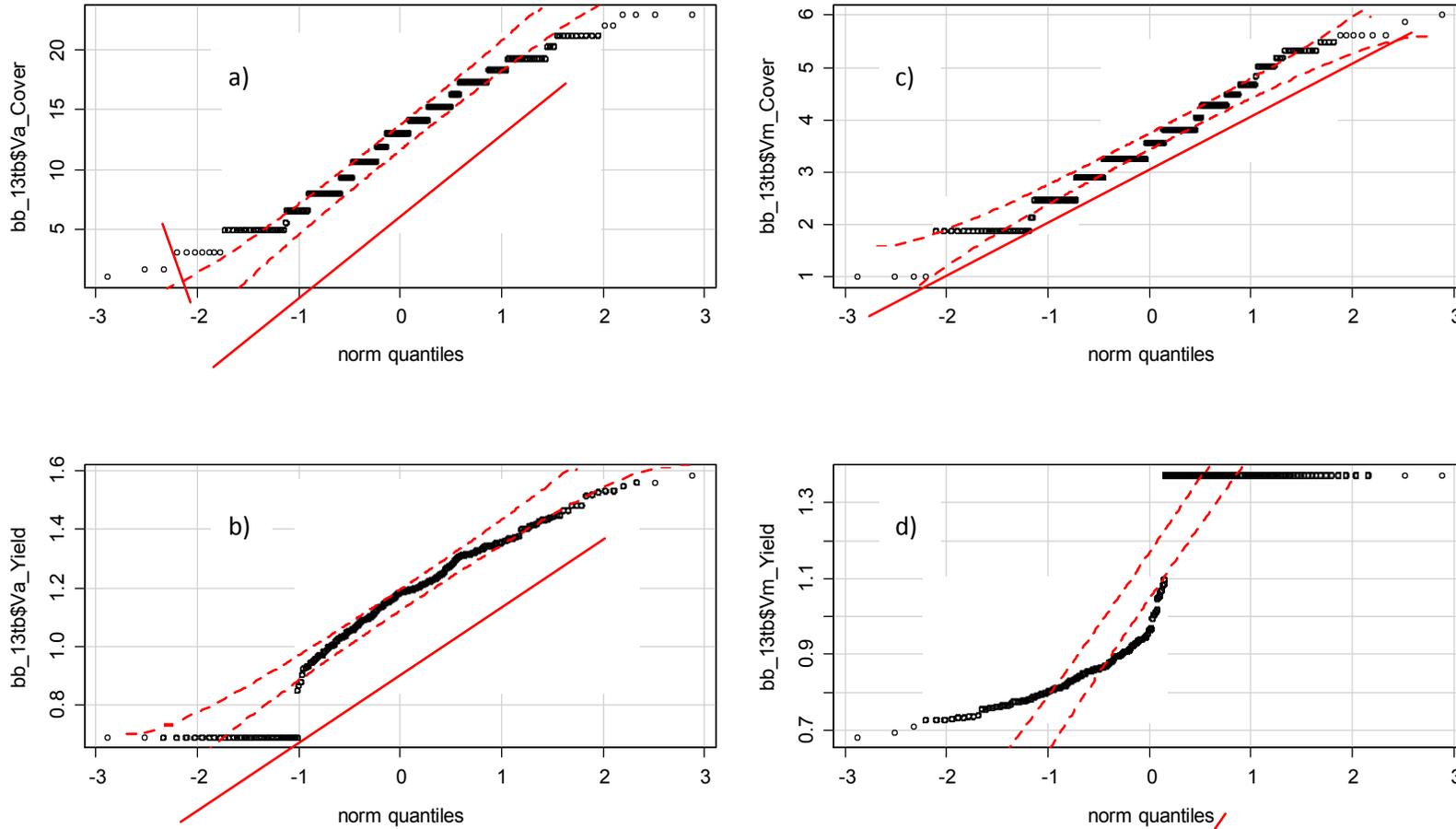
Figure A3-1. qq plots for transformed variables (a) *V. angustifolium* cover (Va_Cover), (b) *V. angustifolium* yield (Va_Yield) , (c) *V. myrtilloides* cover (Vm_cover) and (d) *V. myrtilloides* yield (Vm_Yield) from primary data collected from natural habitats in 2013.

Appendix 3.2. qq Plots of response variables from common garden experiment
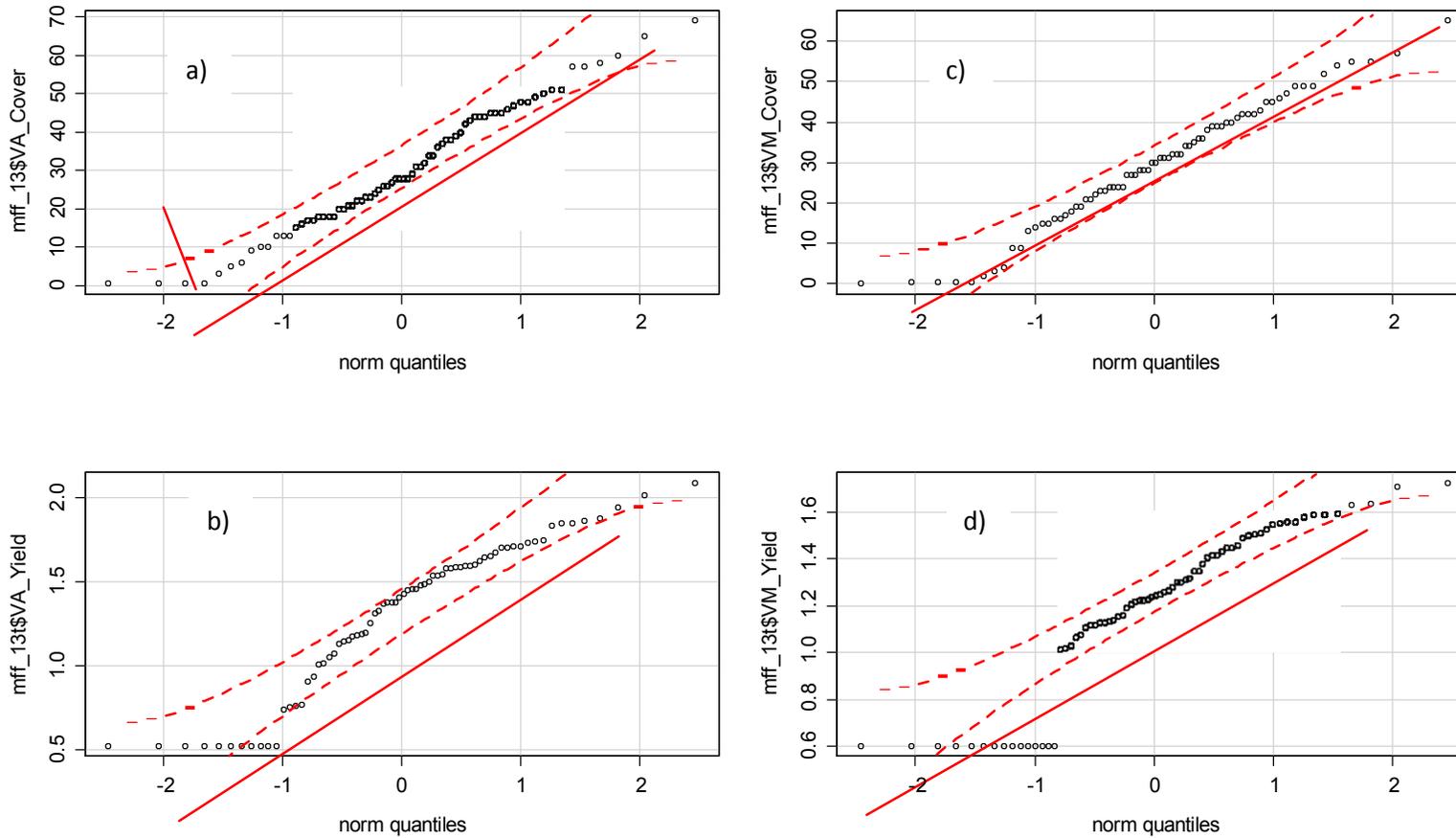
Figure A3-2.qq plots for untransformed variables (a) *V. angustifolium* cover (VA_Cover) and (c) *V. myrtilloides* cover (VM_Cover) and box-cox transformed (b) *V. angustifolium* yield (VA_Yield), and (d) *V. myrtilloides* yield (VM_Yield) from primary data collected from common garden experiment in 2013.

Appendix 4. χ² tests for assessing coexistence congeneric blueberry species

Table A4-1. Expected and observed frequency of occurrence at 20 x 20 cm quadrats

Category	Expected	Observed	DF*	χ^2 -value	p-value	Notes
Both present	7425	7324	1	.69	0.406	Expected presence of both species together was more than 50%, I set expected level at 55%
V. angustifolium present	2363	2815	1	39.5473	3.355e-10	17.5% cases were set for each species to be occurring alone. Observed value more than expected, hence expectation were met.
V. myrtilloides present	2363	1281	1	321.021	< 2.2e-16	Occurrence of *V. myrtilloides* were less than expected
None present	1350	2080	1	155.3644	< 2.2e-16	Expected that 10% cases will be without presence of any species.
Total (n)	13500	13500				Categories were mutually exclusive

* χ^2 test was carried out within each category.

Appendix 5. CCA analysis for conforming key microsite variable

5.1. Significance of CCA analysis

Permutation test for cca under reduced model

Model: cca(formula = bb_13tb ~ CD (light) + SpH + SM + OMD, data = bb_13tb_env)

	Df	Chisq	F	N.Perm	Pr(>F)
Model	4	0.0467	4.3683	299	0.02 *
Residual	355	0.9486			

Significance codes for p value levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

5.2. ANOVA for CCA analysis by "variables"

Permutation test for cca under reduced model

Model: cca(formula = bb_13tb ~ CD(light)+ SpH + SM + OMD, data = bb_13tb_env)

	Df	Chisq	F	N.Perm	Pr(>F)
CD (light)	1	0.0374	13.9787	99	0.01 **
SpH	1	0.0038	1.4311	99	0.48
SM	1	0.0024	0.9019	99	0.65
OMD	1	0.0031	1.1615	99	0.50
Residual	355	0.9486			

Significance codes for p value levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

5.3 ANOVA for CCA analysis by "axis"

Model: cca(formula = bb_13_vamcy ~ light + SpH + SM + OMD, data = bb_13_env)

	Df	Chisq	F	N.Perm	Pr(>F)
CCA1	1	0.0419	15.7247	199	0.005 **
CCA2	1	0.0043	1.6209	99	0.320
CCA3	1	0.0005	0.1768	99	0.970
Residual	356	0.9486			

Significance codes for p value levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

5.4 Correlation matrix of microhabitat environmental variables

	CD (light)	SpH	SM	OMD
CD (light)		-0.14	-0.07	0.05
SpH	-0.14		0.06	-0.14
SM	-0.07	0.06		0.39
OMD	0.05	-0.14	0.39	

Corresponding p- values (n= 360)

	CD (light)	SpH	SM	OMD
CD (light)		0.0075	0.1936	0.3118
SpH	0.0075		0.2788	0.0103
SM	0.1936	0.2788		0.0000
OMD	0.3118	0.0103	0.0000	

5.5 Variance partitioning

Partition of variation in RDA

Call: varpart(Y = bb_13_spe_ord, X = ~CD (light), ~SpH, ~SM, ~OMD, data = bb_13_env)

Explanatory tables: X1: ~CD; X2: ~SpH; X3: ~SM; X4: ~OMD

No. of explanatory tables: 4; Total variation (SS): 2118626 ; Variance: 5901.5;

No. of observations: 360

Partition table:

	Df	R^2	Adj.R^2	Relative contribution	
				R2	Adj.R2
X1(LIGHT(%))	1	0.02424	0.02152	0.563983248	0.645665
X2(SOIL PH)	1	0.0142	0.01145	0.330386226	0.343534
X3(SOIL MOISTURE)	1	0.00909	0.00632	0.211493718	0.189619
X4(ORG. MATTER DEPTH)	1	0.00146	-0.00133	0.033969288	-0.0399
X1(LIGHT(%))+X2(SOIL PH)	2	0.0345	0.02909	0.80269893	0.872787
X1(LIGHT(%))+X3(SOIL MOISTURE)	2	0.03187	0.02645	0.741507678	0.793579
X1(LIGHT(%))+X4(ORG. MATTER DEPTH)	2	0.02544	0.01998	0.591903211	0.59946
X2(SOIL PH)+X3(SOIL MOISTURE)	2	0.02218	0.0167	0.516053979	0.50105
X2(SOIL PH)+X4(ORG. MATTER DEPTH)	2	0.0154	0.00988	0.358306189	0.29643
X3(SOIL MOISTURE)+X4(ORG. MATTER DEPTH)	2	0.01298	0.00745	0.302000931	0.223522
X1(LIGHT(%))+X2(SOIL PH)+X3(SOIL MOISTURE)	3	0.04141	0.03333	0.963471382	1
X1(LIGHT(%))+X2(SOIL PH)+X4(ORG. MATTER DEPTH)	3	0.03566	0.02753	0.829688227	0.825983
X1(LIGHT(%))+X3(SOIL MOISTURE)+X4(ORG. MATTER DEPTH)	3	0.03452	0.02638	0.803164262	0.791479
X2(SOIL PH)+X3(SOIL MOISTURE)+X4(ORG. MATTER DEPTH)	3	0.02433	0.01611	0.566077245	0.483348
All	4	0.04298	0.03219	1	0.965797
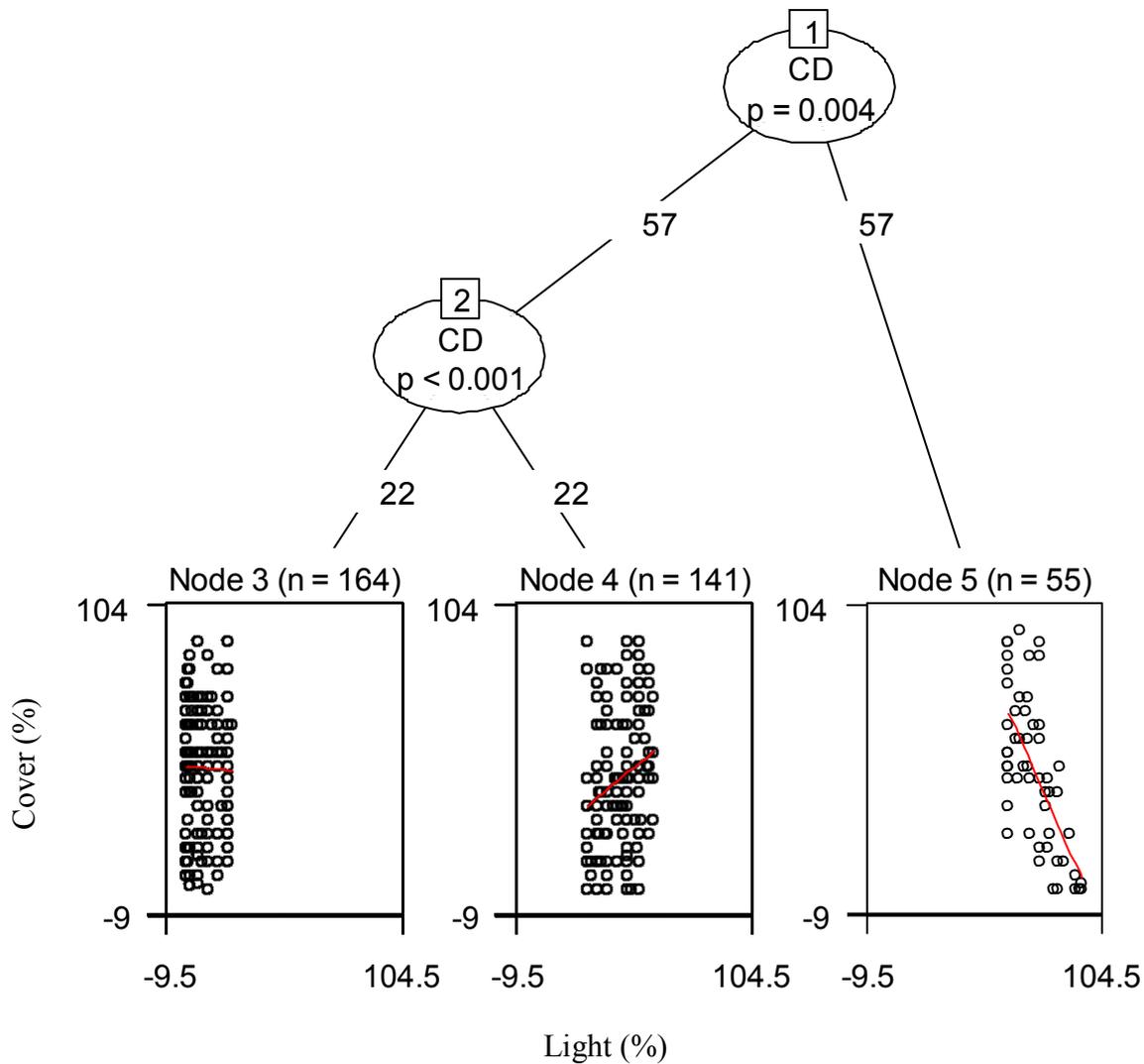
Figure A6-1. Visual diagram of model based recursive partitioning of canopy density (light availability) showing three statistically partitions (2 splits at 22% and 57% canopy density) for linear regression model fits for *V. angustifolium* under natural habitats.

Appendix 7: Analysis of Variance Tables for model selection

7.1. Natural Habitat

7.1.1. *V. angustifolium* cover

Model 1: Va_Cover ~ Light

Model 2: Va_Cover ~ poly(Light, 2)

Model 3: Va_Cover ~ poly(Light, 3)

Model 4: Va_Cover ~ poly(Light, 4)

Model 5: Va_Cover ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	249	6908.8				
2	248	6907.1	1	1.69	0.0671	0.79576
3	247	6354.1	1	552.97	21.9582	4.625e-06 ***
4	246	6222.8	1	131.26	5.2121	0.02329 *
5	245	6169.8	1	53.00	2.1047	0.14813

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	df	AIC
vac_lm	3	1550.396
vac_nl2	4	1552.334
vac_nl3	5	1533.389
vac_nl4	6	1530.150
vac_nl5	7	1530.003

7.1.2. *V. angustifolium* yield

Analysis of Variance Table

Model 1: Va_Yield ~ Light

Model 2: Va_Yield ~ poly(Light, 2)

Model 3: Va_Yield ~ poly(Light, 3)

Model 4: Va_Yield ~ poly(Light, 4)

Model 5: Va_Yield ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	249	14.002				
2	248	13.555	1	0.44728	8.1513	0.004672 **
3	247	13.483	1	0.07162	1.3051	0.254391
4	246	13.448	1	0.03524	0.6422	0.423682
5	245	13.444	1	0.00411	0.0748	0.784655

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	df	AIC
vay_lm	3	-6.143130
vay_nl2	4	-12.291987
vay_nl3	5	-11.621663
vay_nl4	6	-10.278557
vay_nl5	7	-8.355212

7.1.3 *V. myrtilloides* cover

Analysis of Variance Table

Model 1: Vm_Cover ~ Light

Model 2: Vm_Cover ~ poly(Light, 2)

Model 3: Vm_Cover ~ poly(Light, 3)

Model 4: Vm_Cover ~ poly(Light, 4)

Model 5: Vm_Cover ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	249	295.61				
2	248	258.30	1	37.316	35.7986	7.715e-09 ***
3	247	257.12	1	1.177	1.1288	0.2891
4	246	256.89	1	0.228	0.2189	0.6403
5	245	255.38	1	1.508	1.4467	0.2302

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	df	AIC
vmc_lm	3	759.3697
vmc_nl2	4	727.4995
vmc_nl3	5	728.3535
vmc_nl4	6	730.1307
vmc_nl5	7	730.6530

7.1.4. *V. myrtilloides* **yield**

Analysis of Variance Table

Model 1: Vm_Yield ~ Light

Model 2: Vm_Yield ~ poly(Light, 2)

Model 3: Vm_Yield ~ poly(Light, 3)

Model 4: Vm_Yield ~ poly(Light, 4)

Model 5: Vm_Yield ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	249	16.619				
2	248	16.591	1	0.027660	0.4118	0.5217
3	247	16.586	1	0.004965	0.0739	0.7860
4	246	16.530	1	0.056640	0.8433	0.3594
5	245	16.456	1	0.073540	1.0949	0.2964

	df	AIC
vmy_lm	3	36.86592
vmy_nl2	4	38.44781
vmy_nl3	5	40.37269
vmy_nl4	6	41.51410
vmy_nl5	7	42.39492

7.2. Common garden

7.2.1. *V. angustifolium* cover

Analysis of Variance Table

Model 1: Va_Cover ~ Light

Model 2: Va_Cover ~ poly(Light, 2)

Model 3: Va_Cover ~ poly(Light, 3)

Model 4: Va_Cover ~ poly(Light, 4)

Model 5: Va_Cover ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	70	19907				
2	69	14082	1	5825.4	37.4465	5.753e-08 ***
3	68	11069	1	3012.8	19.3669	4.031e-05 ***
4	67	10746	1	323.4	2.0787	0.15409
5	66	10267	1	478.2	3.0741	0.08419 .

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	df	AIC
mff_vac_lm	3	615.1232
mff_vac_nl2	4	592.1969
mff_vac_nl3	5	576.8638
mff_vac_nl4	6	576.7290
mff_vac_nl5	7	575.4512

7.2.2 V. angustifolium yield

Analysis of Variance Table

Model 1: Va_Yield ~ Light

Model 2: Va_Yield ~ poly(Light, 2)

Model 3: Va_Yield ~ poly(Light, 3)

Model 4: Va_Yield ~ poly(Light, 4)

Model 5: Va_Yield ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	70	81480				
2	69	78564	1	2915.94	2.4555	0.1219
3	68	78554	1	10.00	0.0084	0.9272
4	67	78513	1	40.59	0.0342	0.8539
5	66	78377	1	136.64	0.1151	0.7355

	df	AIC
mff_vay_lm	3	716.5911
mff_vay_nl2	4	715.9672
mff_vay_nl3	5	717.9580
mff_vay_nl4	6	719.9208
mff_vay_nl5	7	721.7954

7.2.3. V. myrtilloides cover

Analysis of Variance Table

Model 1: Vm_Cover ~ Light

Model 2: Vm_Cover ~ poly(Light, 2)

Model 3: Vm_Cover ~ poly(Light, 3)

Model 4: Vm_Cover ~ poly(Light, 4)

Model 5: Vm_Cover ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	70	16135.5				
2	69	12072.3	1	4063.1	32.5183	3.006e-07 ***
3	68	9696.5	1	2375.8	19.0141	4.651e-05 ***
4	67	8459.8	1	1236.8	9.8981	0.002482 **
5	66	8246.6	1	213.1	1.7057	0.196081

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	df	AIC
mff_vmc_lm	3	599.9990
mff_vmc_nl2	4	581.1115
mff_vmc_nl3	5	567.3328
mff_vmc_nl4	6	559.5087
mff_vmc_nl5	7	559.6716

7.2.4. V. murtilloides yield

Analysis of Variance Table

Model 1: Vm_Yield ~ Light

Model 2: Vm_Yield ~ poly(Light, 2)

Model 3: Vm_Yield ~ poly(Light, 3)

Model 4: Vm_Yield ~ poly(Light, 4)

Model 5: Vm_Yield ~ poly(Light, 5)

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	70	62167				
2	69	56595	1	5572.3	6.8379	0.01105 *
3	68	56202	1	393.1	0.4824	0.48977
4	67	56201	1	0.7	0.0008	0.97724
5	66	53784	1	2417.	0 2.9660	0.08972 .

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	df	AIC
mff_vmy_lm	3	697.1134
mff_vmy_nl2	4	692.3520
mff_vmy_nl3	5	693.8502
mff_vmy_nl4	6	695.8493
mff_vmy_nl5	7	694.6843

Appendix 8: Producing error bars for optimum performance levels

First I fitted lines for response curves with predicted upper values at 95%confidence interval level. The line crosses the optimum level (1) at two points while going upslope and downslope. These two points are onsidered to be the interval between which the optimum level can be found.
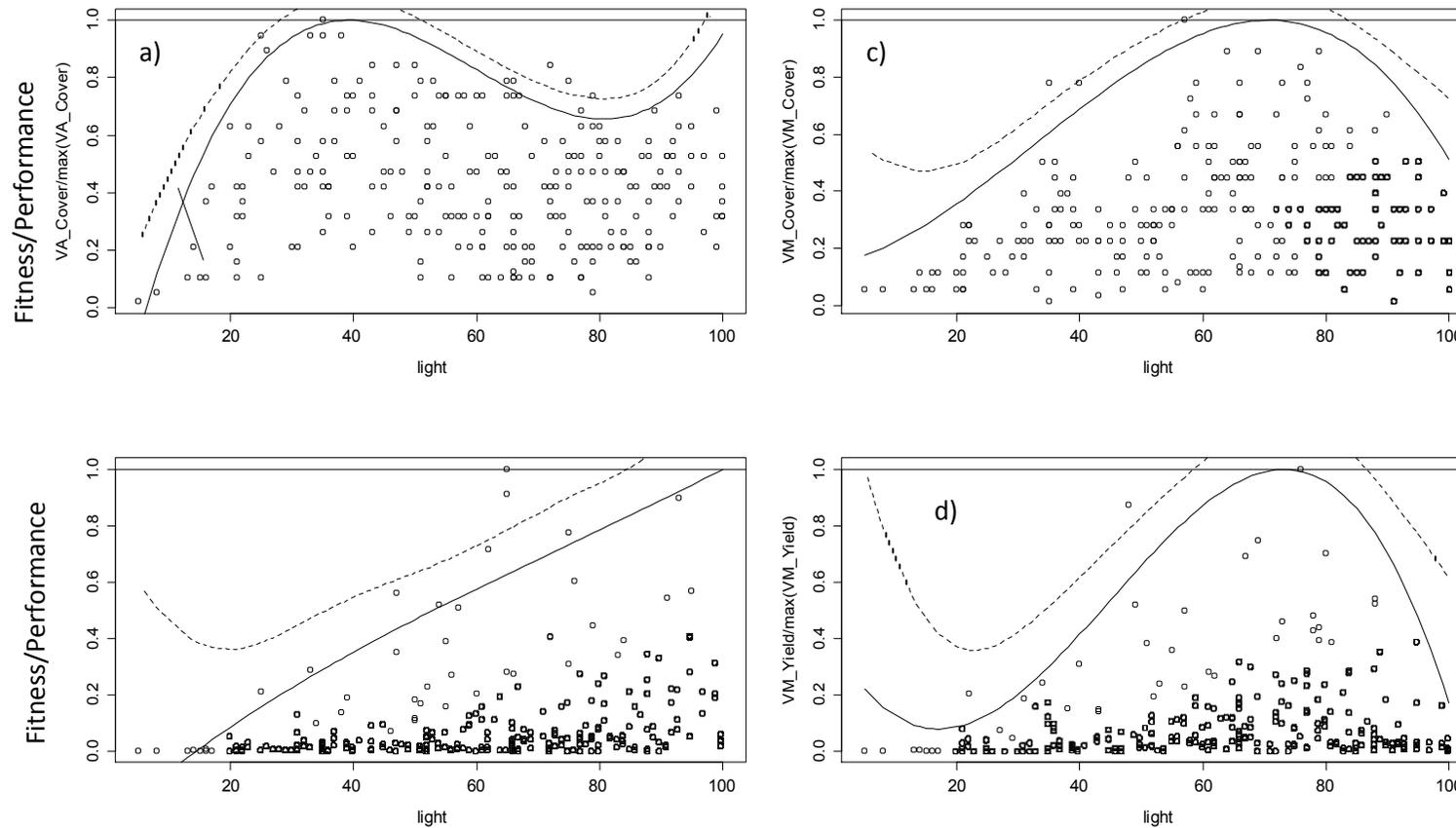

Figure A8-1. Fitting lines with confidence interval of 95% for response curves (Fig 16 a) and finding the error bars for optimum performance level for functional niches (16 b). The spread of error are the two points where the line fitted with upper values cuts the optimum performance level (in this case, for *V. angustifolium* cover in common garden the error bars would be 34% and 48%) light.
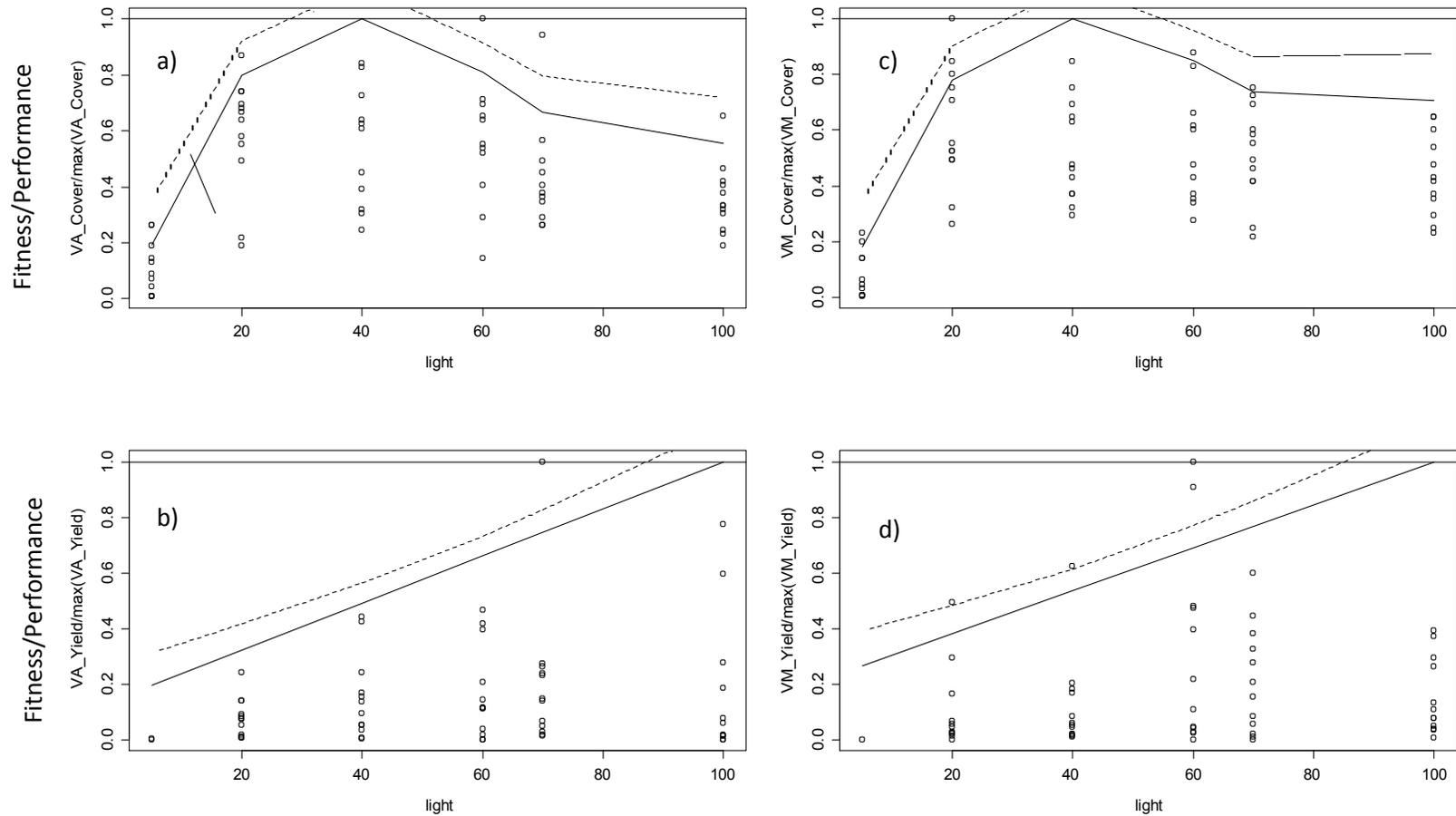
Figure A8-2. Fitting lines with confidence interval of 95% for response curves (Fig 16 a) and finding the error bars for optimum performance level for functional niches (16 b). The spread of error are the two points where the line fitted with upper values cuts the optimum performance level (in this case, for *V. angustifolium* cover in common garden the error bars would be 34% and 48%) light.

Natural habitats
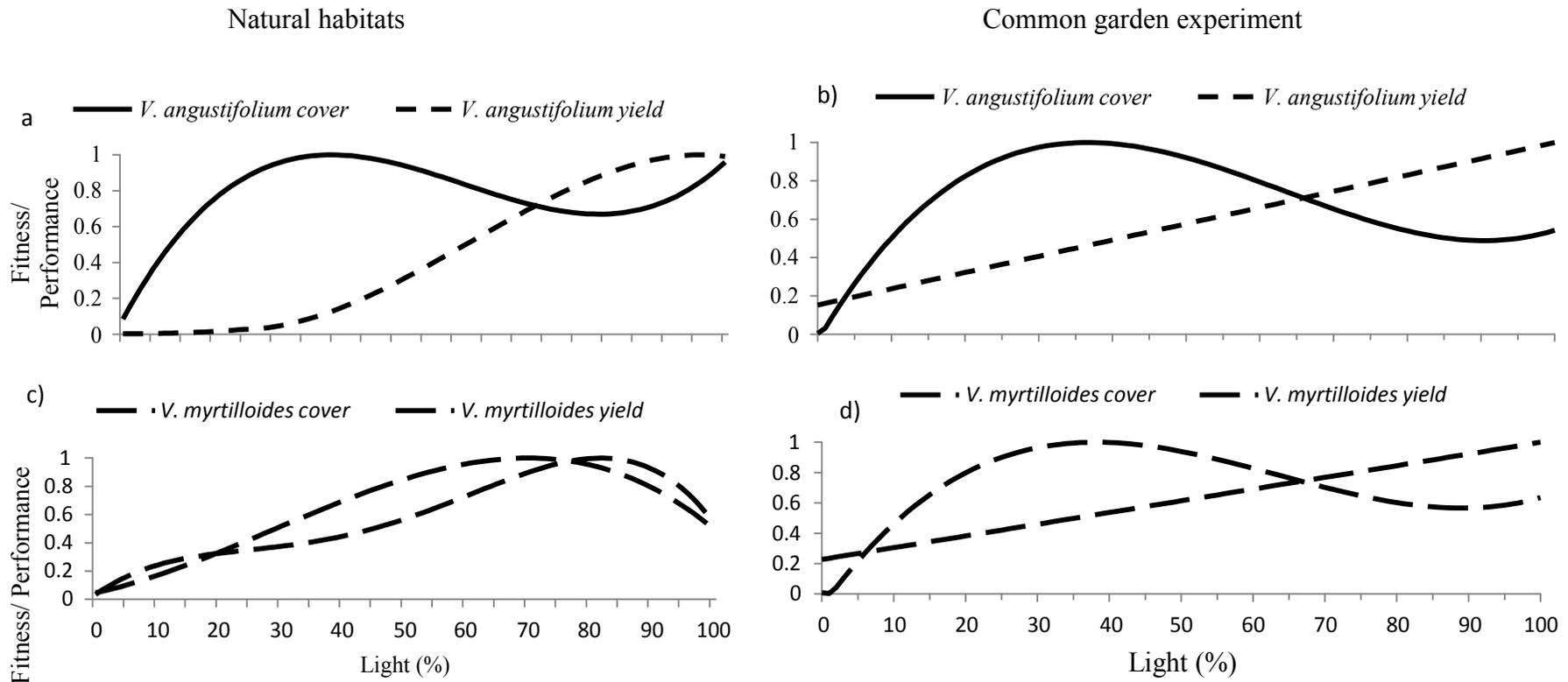
Common garden experiment

Figure A9-1. Function-wise fitness/performance curves for comparing niche preferences for growth and reproduction between *V. angustifolium* (Va) and *V. myrtilloides* (Vm). In natural condition (A9-1 a), growth (cover) had contrasting optimum condition between species; *V. angustifolium*'s high growth performance in open lit and lower light (30%) corresponds with less yield of *V. myrtilloides*. *V. myrtilloides'* growth increase is in line with the dip in growth performance of Va in between 75-80% light. In common garden (A9-1 c), the growth niches of these two species are strikingly similar. In common garden, the similarity is also evident for reproductive niche (17 d) with both Va_Yield and Vm_Yield preferring open condition then gradually declining. In natural habitat, Va's yield was optimum at open light condition while Vm's reproductive effort was optimum at low (15-20%) shade.