Importance of Bumble Bee Community Evenness for Crop Pollination

– A Simulation Analysis of Swedish Red Clover Seed Production

Vivek Babu

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In Deep Gratitude To

Each People & Organisation, Who Facilitated My Interest in Science

(Beloved Teachers, Guides, Seniors and Organisation)

1994 - 2002	1998 - 2002	2002 – 2005	2005 - 2007
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	Tamil Nadu Science Forum	**Pedestrian Pictures**	

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Abstract

The red clover seed production systems are dependent on pollinators for increase in red clover seed yield and its stability. When compared to domesticated honey bees, the wild bumble bees are highly efficient in pollinating the red clover crop due to its relatively longer tongue length. Longer dependence on single pollinator species i.e., honey bees has proved that reliance on single pollinator population is highly inefficient especially when the highly managed systems are prone to ecological surprises like colony collapse disorder. Therefore, global agro-ecosystem management has begun to increase their efforts of harnessing the pollination potential from diverse wild pollinator communities like bumble bees and non-bee pollinators. However, the agricultural intensification led landscape and environmental homogenisation has caused the populations of the wild pollinators decline, resulting in reduced pollination service from wild bumble bee diversity, necessitating conservation of bumble bees.

Among bumble bees the long tongue (LT) bumble bees are highly efficient pollinators, whereas short tongue (ST) bumble bees are relatively least efficient or unproductive because of their short tongue length and their one third proportion engages in robbery of nectar without pollinating the flowers. However, ST bumble bees are highly mobile and highly populated generalist functional group, contrasting specialist LT species in red-clover production systems. To investigate the impact of declining evenness in this 10-species community comprising of 5 LT and 5 ST, the empirical proportional abundance data from historic field investigations (1940's, 1960's & 2010) were modelled as temporal replication scenarios for 100 years in a model called FunBumble prepared for this study using empirical parameter estimates. The early 1940's & 1960's scenarios had one dominant and 3 co-dominant identities and the contemporary 2010 scenarios had one dominant and co-dominant identity. Throughout since 1960's to 2010, *B. terrestris* is the dominant species. Thus, the 10-species community comprised of totally 5 dominant species, these each dominance identities taken as scenarios were designed as nested evenness levels namely, high evenness, medium evenness and low evenness scenarios.

The FunBumble model investigation of these scenarios, showed that as community evenness increased the temporal seed yield stability too increased due to portfolio effect and species asynchrony in the presence high evenness. Whereas, the low magnitude increases or decreases of temporal productivity depended largely on sign of selection effect and contributions of co-dominance identities. For example, when unproductive ST species *B. terrestris* is dominant due to negative selection effect, the co-dominant highly productive LT species contributed positively resulting in over yielding of productivity and enhanced species co-existence causing positive influence on biodiversity. This mechanistic understanding of biodiversity, productivity and stability relationship of realistic *B. terrestris* dominance identity scenarios showed that the bumble bee community composition since 1940's in red clover production system had acted as species co-existence promoting buffering mechanism under the presence of selection processes like landscape and environmental homogenisation due to agricultural intensification. Especially the contemporary (2010) least evenness scenario with no LT species as co-dominant illustrates the reasons for current decline in both stability and productivity of red clover seed yield. This necessitates, the need for local and landscape scale management measures for increasing relative abundance of LT species, through nesting and floral resource facilitation in crop production systems.

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1. Introduction

பகுத்துண்டு பல்லுயிர் ஓம்புதல் நூலோர்

தொகுத்தவற்றுள் எல்லாந் தலை

Paguththundu palluyir oambudhal nooloar

Thoguththavattrul ellaandh thalai

Equally Shared Consumption of Food to Protect Diverse Living Beings

Is, The Prime Principle Amongst All Compiled by Scholars

<div align="right">(Chapter 33: Couplet 322, Thirukkural by Thiruvalluvar)</div>

The importance of conserving the biodiversity in human dominated systems is being increasingly appreciated in recent decades to facilitate a safe operating space within the planetary boundaries, e.g. through sustaining ecosystem service value of agricultural landscapes (Loreau *et al.*, 2001; Fischer *et al.*, 2006). The current paradigm of policy making necessitates evidence-based conservation frameworks which also enables conservation researchers to explore and prioritize the key ecosystems for stewardship, based on understanding from basic ecological sciences. Hence, it becomes vital to explore the mechanistic role of biodiversity in maintaining the key ecosystem functions that has direct effect on the ecosystem services which are vulnerable to anthropogenic global change (Loreau *et al.*, 2001). The biodiversity (Species Richness & evenness) & ecosystem function (BEF) research has produced compelling evidences that biodiversity enhances ecosystem functions and interestingly, now in recent years it has moved ahead from the question of "whether biodiversity matters?" to "how does it matter in specific systems?" (Reiss *et al.*, 2009). And my study addresses the latter, -question "how"- to draw a mechanistic understanding of functional processes.

The prediction that the impact of anthropogenic forcing would be more rapid on species abundance, evenness/relative-abundance more than species richness and sometimes evenness decline would cascade into subsequent decline in species richness (Chapin *et al.*, 2000) had attracted the attention of BEF research (Wilsey & Potvin, 2000). However, since pioneering BEF studies, in contrast to species richness there are very few on evenness, that too have given contrasting and inconclusive evidence for the links between the evenness and ecosystem functions, which emphasizes the need for improved focus on the latter (Hillebrand *et al.*, 2008; Reiss *et al.*, 2009).

The long-held two fundamental and complex questions in ecology are diversity-productivity relationship and diversity-stability relationships, which were also addressed by the BEF research., rightly the seminal diversity (evenness)-productivity (DEP) & diversity (evenness)-stability (DES) investigations started to address the question whether diversity(evenness) or sampling effect of highly productive species identities drives productivity dynamics by keeping the

variability in species identities/richness constant in diversity (evenness)-productivity relationship experiments and concluded that biodiversity, productivity and stability is driven by diversity above and beyond sampling effect of species identities (Wilsey & Potvin, 2000; Polley *et al.*, 2003; Wilsey & Polley, 2004; Isbell *et al.*, 2009). Hence, the objective of this paper is to test the importance of evenness in relation to a specific ecosystem function.

The exercise of quantifying the influence of community evenness in delivering ecosystem services, is analogous to the half a century old practice of assessing financial system dynamics driven by mean-variance portfolio theory's "portfolio effect" (Markowitz, 1952; Figge, 2004; Schindler *et al.*, 2015). According to a seminal "portfolio effect" paper in basic ecological sciences research by Doak *et al.*, (1998), the statistical averaging of the several randomly &nonrandomly varying individual species identities would yield less variable aggregate-sum causing a portfolio effect in overall function/service delivery, that is interpreted also as community stability in the field of community ecology, or further recently incorporated into efforts of theorizing invariability (Haegeman *et al.*, 2016; Delsol *et al.*, 2018; Wang *et al.*, 2017). Importantly, this portfolio theory is being used as a "simulation tool" for understanding & managing system dynamics in the present risk & uncertainty prone global change scenario by quantitatively investigating, the relative magnitude and reliability (stability) of specific spatio-temporal ecosystem-service delivery, catered by the relative proportion of each species and their aggregate sum dynamics in diverse ecosystems (Tilman *et al.*, 1998; Tilman, 1999; Hildebrandt & Knoke, 2009; Moore *et al.*, 2010; Schindler *et al.*, 2010).

Globally, pollinator declines have raised concerns among scientists about the stability of pollination service that is vital for maintenance of both wild plant communities as well as agricultural productivity (Potts *et al.*, 2010; Winfree *et al.*, 2011). Worldwide, 75% of the crop plants rely on animal mediated pollination (Klein *et al.*, 2007), among them the pollination services of many crops are perceived to be dependent on the single domesticated species *Apis mellifera*. Such, reliance on any single domesticated pollinator species is risky, because pollinators are vulnerable to various diseases and parasites, that may lead to uncertainty in crop pollination service efficiency and the resultant loss of crop productivity (Winfree *et al.*, 2007). The conservation of native pollinators or wild bees has been the management practice advice over the last many decades (Bohart, 1972), albeit the increasing impact of intensive conventional farming on wild bees, has further emphasized vitality of prioritizing the conservation management of these native wild pollinators for pollination service insurance (Winfree & Kremen, 2009; Winfree *et al.*, 2011; Garibaldi *et al.*, 2013).

In Europe out of the total 68 bumble bee species, 24% are threatened with extinction (IUCN, 2014). Agricultural intensification driven low effective population sizes of bumblebees render the local populations to experience inbreeding and stochastic extinctions due to poor habitat quality by reducing the diversity of floral resources, loss of nest sites, pesticide pollution and

habitat fragmentation (Goulson *et al.*, 2008). However, notwithstanding the general impact of agricultural intensification over the agroecosystem quality, the cultivation of mass flowering crops (MFC) is also evidenced to be an additional floral resource aiding wild bumble bee conservation (Westphal *et al.*, 2003; Holzschuh *et al.*, 2013).

Thus, to study the effect of evenness on the ecosystem function, the choice of bumble bees dependent on MFC landscapes is appropriate because, the historic economic importance of this production system had made available historic community-wide abundance trends for this community. Investigations recently conducted at different (local and regional) landscape scales has analysed such temporal empirical data to prove the historic decline in population abundance of many species and also the drastic structural changes in community of the bumble bees in red clover (*Trifolium pratense*) agro-ecosystems (Dupont *et al.*, 2011; Bommarco *et al.*, 2012). Therefore, in this study simulation approach is used to theoretically understand the ramifications of such temporal community structure changes on red clover seed production, and to advance the applied ecological implications of these understandings.

The red clover is an important forage legume crop as well as a rotation crop for soil improvement. Both honey bees and bumble bees pollinate this crop, but comparatively the latter is more efficient pollinator of red clover specifically because of their relatively long tongue length (Rao & Stephen, 2009). Also, each bumble bee species has a pollinator identity, which is due to their distinct differences in morphology, physiology and foraging behaviour (Bergström, 2010).

Objective of this study is to conduct simulation experiment for the effect of bumble bee evenness variation over the red clover seed production to address the following questions,

1. How varying levels of bumble bee community evenness affect ecosystem function (Seed yield temporal variability)?

2. How the identity of a dominant pollinator influences the evenness levels and seed yield temporal variability?

3. What is the role of species tongue length in mediating evenness levels and seed yield temporal variability?

2. Materials and Methods

2.1 Study System

The self-sterile red clover (*Trifolium pratense*) crop is pollinated by bumble bees, which are considered to be primary pollinators than the relatively shorter tongue length honey bees (McGregor, 1976). Bumble bee community are also said to be the, most efficient pollinators among the various flower visiting insects of temperate and cold climatic zones (Wolf & Moritz, 2014). The functional identities of this community are given rise by the morphological trait tongue length determined foraging behavioural trait (Inouye, 1980). The community is classified by former as short tongued (ST, e.g. *B. terrestris*) & long tongued (LT, *B. subterraneus*) (See Table 1) species and by the latter as legitimate nectar feeders & nectar robbers (Rao & Stephen, 2009). Nectar robbing is a foraging behavioural trait of short-tongued pollinators (e.g., *B. terrestris* & *B. lapidarius*), that feed the nectar by making holes in floral parts without engaging in pollination service as the legitimate nectar feeders. For example, the ST *B. terrestris*, besides consuming nectar and pollen legitimately, a significant proportion of its individuals additionally involves in robbing behaviour, whereas few other ST species like *B. lapidarius* being smaller in body size and the resultant weaker jaw strength relatively, makes them secondary robbers by using primary robber *B. terrestris* robbing holes (Bergström, 2010).

The bumble bee pollinator identity and efficiency study in red-clover crop had been conducted by Bergström, (2010) using a representative subset, such as the long tongued species *B. hortorum* & *B. subterraneus* and short tongued species *B. lapidarius* & *B. terrestris.* Investigation of pollinator identities for key parameter estimations in this study shows that, individual pollinator efficiency (IPE) is influenced by the behaviours such as (i) tongue length determined nectar robbing behaviour and (ii) seed set success (iii) flower handling time. Among these three key processes, only the seed set success had no distinct differences and effect among the species identities and their IPE respectively. Therefore, the vital differences among each species and their functional identities is contributed by combination of variability of flower handling time (VFHT) and variability of nectar foraging/robbing behaviour (VNFRB). Bergström (2010) generalized that, relatively among functional identities the long-tongued species are quicker in pollinating the florets, whereas short tongued species had relatively less seed set efficiency due to nectar robbing behavior. Therefore, the IPE that is calculated combining the pollination efficiency estimates for both legitimate visits & robbing visits shows that, the pollinator identities of long tongued traits are several times highly efficient than the short-tongued. Thus, IPE turned out to be highly efficient for *B. hortorum* (LT), closely followed by *B. subterraneus* (LT) and *B. lapidarius* (ST) is moderately efficient, whereas *B. terrestris* (ST) is least efficient. However, when Bergström (2010) assessed the field abundance weighted IPE i.e., the population pollination effectiveness (PPE), the highly abundant *B. terrestris* (ST) followed by *B. lapidarius* (ST)

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species has higher pollination effectiveness than the long tongued. In summary, LT species are most efficient as individuals, but given the current scenario of global pollinator decline increasingly being contributed by LT bumble bee population abundance, their IPE therefore doesn't translate into PPE.

From the above understanding of the study by Bergström (2010), for any ideal and comprehensive forecast modelling for red clover seed yield, the individual pollinator efficiency (IPE) estimates would be used to model with empirical proportional abundance. Because, comparatively IPE also accounts for inter-species variability in the flower handling time (VFHT), that contributes significantly to the pollination efficiency difference among species besides foraging behaviour. Instead, in this study seed set parameter alone used, which doesn't have statistically significant inter-species difference. Though this is a shortcoming, nevertheless this study could provide the preliminary understanding about portfolio effects on stability of red-clover seed production affected by foraging trait difference and evenness. Bergström, (2010) obtained the seed set estimates as pollinator specific "mean seed set per visit" per flower head by calculating the proportion of florets that set seeds among the total number of florets in the visited virgin flower head by an individual bumble bee.

In this modelling study, the bumble bee community feedstock data of empirical proportional abundance signifying their historical (1940, 1960 & 2010) composition shifts at regional scale is gathered from the recent investigations in red-clover production system of Sweden by Bommarco *et al.*, (2012). To gain a categorical understanding about the influence of demographic identities constituting composition shifts (such as dominant, intermediate and rare), the species which are higher than 10% proportion were classified as dominant; the species which are higher than 1.0 % is taken as intermediate and less than 1.0 % as rarer species (See Table 1). To compensate for non-inclusion of the key parameter VFHT that account for tongue length correlated variability (Bergström, 2010), the community is merely classified into LT and ST to gain a categorical understanding of them on distinct evenness scenarios, based on the tongue length functional traits.

2.2 Simulation design

The simulation design comprises of constructing a mechanistic model - "FunBumble" - of the community portfolio dynamics and designing the feedstock scenarios for simulation experiment. The following sections are description of these two tasks.

2.2.1 Simulation design Overview

FunBumble Model –Part 1

Peak Pollination/ Day (D) =	0.1 Visits/FH/Hr / 5 Hrs/D	
Pollination Days / Mass Flowering Period (MFp) =	0.5 Visits/FH/D / 5 Day	
4 MFp/Mass Flowering season (MFs) =	2.5 Visits/FH/MFP / 4 MFp	
1 Potential(p) MFs of seed production out of 2 MFs per Year =	10 Visits/FH/ MFs / 1 pMFs/yr	
23,650 FH/100 m² =	10 Visits/FH/Yr / FH/100 m²	
	236,540 FH Visits/100 m² /Year	

ST_B. terrestris
ST_B. lapidarius
40%(B.ter.) + 16%(B.lap)
LT_B. pascuorum
LT_B. distinguendus
LT_B. hortorum
LT_B. subterraneus
LT_B. sylvarum
ST_B. hypnorum
ST_B. pratorum
ST_B. sp. (B. Jonellus)

SPECIES SPECIFIC (SS)
STANDARD ERROR _SE

Yearly Visits
TEMPORAL VARIABILITY

Inter-annual Demographic Dependency of Visits
Visits of a species in a year is relative to its old visits frequency

New Mean Visits(t) = VISITS[S](t) Old (Mean Visits [S](t-1))

VISITS[S] = Visits_S.E New_Mean (Visits) Year_S.E **Jitter: Noise**

(t) = 100 years

Total Visits ✖ Species-Specific [SS] Relative Abundance

SS Temporal Variability

Correlation of yearly visits

SS Visits Constrained By Demographic and Yearly Variability

SS Mean Visits
Total Visits spread across all species proportional to relative abundance of the community

Visits_S.E
SS empirical abundance standard error translating into variability in visists

Year_S.E
Community wide common good & bad Year for bumble bee visits

Visits [S]
Species Specific - SS

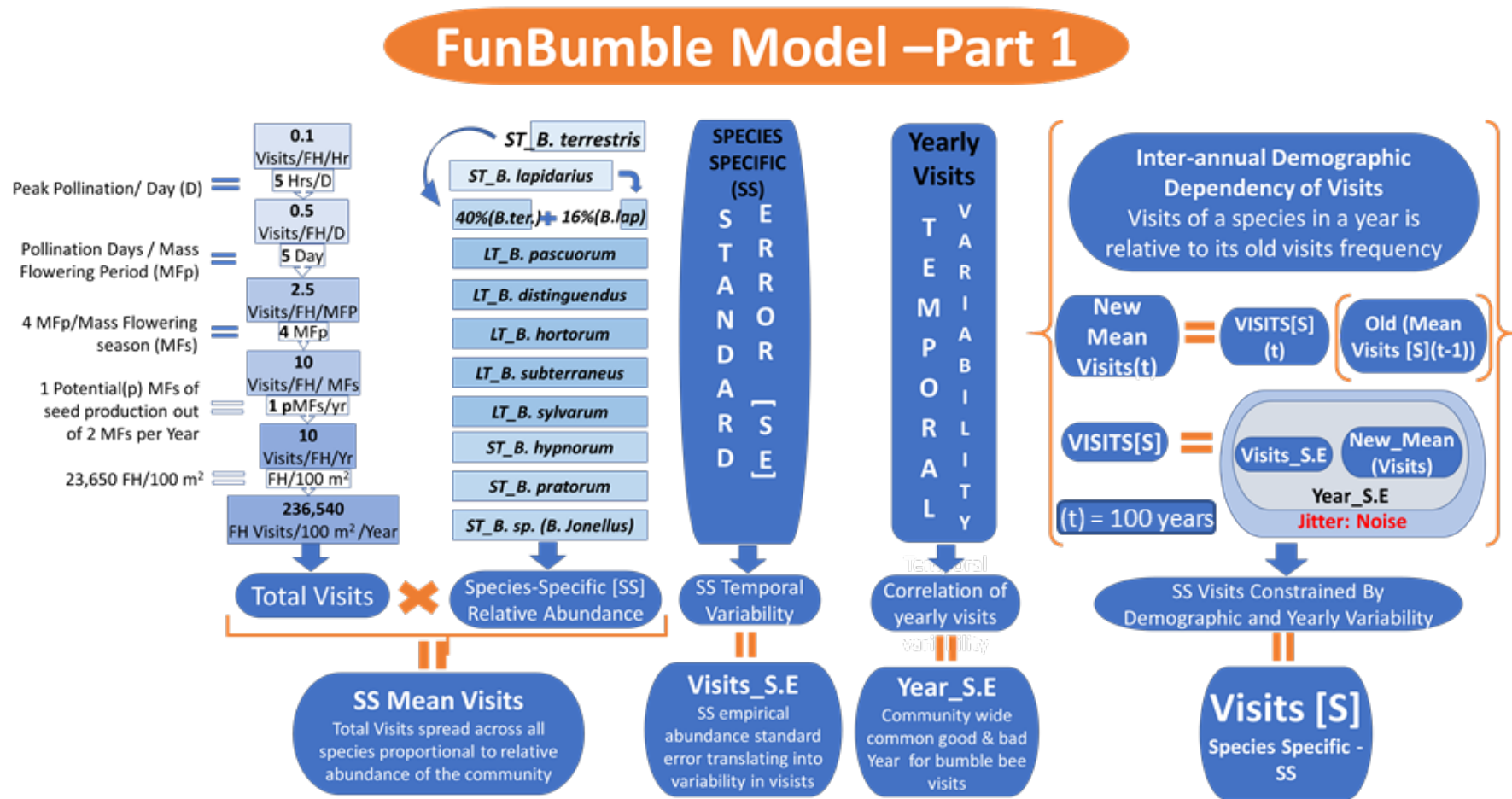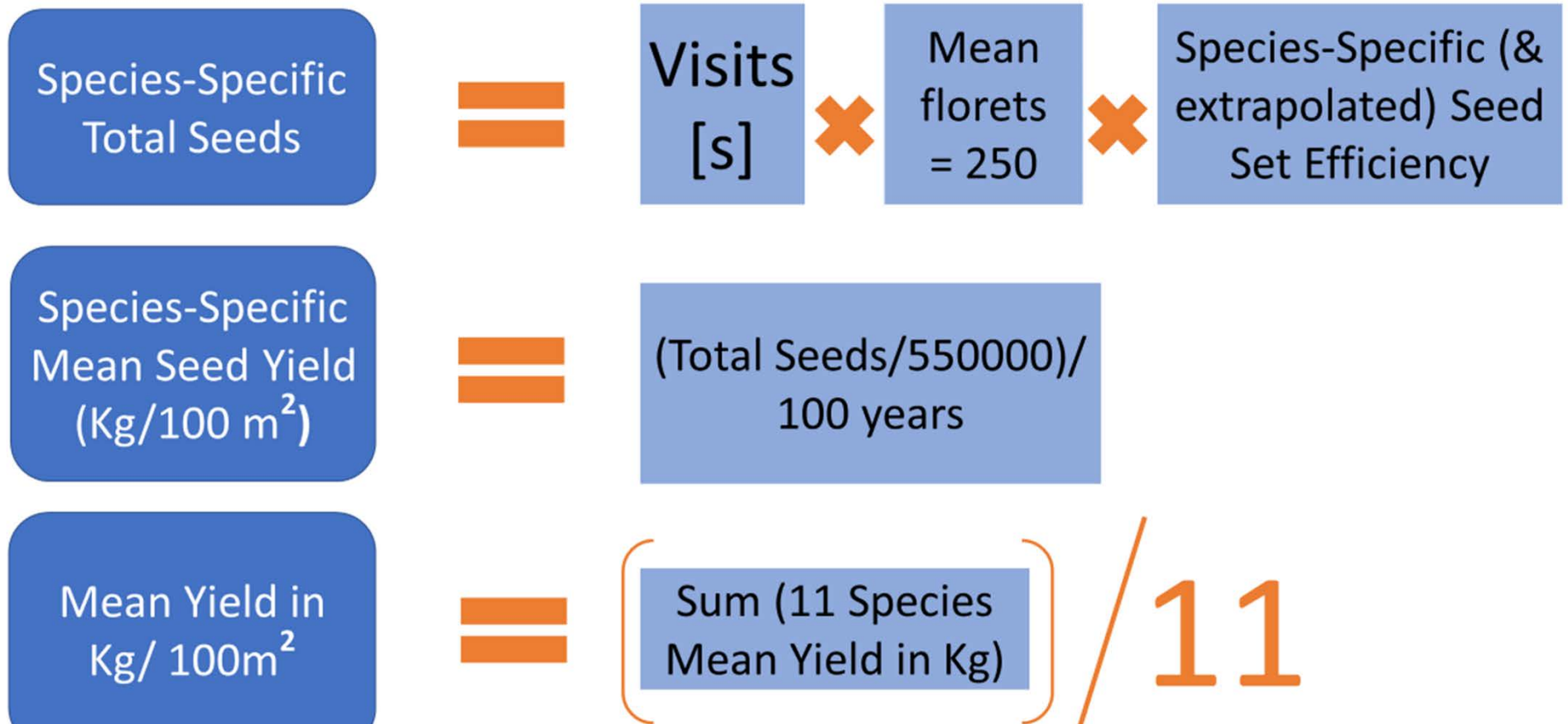*Fig: 1: Simulation model flow-chart - part 1*

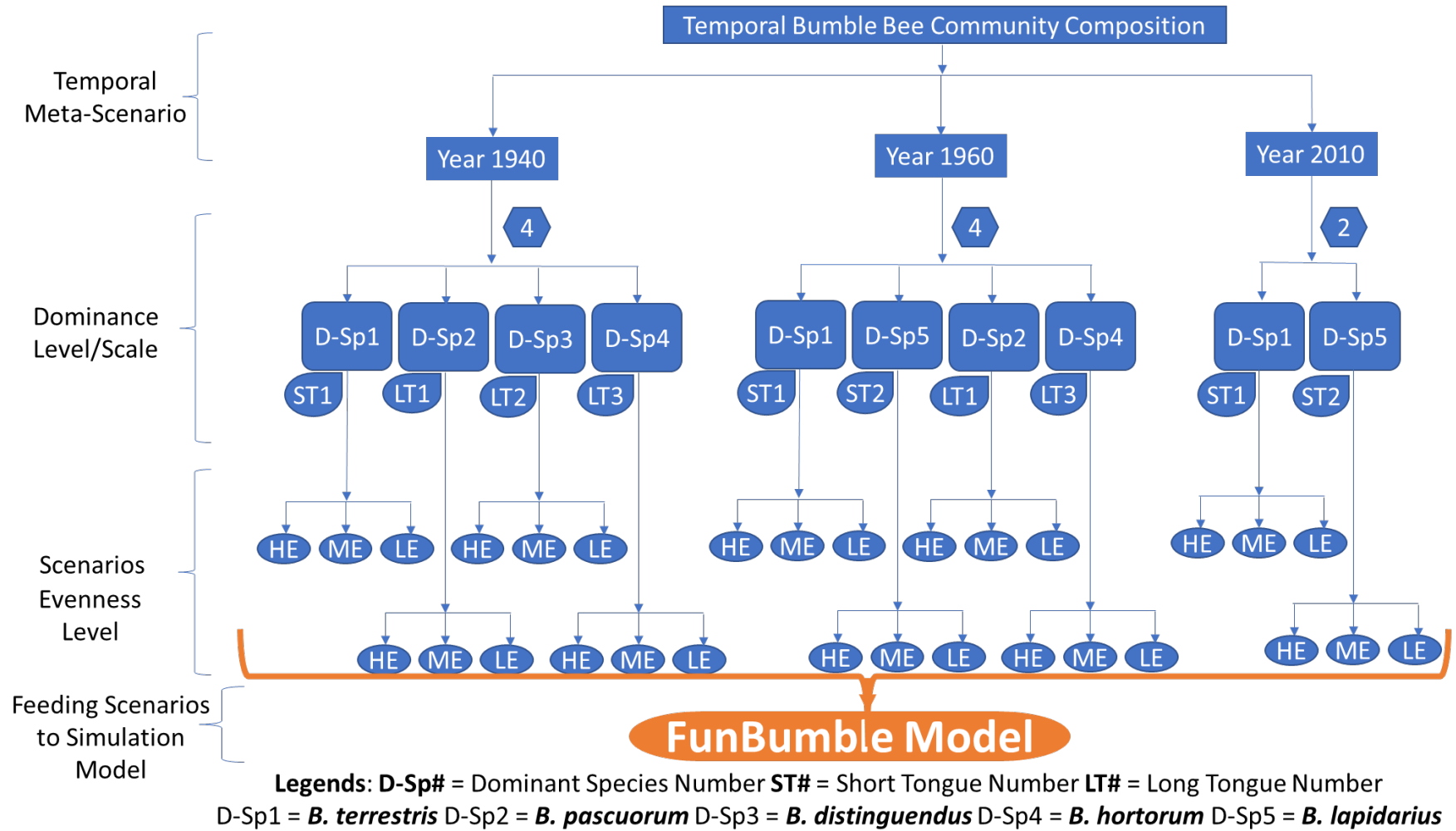*Fig: 2: Simulation model flow-chart - part 2*

Fig: 3: Simulation meta-scenarios (12+12+6=30) classification

2.2.2 *FunBumble: Red clover seed yield model*

The production of red clover seeds starts with the individual bumble bee visits to flowerheads for consumption of nectar (See Fig 1 & 2: FunBumble flowchart part 1 & 2). The biological constraints that determine the red clover seed yield are accounted for in the FunBumble ecosystem function model, as shown in the following description of the model.

2.2.2.1 Bumble bee visits: from an individual frequency to spatial frequency

The total numbers of floral (flower-head -FH i.e. inflorescence) visits of the bumble bees (BB) were obtained empirically (Collected from field study of Ola Lundin) as 0.1 bumble bee visits per flower-head per hour (See Fig.1 Flowchart of FunBumble Model part 1). This was computed with the 5 hours of peak pollination period in a day to get bumble bee visits per FH per day as 0.5 visits/flower head/day. The florets of the flower head, that opens from bottom to top at the rate of 18 florets per flower head per day, each unpollinated florets before wilting remains open for 6 pollination days according to Clifford & Scott (1988), 8 pollination days according to McGregor, (1976) and 10 pollination days according to Taylor & Quesenberry, (1996) and these pollination days could be considered as a flowering period. However, in this model each mass flowering period (MFP) is composed of 5 days as peak pollination days. Therefore, bumble bee visits of each mass flowering period computed as 2.5 visits/FH/MFP. Each year consists of early, mid and late mass flowering sub-seasons (MFS). It is assumed in this model, that each mass flowering sub-season, consists of 4 mass flowering periods, which is lower than the reality of approximately 60 days of main flowering period (Bommarco *et al.*, 2012). Based on this assumption bumble bee visits are computed as 10 visits/FH/MFS. Further, there is one potential high yielding seed production season for temperate cropping system in a year i.e., late mass flowering season before overwintering (Taylor & Quesenberry, 1996; Ohberg *et al.*, 2005), therefore one potential mass flowering sub-season (1 pMFS) computed for visits as 10 visits/FH/Year. Finally, the empirical spatial estimate that there are 23654 flower heads per 100 m^2 (Rundlöf *et al.*, 2014) in a full bloom red clover crop system, which yielded spatial computation of FH visits as total bumble bee visits per year per 100 m^2, which gives spatio-temporal total-visits 236,540 visits/year/100m^2.

2.2.2.2 Proportional abundance weighted visits

The historic empirical proportional abundance was taken from the study of Bommarco *et al.*, (2012) paper's Table S1 to feed the FunBumble model for temporal seed yield. Also, the study by Bergström, (2010) estimated that, 40% & 14 % population of the *B. terrestris* & *B. lapidarius* species respectively are robbing individuals. To enable explicit modelling of relative robbing behaviour's effect, the respective combined proportions of these two species, where taken as a distinct species (See Table 1, Fig 1 & Sample Scenarios in Table A2 of Appendix) from legitimate proportions of the

same species, which is used for both experimental scenarios and empirical temporal seed yield forecast. Thus, there are totally 11 species composed of 10 natural species identities and one robbing species. So, the total numbers of flower head visits per year were distributed among the 11 bumble bee species in accordance to the proportional abundance to obtain the species-specific mean visits per year per species (See the Fig 1 & FunBumble R Script in Appendix).

Table: 1 Bumble bee community composition structure

Pollinators	Tongue Length	Demographic Identity		
		1940's	1960's	2010's
B. terrestris	ST	Dominant	Dominant	Dominant
B. lapidarius	ST	Intermediate	Dominant	Dominant
B. pascuorum	LT	Dominant	Dominant	Intermediate
B. distinguendus	LT	Dominant	Intermediate	Rare
B. hortorum	LT	Dominant	Dominant	Intermediate
B. subterraneus	LT	Intermediate	Intermediate	Intermediate
B. sylvarum	LT	Intermediate	Intermediate	Rare
B. hypnorum	ST	Rare	Rare	Rare
B. pratorum	ST	Rare	Rare	Rare
B. sp. (B. jonellus)	ST	Rare	Rare	Rare
Robbing Species	ST	Dominant	Dominant	Dominant

2.2.2.3 Stochasticity in visits

The FunBumble model is designed to run for t = 100 years as temporal replication. Throughout these replications, the model contains different sources of variability. First, the empirical standard mean error (SME) of the species-specific proportional abundance obtained from Bommarco *et al.*, (2012) paper's Table S1 for introducing species-specific temporal population variability in the community. The standard mean error is introduced also to the robbing species from the standard mean error of *B. terrestris* since this species contributes relatively more to the robbing identity. So this introduction of standard mean error of visits to each species forms FunBumble model variable visits_s.e (See Fig 1 and FunBumble Script in Appendix).

Second, the FunBumble model accounts also for yearly temporal correlation across pollinators, so a bad year is equally negative for all species. This temporal variability adds to the model as the variable Year_S.E (See Fig 1 and FunBumble Script in Appendix), computed using random normal distribution (rnorm) function in R programming platform to introduce 25th percentile as bad year and 75th percentile as good year for species specific visits computation as Visits[S].

Third, the inter-annual demographic dependency of bumble bee visits i.e., the visitation rate in a year is calculated by taking account of last year's visitation rate, so the visitation in a specific year is not independent of previous years. This is computed as model variable named "New Mean Visits(t)"

of the year t. It was computed by taking the past year Visits [S] of specific species as the precursor for current year's visits. In that way the mean expected visitation at year t, takes the value at t-1.

Finally, stochasticity is implemented using the jitter function. This function is to introduce the statistical noise around the yearly community wide correlated variability. Total visits are assigned to the different species using function qnorm. qnorm function compute is used to match the evenness distributions.

2.2.2.4 Species Specific Visit frequency

The visit frequency was computed for 100 years as temporal replication. In summary, the total visits of specific bumble bee identities are calculated by considering the spatial flower head density, temporal visit frequency per flower head and variability in visit frequency, which is computed from standard mean error of the proportional abundance and correlated community wide temporal variability and inter annual dependence of bumble bee visits. (See Fig 1 FunBumble flowchart part 1)

2.2.2.5 Mean florets per flower head

The total number of florets are highly variable depending on red clover varieties such as diploid and tetraploid varieties (Taylor & Quesenberry, 1996). The floret numbers in each flower head ranges between 55 to 300 (McGregor, 1976; Taylor & Quesenberry, 1996). In our FunBumble model, the mean florets 250 is used for modelling. (See Fig 2 FunBumble flowchart part 2)

2.2.2.6 Mean seed set efficiency estimate

The estimation of mean seed set efficiency parameter done only for 4 representative species, 2 for LT and 2 for ST tongue length by the study of Bergström, (2010). Therefore, the estimate ranges of those few species where used to extrapolate for the remaining species. The mean seed set efficiency range of ST species *B. terrestris* and *B. lapidarius* were also used for the remaining 3 ST bumble bees (See Table 1A). And similarly, the mean seed set efficiency range of LT species *B. hortorum* and *B. subterraneus* were extrapolated to the remaining three LT bumble bees. "Mean seed set efficiency" of robbing species is 0.1 whereas the mean seed set efficiency of the ST species ranges from 0.50 to 0.54 and the LT species ranges from 0.41 to 0.49. Mean seed set efficiency is kept constant throughout all designed scenarios of simulation experiment as well as while modelling three empirical scenarios for temporal seed yield.

2.2.2.7 Computing mean yield & coefficient of variation in kg

The total species-specific seeds per year were calculated by the product of species-specific total visits (Visits[S]), mean florets per flower head (250) and species-specific mean seed set efficiency (See Fig 2 FunBumble flowchart part 2) throughout the 100 years temporal replication. The 100 years sum of the obtained species specific total seed numbers per 100 m^2 per year is divided by 550,000 seeds (McGregor, 1976) to obtain the seed yield in kilograms for 100 years, which is further divided by 100 to obtain species specific, mean seed yield in kilogram per year. The bumble bee community

ecosystem function mean yield in kg/100m^2 is obtained through average of species-specific mean yield in kg of all the 11 species.

Finally, the mean yield in kg and its coefficient of variation is computed through 100-year temporal replication where not tested for statistical significance. Because the frequentist statistical hypothesis tests are inappropriate for simulation experiments, where high replication of experiments produces miniscule p-value irrespective of its effect size and additionally the differences between parameters are known a-priori, which makes hypothesis testing irrelevant for modelling investigations (White *et al.*, 2014).

2.2.3 Simulation experiments

Since, last decade the diversity-productivity/stability relationship researchers were cautioned about two problems, first is against using unrealistic maximally even scenarios in evenness level treatments of field experiments (Huston, 1997; Wardle, 1999; Huston *et al.*, 2000) , that hamper the translatability of results from basic ecological sciences to applied and conservation ecology (Huston, 1997; Schwartz *et al.*, 2000; Srivastava & Vellend, 2005) and second, inevitability of evenness level decomposition through the successive years had been noted as limitation of evenness treatments in laboratory & field experiments (Isbell *et al.*, 2009; Wittebolle *et al.*, 2009). The first concern was addressed through, mimicking the realistic community structure from natural systems (Wilsey & Polley, 2004; Zavaleta & Hulvey, 2004; Isbell *et al.*, 2008). The second problem could be addressed only through simulation modelling with temporal replication of persistent evenness levels, to gain complementary understanding besides the field experiments of BEF. Additionally, simulation based experiments enable us to advance the conceptual realism to empirical realism of rarity-extinction scenarios (Isbell *et al.*, 2008).

Therefore, scenarios, each with unique combination of evenness level and dominant species identity is taken as the fundamental unit of the experiment (See Fig 3 Simulation Scenario's Classification), nested under the temporal meta-scenarios, that are provided by the historic (1940, 1960 & 2010) empirical relative abundance data (Bommarco *et al.*, 2012). The various levels of evenness (High evenness-HE, Medium evenness-ME and Low evenness-LE) were generated manually as realistic to semi-realistic rarity-extinction scenarios, mimicking the empirical community structure of respective temporal meta-scenario. The evenness level ratios of demographic identities dominant, intermediate & rare species (D: I: R) were respectively classified and kept constant through each scenario as HE 50:27:23, ME 79:13.50:7.50, LE 91:7.20:1.80. The proportions of each bumble bee species were manually adjusted to match these listed evenness level ratios. In addition to the evenness level ratios, the proportional abundances of each species were manually manipulated to obtain constant pielou's evenness index values for all evenness levels throughout each scenario. For example, the 1940's and 1960's populations were composed of 4 dominant species (See Table 1) (Pielou's index of HE = 0.98, ME=0.76 and LE=0.45) and for 2010's data there were only 2 dominant species

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(Pielou's index of HE = 0.87, ME=0.75 and LE=0.53). The level of dominance (4 & 2), constrained the ability to retain constant pielou's index across all three meta-scenarios. Hence coercing & obtaining same evenness was difficult but the evenness levels are qualitatively comparable. So, each scenario unit is part of respective evenness levels and dominance levels. To test the effect of dominance identity, the scenarios were also made to represent one among 4 or 2 dominant species belonging to respective temporal meta-scenarios.

So, among the 10 species identities of 1940's there were 4 dominant species, for example the dominant species identity *B. terrestris* proportional abundance kept as dominant species through each evenness levels (HE, ME & LE) rendering three distinct scenarios of this specific dominance identity. Therefore, the similar process of scenario preparation for other three dominant species identities under the 1940's meta-scenario produced totally 12 scenarios. In the case of 2010 temporal meta-scenario, the 2 dominant species generated only 6 scenarios. Totally there were 12 scenarios for each 1940's and 1960's data, i.e., 4 dominance identities for each evenness levels (HE, ME and LE). Whereas for the 2010's data there were only 6 scenarios i.e. 2 dominance identities for each evenness levels.

Among the five dominance identities of this bumble bee community, only *B. terrestris* is represented in all three meta-scenarios (See Scenario Classification in Fig 3), whereas *B. lapidarius (1960's and 2010's)*, *B. pascuorum (1940's and 1960's)*, *B. hortorum (1940* 's & 1960's) are present only in two temporal meta-scenarios. Finally, *B. distinguendus* is represented only in one temporal meta-scenario of the year 1940's. And, totally there were 30 scenarios in this simulation experiment. Among these scenarios of dominant species identities, except *B. terrestris* all other dominant species identity scenarios are semi-realistic rarity-extinction scenarios.

While manipulating the proportional abundance for each dominant species identity, the intermediate species and rare species proportions were kept constant throughout all the specific dominant species identity scenarios in each evenness level (See the sample Scenarios attached in Appendix I as Table A1). This enables the ability to categorically understand the effect of the respective dominance identities in each evenness levels and dominance levels. The FunBumble model is designed to retain empirical standard mean error constant for the species abundance distributions of all the scenarios across all evenness levels in each temporal meta-scenario.

Each scenario was simulated for t = 100 years, which is temporal replication for 100 years, where at each year the productivity of each species is subjected to statistical averaging at aggregate community portfolio, further this 100-year replication is to quantify the variance in the mean productivity of bumble bee community caused by evenness levels as CV of red clover seed yield beyond the constraints of non-random biological and statistical dampening of variance. Therefore, this eliminates the need for redundant replication of the simulation runs of each scenario. These results were presented as box plots of the seed yield's coefficient of variation and mean seed yield of each dominant species identities, tongue length functional group and evenness levels.

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Additionally, the historic empirical proportional abundances from Bommarco *et al.*, (2012) paper's Table S1 was taken as empirical natural scenarios (1940's, 1960's & 2010's, Pielou's evenness (J) are 0.76, 0.65 and 0.41 respectively), while all other components of FunBumble model are similarly kept constant as designed scenarios and their performance in the FunBumble model was comparatively tested in terms of 100 years temporal seed yield with designed scenarios of evenness level gradient. This enables comparative mechanistic understanding of the effect of evenness level gradients in natural system and its productivity.

3. Results

3.1 Simulation experiment results

3.1.1 Effect of community evenness levels on temporal seed yield

The species evenness levels have higher impact on the CV(yield) than the mean yield in kg (See Fig 4A & 4B). It's necessary to note that, there are only 6 scenarios under 2010 community composition structure, where only two species are dominant contrasting the 4-dominant species of 1940/1960's community structure resultantly 12 scenarios (See Fig 3), however, there are equal number of scenarios for each evenness levels (10 scenarios each for HE, ME, LE, See Fig 3). Additionally, the unequal scenarios between the final meta-scenario and others is caused by the constrain of not being able to achieve constant pielou's evenness levels across the meta-scenarios, which doesn't however constrain the ability to glean the effect of evenness levels across meta-scenarios (See Fig A1.8 & A1.9).

Fig: 4: CV(Yield) & mean(Yield) in kg Vs community evenness levels

Aggregated meta-scenario comparison of 100 years temporal CV(Yield) & mean (Yield) in kg aggregated across dominance level and dominant species identity scenarios plotted against evenness levels. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually. Refer Fig A1.11 & Fig A1.12 to see the meta-scenario comparison of this plot.

The aggregated CV(yield) and mean yield in kg of all meta-scenarios shows that, the CV(yield) increases with large magnitude as the evenness level decreases and whereas the mean yield in kg shows confounded positive and negative effect as the evenness level decreases (See Fig 4A & 4B). However, under the disaggregated view of each meta-scenario contrasts the aggregated meta-scenario results, because there is low magnitude positive & negative relationship between the evenness levels and mean yield in kg across all meta-scenario determined by the proportion of robbing behaviour (See Fig 4B, A1.9 & A1.11), whereas CV(yield) relationship with evenness level is consistent in both aggregated and disaggregated view of the meta-scenario results (See Fig 4A & A1.10).

Besides the portfolio effect caused evenness level effect on stability, there is contribution of population fluctuation too in the form of species total visits asynchrony, which is determined by the standard mean error of the proportional abundances. The realistic population fluctuation/realistic standard mean error structure at regional scale is empirically shown in the Table S1 of Bommarco *et al.*, (2012) study shows that, through historic (meta-scenarios) increase of proportional abundance of super-generalist dominant/co-dominant ST identities (*B. terrestris* & *B. lapidarius*), the standard mean error declined. Similarly, for LT co-dominant species, ST and LT intermediate and rare demographic identities, with decreasing proportional abundance the standard mean error relatively decreased historically.

This empirical inter-species standard mean error characteristic of dominance identity is impaired in this study's scenario design by having realistic standard mean error for *B. terrestris* scenarios alone, but unrealistically constant standard mean error for all other 4 dominant species identity (both ST and LT) scenarios, which is due to making *B. terrestris* dominance identity scenario's realistic standard mean error as constant across all the other dominance identity scenarios under each meta-scenario.

Though, the inter-species standard mean error become unrealistic due to its constant nature in scenario design across each meta-scenario, the overall realistic standard mean error structure across each meta-scenario contributes to realistic population fluctuation and its categorical effect across evenness levels. Through all meta-scenarios the population fluctuation declines as the standard mean-error declines, with 2010 meta-scenario showing least population fluctuation.

Thus, our simulations indicate that there is a positive diversity-evenness-stability relationship causing the stability of ecosystem function red clover mean seed yield, due to portfolio effect and compensatory population fluctuation as standard mean error under the high evenness scenarios. Whereas, the positive or negative diversity-evenness-productivity relationship is determined by the robbing identity proportion in scenarios.

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3.1.2 Effect of tongue length on temporal seed yield

In this simulation experiment, there were 2 short tongue dominant species and 3 long tongue dominant species. The dominant long tongue bumble bees were not present as dominant in 2010's data (See Fig 3).
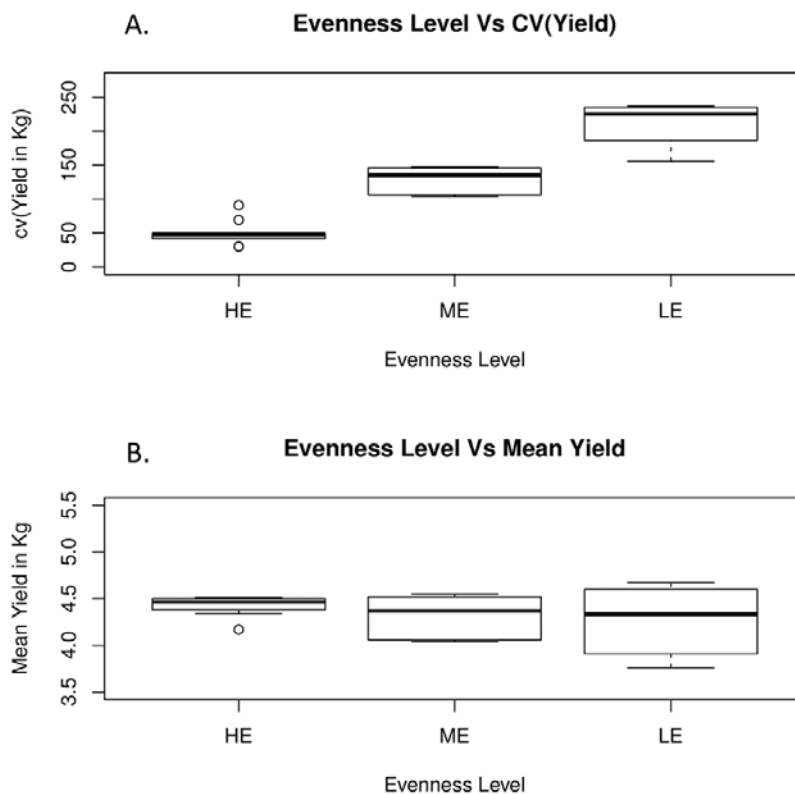

Fig: 5: *CV(Yield) & mean(Yield) in kg Vs. tongue length trait*

> *Aggregated meta-scenario comparison of 100 years temporal CV(Yield) & mean (Yield) in kg aggregated across evenness levels, dominance levels and dominant species identity scenarios, plotted against tongue length trait. Refer Fig A1.17 & Fig A1.18 to see the meta-scenario comparison of this plot. The box-plots show the median (horizontal line in the box) value for each species evenness level. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.*

The short tongue dominance scenario shows low magnitude difference CV(yield) with long tongue dominance identity scenarios (See Fig 5A & FigA1. 12). This long spread of the CV(yield) in both ST and LT is contributed by the evenness levels and additionally the unrealistic standard mean error of co-dominant robbing proportion contributes to the increase in CV yield of LT dominance identity scenario. Whereas in the case of mean yield, the LT dominance identity scenarios increases productivity dampening the co-dominant ST robbing proportion even with unrealistic standard mean error. The robbing behaviour of the short tongue bumble bees decreases the mean yield of the ST dominance identity scenarios (See Fig 6B & FigA1. 13) with relatively high variability due to realistically high standard mean error of super-generalist ST dominance identities.

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3.1.3 Effect of dominance identity on temporal seed yield

The low magnitude mean yield decrease (See Fig 4B & FigA1.15) of the short tongue dominance identities is caused more by proportion of robbing behaviour, which is evident from both disaggregated & aggregate plot. Distinctly from other dominant species identities, *B. terrestris* boxplot alone shows long spread of mean yield in kg, which is contributed by the aggregation of evenness levels across meta-scenarios under this dominant species identity.
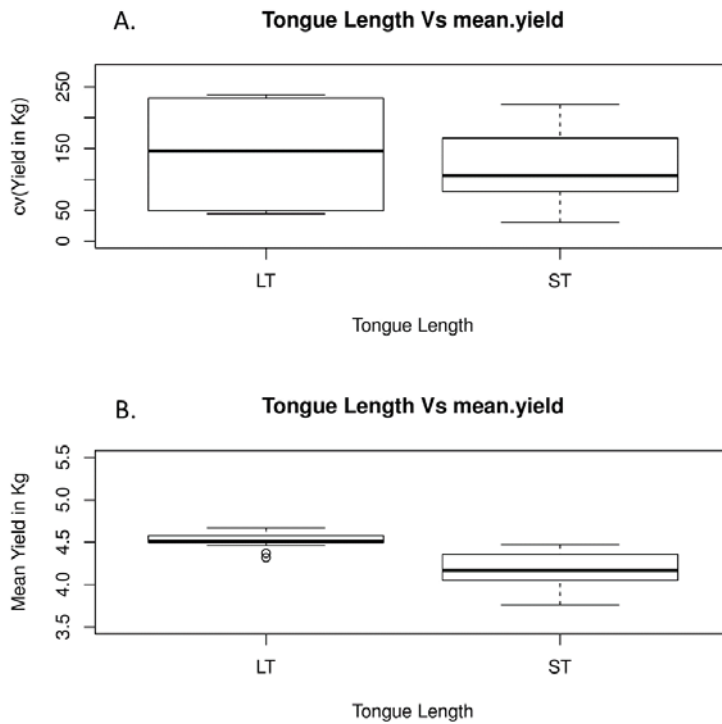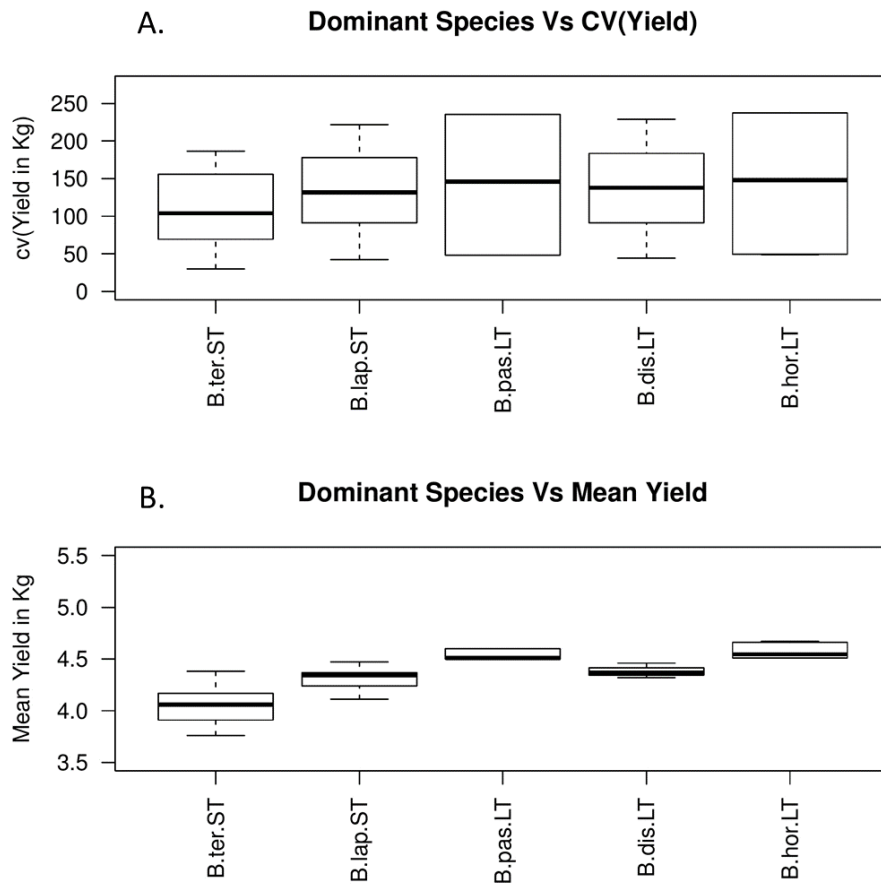

Fig: 6: CV(Yield) & mean(Yield) in kg vs dominant species identity

Aggregated meta-scenario comparison of 100 years temporal CV(Yield) & mean (Yield) in kg aggregated across dominant species identity scenarios, across evenness and dominance levels plotted against dominant species identity. Refer Fig A1.13 & Fig A1.14 to see the meta-scenario comparison of this plot. The box-plots show the median (horizontal line in the box) value for each species evenness level. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.

The short-tongued species *B. lapidarius* and *B. terrestris* show lower CV(Yield) than the long-tongued bumble bees (See Fig 4A & FigA1.14). However, the magnitude of difference in CV(yield) is not much between each dominance identities or among tongue length trait groups (ST & LT). Beyond the evenness-level aggregation caused long spread of box plots, the important cause for the

increased CV(yield) in LT scenarios is, the proportion of robbing behaviour of co-dominant ST species. The *B. terrestris* & *B. lapidarius* identity that has larger proportion of robbing identity due to their co-dominance demographic identity in all LT scenarios resulting in long spread of CV(yield).

The second cause is positive and negative contribution among the portfolio components. When short tongue species are dominant in the first two meta scenarios, the other co-dominant long tongue species contribute to productivity in a positive manner and relatively equally contribute to stable delivery of ecosystem function, that results in the decrease of the CV(yield) for short tongue species dominance identity alone. Whereas, in the scenarios of long tongue species dominance identity, the co-dominant short tongue species proportional abundance is split as legitimate and robbing, the latter contribute to ecosystem function in negative manner and also additively both foraging identities share the same unrealistically constant & highest standard mean error similar to dominant *B. terrestris* in all three meta-scenarios, which contributes to the increase in CV(yield) of long tongue dominance identities, thereby causing decrease in the stability of ecosystem function delivery of long tongue dominance identity scenarios.

The other possible contribution of difference among the identities might be impaired by population fluctuation due to the reason that, the standard mean error remained constant for all species in all dominance identity scenarios, because of this, the *B. terrestris* species that has highest standard mean error with larger robbing proportion than other species in all three meta-scenarios, which contributes to the increase in coefficient of variation in the scenarios of other dominance identities.

Future investigations of the dominance identities in the presence of individual pollinator efficiency estimate (IPE), could be conducted using uniform dominance level meta-scenarios as well as with realistically variable standard mean error, so that exact differences could be explicitly investigated among the species dominance identities.

3.2 Temporal seed yield of empirical proportional abundance

This study's FunBumble simulation model was fed with the original proportional abundance data of Bommarco *et al.*, (2012) and the model's output temporal seed yield trend is given in the Figure 7 for the three temporal periods. This scatter-plot (See Fig 7) shows the decrease in seed yield from 1940's to 2010's as the species evenness decreases. (See the Pielou's evenness (J) in Fig 1 description). CV (Yield) of the year 1940, 1960 and 2010 is 103.06, 120.54, and 188.89 respectively; also, the mean yield in kg is 4.24, 4.06 and 3.74 respectively.
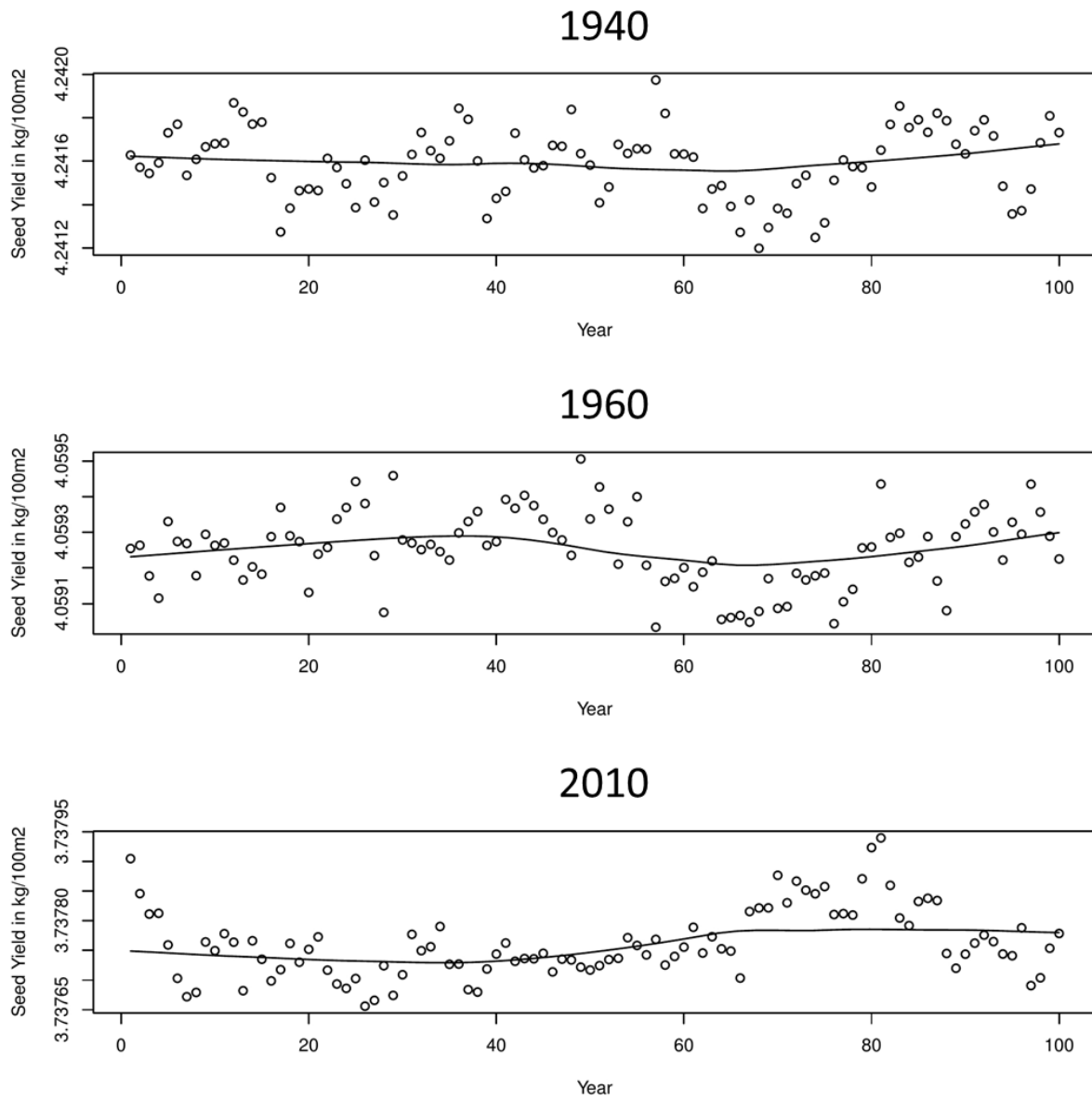
![1940 plot]

![1960 plot]

![2010 plot]

Fig: 7: Empirical historic community evenness level predicted red clover seed yield

4. Discussion

The bumble bee community composition structural features in the natural systems has been taken as the template for experimental simulation of three meta-scenarios & 30 scenarios for realistic design that were investigated in this study of portfolio effect on ecosystem function. The disaggregated view of the structural features of the portfolios has been discussed in the first section of this chapter and its resultant insights is used in second section to tease out the possible mechanistic understanding about temporality of seed yield using the historic empirical data obtained from the Bommarco *et al.*, (2012) study. In the third section, B-EF simulation results implications for wild bumble bee conservation is discussed.

4.1 Influence of community composition's structural features

Important structural features of the community composition such as (i) dominant species identities, (ii) tongue length trait and (iii) evenness levels, which has been used to design the scenarios and to observe their influence on overall portfolio effect are discussed below.

As stability increases, magnitude too increases in the measure of Temporal stability as inverse of CV. (Lehman & Tilman, 2000; van Ruijven & Berendse, 2007; Isbell *et al.*, 2009) Henceforth, CV would be mentioned as stability, to differentiate it from precise measure of temporal stability (inverse of CV). Species interactions (i.e., overyielding mechanisms), species asynchrony effect (SA) and portfolio effects (PE) are predicted by theory as influencing mechanisms of diversity-stability relationships (Doak *et al.*, 1998; Lehman & Tilman, 2000; Loreau & de Mazancourt, 2008). To increase the stability of productivity, any of these three mechanisms should do so by either or both increasing the mean productivity, decreasing the variance in productivity (Isbell *et al.*, 2009).

The species interactions in the form of overyielding mechanisms increases mean productivity of communities more than the expected productivity of the individual species (Lehman & Tilman, 2000). Two types of overyielding mechanisms influence biodiversity, productivity & stability (BPS), that are identified as (i) selection effect (SEL) and (ii) complementarity effect (COM), which are summed as net-biodiversity effect (NBE) (Loreau & Hector, 2001). In this simulation study, evenness levels acts as the source for species interactions based overyielding mechanisms, with random species identities being subjected to selection effect in each scenario. The complementarity effect between species is not applicable to the simulation design of this study, since the design of the Fun-Bumble model is additive in nature through investigation of each species identities dependence on single floral resource, red clover.

The selection effect (SEL) occurs when species with extreme traits are favoured by selection process, which results in either increased or decreased productivity of whole community, when compared to the expected productivity of the same specific extreme trait individual faunal species population (Loreau, 2000). For example, empirically dominant species identity *B. terrestris* of this study with a primary robbing & highly mobile super-generalist trait (Bommarco *et al.*, 2012) is empirically

extreme trait species that is subjected to selection effect at regional scale in this bumble bee community of red clover production system. The expected productivity of the extreme trait species identity is computed analogous to monoculture in manipulated or managed in-situ BEF studies. Similarly, in this study, the non-empirical random species identities were also subjected to selection effect based simulation modelling.

Whereas species asynchrony (SA) effect decreases the variance in productivity when fluctuations of each species populations varies in contrast to another, i.e., when productivity of a species decreases, the productivity increase by another species compensates for the decrease, resulting in asynchrony in fluctuations, whereas when all species either decrease or increase in productivity together, results in perfect synchrony that doesn't dampen the variance in productivity (Loreau & de Mazancourt, 2008).

The portfolio effect (PE) enhances the stability, by statistically averaging the aggregate productivity of the community portfolio's each component species productivity, freely from the influence of each species synchronous, asynchronous or independent fluctuations in mean productivity. Also, there are evidence for portfolio effect, especially when there is scaling of temporal variance of productivity by a species with its mean productivity based on Taylor's (1961) power function (Doak *et al.*, 1998; Tilman *et al.*, 1998).

Empirical inter-species standard mean error characteristic becoming unrealistic to all species identities except *B. terrestris*, this might also have contributed to the higher fluctuation of the *B. terrestris* co-dominance identity (legitimate and robbing), in all those ST and LT dominance identity scenarios causing huge negative-effect on diversity(evenness)-stability (DES) relationship, which could be rectified by making standard mean error of proportional abundance as realistically variable in future investigations. However, in the simulation there is enough magnitude of difference in stability signalled between the evenness levels possibly contributed by the mean productivity increase across increasing evenness levels due to increase in abundance of component species, resulting in respective magnitude of portfolio effect throughout all scenarios, even in the presence of this unrealistically constant standard mean error. In this study, dominance identity, selection effect, species asynchrony and portfolio effect are qualitatively discussed, therefore the quantitative analysis & discussions of all, selection effect, net-biodiversity effect, portfolio effect & computation of monoculture productivity of respective dominant species identities are essential for future simulation investigations of this system (Loreau & Hector, 2001; Anderson *et al.*, 2013; Fung *et al.*, 2015).

The theory predicts that than richness-levels, the evenness-levels show larger magnitude of portfolio effect due to statistical averaging and resultant increase in stability (Doak *et al.*, 1998; Hillebrand *et al.*, 2008). However, along with aggregate pattern of portfolio effect, all the above discussed mechanisms at the scale of evenness levels, and the other scales of community structure too need to be explored to understand the potential non-random patterns and processes (See Table 2).

Table: 2: Biodiversity, Productivity & Stability Mechanisms

Mechanisms affecting	Productivity		Stability
Community Structure	**SEL**	**SA**	**PE**
Evenness Level			
As Evenness Level decreases	confounded	*decreased*	*decreased*
HE	confounded	*Strongly Positive*	*Strongly Positive*
ME	confounded	*Positive*	*Positive*
LE	confounded	*Weakly Positive*	*Weakly Positive*
Tongue Length			
ST	*Negative*	confounded	confounded
LT	*Positive*	confounded	confounded
Dominance Identity			
B.terrestris	*Negative*	confounded	confounded
LT	*Positive*	confounded	confounded

4.1.1   Influence of evenness levels on biodiversity, productivity & stability

The aggregated meta-scenarios results of this study is consistent with the seminal realistically low evenness levels study of Polley *et al.*, (2003) regarding diversity(evenness)-productivity (DEP) relationship not influenced by selection effect. However, this generality applicable across meta-scenario aggregate results isn't applicable when disaggregated view of each meta-scenarios, where selection effect influence productivity, though in low magnitude. The scenarios with negative selection effect due to unproductive species recruited by selection process, has positive trend in yield caused by productive co-dominant species resulting in positive diversity-evenness-productivity relationship resulting in overyielding of productivity. For example, contemporary 2010 meta-scenario results are demonstrating the presence of negative selection effect which results in positive diversity-evenness-productivity relationships.

In this bumble bee community of red-clover production systems, the potential niche space partitioning mechanism (alike facilitation, plant height, phenology and rooting depth) is landscape complexity moderated spillover or subsidy that contribute to the enhanced complementarity through increase in evenness of functionally diverse bumble bee population from complex agro-ecosystems in the landscape matrix of local production habitat (Öckinger & Smith, 2007; Ockinger *et al.*, 2010; Marini *et al.*, 2014).

The positive diversity-evenness-stability relationships in all dominance identity scenarios are contributed mainly by the aggregate productivity contribution of each portfolio components as evenness level increases irrespective of the selection effect type (Positive or Negative). Also, the aggregate effect of strongly positive species asynchrony and portfolio effect acts upon high evenness scenarios. As discussed by the seminal paper on portfolio effect the aggregate ecosystem function delivery is from each species comprising a community portfolio, productivity of those each species subjects to variability dampening statistical averaging and consequently contributes to the stability of red clover

seed yield, through positive diversity-evenness-stability (DES) relationship as evenness level increases (Doak *et al.*, 1998).

The dampening effect of portfolio components on productivity decrease is weaker than for stability decrease because productivity is an additive process whereas stability is an aggregate process, which means the former gets dampened just by positive contribution from single productive dominant species or group of co-dominant species, whereas for stability the contribution is from all component species in a community, each individual productivity aggregating to result in community wide stability. Therefore, for the aggregate effect of species asynchrony and portfolio effect to be robust on stability the increase in evenness levels is essential.

Interestingly, Isbell *et al.*, (2009) discussed that species asynchrony might act as compensatory mechanism even when portfolio effect decreases with decreasing evenness level (Doak *et al.*, 1998), however such compensatory mechanism is not feasible for the regional proportional abundance data of Bommarco *et al.*, (2011) since standard mean error that causes species fluctuations too decreases as evenness levels decreases temporally, thus the correlated decrease of SA and PE causes concern about stability bumble bee community ecosystem function.

In summary, this pollinator evenness simulation study rejects the potential generality of Polley *et al.*, (2003) in vegetation evenness investigations and of other studies (Huston, 1997; Grime, 1998; Smith & Knapp, 2003), that under realistically low evenness level there is no diversity-evenness-productivity relationship. Also, the stability of red clover seed yield increases temporally as evenness level increases realistically, which contrasts the conclusion of Isbell *et al.*, (2009) about no influence of realistically low evenness levels on diversity-evenness-stability. The possible reason is the key difference of this study from seminal realistically low evenness investigations that brought these key insights forward are, mainly the taxa investigated are different, second reason could be the type of competition affecting productivity is different, third this study is a simulation experiment that enables consistent evenness level difference across 100-year temporal replication contrasting initial evenness investigations in in-situ and in-vitro studies (Polley *et al.*, 2003; Wilsey & Polley, 2004; Wittebolle *et al.*, 2009). Also, vitally this study isn't realistic only in terms of evenness levels, but also in terms of community structure. So, the combined investigation of realistically low evenness and realistic community structure in the scenario design & consistent evenness level difference through 100-year replication enables the ability to determine the potential role of selection effect on diversity-evenness-productivity positive relationships and the role of species asynchrony and portfolio effect on diversity-evenness-stability positive relationship.

Therefore, the ecological integrity from the dimension of healthy evenness level has huge effect on the stability of the ecosystem service, though low magnitude increases in productivity. Therefore, biodiversity's effect on the ecosystem function ensures the insurance effect (Yachi & Loreau, 1999) thereby preventing the system from incurring extreme/surprise pollination disservice events.

4.1.2 Influence of dominance identities & tongue length trait on biodiversity, productivity & stability

So far investigations of species identity influences through evenness levels had assessed only the dominant species identities (Wilsey & Potvin, 2000; Isbell *et al.*, 2008, 2009), but understanding from the designed & empirical scenarios of this study calls for explicit discussions about the influence of even the co-dominant species identities. The investigation of total 5 dominant species identities representing 2 ST and 3 LT, the ST species identities show distinct performance in the simulation experiment scenarios, especially based on the proportion of robbing foraging behaviour in scenarios.

Since this study didn't include statistically significant parameter estimate namely individual pollinator efficiency of Bergström's (2010) study, it is difficult to glean the difference between each species identities per se. Additionally, this study's modelling limitation of having unrealistically constant standard mean error in scenarios other than *B. terrestris* dominance identity might also have contributed to the higher fluctuation of the *B. terrestris* co-dominance identity (legitimate and robbing) with highest standard mean error in total visits, than from other ST and LT identities relatively in all scenarios across all meta-scenarios.

Nevertheless, the current low magnitude distinct difference in mean yield & CV(yield) of species identities between the ST & LT and *B. terrestris* & *B. lapidarius* is contributed by the proportion of robbing behaviour. Whereas, negative trend through high standard mean error and high proportion robbing behaviour of co-dominant ST species, possibly contributes to the instability through relatively high CV(yield) in all LT scenarios. However, in the natural systems exemplified by Bommarco *et al.*, (2012) study, empirically there is no any evidence in known regional ecological history data for LT species being prime dominant species. However, LT scenarios might aid for understanding unknown regional paleo-ecological history through the eco-evolutionary dynamics that might resulted in the current known scenario of ST dominance identity in bumble bee community. Both in known & unknown ecological history the secondary robbing species *B. lapidarius* could never be a dominant species identity in long tube red clover system. Therefore, *B. lapidarius* scenario is not discussed.

The negative selection effect decreases the productivity of the realistic *B. terrestris* scenarios due to selection process favouring unproductive species, whereas positive contribution of co-dominant LT species increases the productivity through overyielding mechanism. In the case of both productivity and stability, the positive contribution of LT co-dominant species identities determines the scenario performance, dampening the negative selection effect in *B. terrestris* scenarios under high evenness levels. This shows that the positive contribution of LT co-dominant identities is key in increasing the productivity & stability of ecosystem function, which could be possible only in the presence of high evenness, where LT co-dominant species enhances the productivity of ST dominance identity scenarios. Along with the dampening effect of LT co-dominant identities, positive

species asynchrony and portfolio effect too dampens the negative selection effect of ST dominance identity scenarios, consequently increasing productivity & stability in the presence of high evenness.

So, *B. terrestris* scenario's combination of realistic community composition structure as well as realistic standard mean error distribution, make it clear, the important contribution for higher stability of this scenario is from the presence of co-dominant LT species. However, the unproductive dominant *B. terrestris* scenario's negative selection effect causes low magnitude decrease in the productivity than any other species identity, even the presence of LT co-dominant identities could not match the productivity levels of positive SEL in the LT scenarios.

This stability and productivity response of this empirically realistic *B. terrestris* dominance identity scenario shows that the selection process selected the unproductive species, thereby though initially replacing the demographic proportion of other selectively (by selection process) declined species identities, eventually the species co-existence is ensured by overyielding mechanism resulting in promoting biodiversity as evidenced by previous studies (Isbell *et al.*, 2009b). Even the species fluctuations in the form of standard mean error contributed to positive species asynchrony (SA) effect in the high evenness scenarios, along with overall portfolio effect resulted in increased stability of *B. terrestris* scenarios only in the contexts of high or medium evenness levels. As evidenced by Isbell *et al.*, (2009a), the species interaction causing overyielding mechanism through *B. terrestris* dominance identity scenario of this study promotes the productivity, stability and biodiversity (Isbell *et al.*, 2009b) as evenness level increases.

Therefore, negative selection effect of *B. terrestris* dominance identity itself could be a buffering mechanism at relatively high evenness meta-scenarios (1940's & 1960's) in the predominance of selection processes like decline of ecosystem heterogeneity and raise of mass flowering crops, thereby ensuring buffering of both productivity & stability by positive contribution through increased co-dominance and ensuring persistence of species co-existence despite the presence of exploitative competition among bee species (Balfour *et al.*, 2015). The environmental, landscape & resource complexity decline acting as selective stressors could be the primary selection process moderating the exploitative competition. However, under the low evenness scenario for *B. terrestris* dominance identity in contemporary period (2010) reduces the insurance/portfolio effect or buffering ability of biodiversity, thereby decrease in both productivity and stability (Yachi & Loreau, 1999), through selective stressors mentioned above and potentially non-selective stressors that affect all species alike such as pesticide exposure together threaten bumble bee community with non-random rarity-extinction trajectory (Wittebolle *et al.*, 2009).

While investigating the scenario performances of LT dominance identities that were represented only in the 1940 and 1960 meta-scenarios, the LT scenarios experienced strong positive selection effect due to productive species being the dominance identity and strong negative contribution due to the presence of robbing ST co-dominant identities with additive negative contribution from unrealistic & relatively higher standard mean error of *B. terrestris* & *B. lapidarius* robbing identities,

consequently underyielding of productivity. However, the strong positive selection effect dampened the negative contributions from ST robbing identities affecting the productivity increase for LT scenarios with low magnitude of underyielding, but the same dampening effect is weaker for stability because productivity is an additive process whereas stability is an aggregate process, which means the former gets dampened just by positive selection effect from single productive dominant species or group of co-dominant species, whereas for stability the contribution is from all component species in a community, each individual productivity aggregating to result in community stability. In the presence of negative co-dominance & unrealistic standard mean error, weakens the portfolio effect and species asynchrony ability to dampen or atleast buffer the stability decrease of LT species scenarios is reduced.

However, our results concur with Polley *et al.*, (2003) about the influence of dominant species identity on productivity, additionally co-dominant identity too contributes as the evenness level increases due to positive effect of co-dominance identities.

4.2 Historic empirical evenness seed yield modelling

The portfolio effect under the respective natural evenness levels of historic community structure shows, there is clear indication from the simulation experiment that the magnitude of the ecosystem function stability decreases drastically as the evenness decreases, though the mean yield in kg doesn't differ much through 100 years temporal replication of these natural species abundance distribution. The decline in stability of temporal productivity between the current scenario (2010) against 1960's and 1940's is 36% and 45% respectively, almost 50% decline in potential natural stability, this necessarily raises concern about the ability to achieve safe operating space in terms of multiple planetary boundaries associated with red-clover production systems. These predictions of the FunBumble model is typical characteristic of portfolio effect in various ecological systems through temporality of community portfolio. Especially, the difference in the dominance levels (4 & 2) between the two early species abundance distributions (1940's & 1960's) and the current (2010) species abundance distributions indicate that the magnitude of decline in stability between these two, emphasizes the vitality of restoring the level of dominance in the systems through local and regional target species specific management efforts for restoring previously dominant species identities. Also, along with restoration of the dominance levels, restoring the ecological integrity of evenness levels captured by the 1960's empirical proportional abundance data, would necessitate protection of habitats and species itself, through conservation efforts in the form of natural and semi-natural agro-ecosystem reserves.

In summary, comparing evenness level decrease across meta-scenarios (1940's, 1960's & 2010), the negative selection effect become stronger and positive contribution of co-dominance identities become weaker on the realistic *B. terrestris* dominance identity bio-folio, resultantly decreased productivity and stability due to the constraint of selection processes like landscape & ecosystem homogeneity (Öckinger & Smith, 2007; Ockinger *et al.*, 2010; Marini *et al.*, 2014). This study's

empirical evenness level investigation agrees with Mulder *et al.*, (2001) that under low evenness the communities with higher relative abundance for one or more dominant species behave more like monoculture, i.e., the contemporary (2010 -meta-scenario) bumble bee community composition behave more like monoculture of dominance identity *B. terrestris*, thereby reducing the species co-existence potential of negative selection effect scenarios. Recent investigation of the effectiveness of the semi-natural habitat restoration for pollinators, had provided evidence for persistence of functional composition (Winsa *et al.*, 2017), however to achieve the target community structure of high evenness, crop production systems & agro-ecosystems might need functional trait based local scale pollinator conservation management (Jönsson *et al.*, 2015).

The FunBumble model in this study, considers only the proportional abundances of bumble bee community, instead accounting for the decline of total abundance in terms of absolute average abundance per year in field (as shown in Table 1 of Bommarco *et al.*, (2012)) through each temporal meta-scenario (1940's, 1960's and 2010), would enable understanding about the impact population abundance decline and resultant impact of species asynchrony and portfolio effect (Schindler *et al.*, 2010).

4.2.1 Limitations of Portfolio Theory based simulations

Bumble community's population enhancement through optimized decisions of management actions are appropriate and needed for production landscape habitat management. However, caution is needed in using predictions or forecasts from portfolio theory based simulations to optimize efficient pollinator community composition in natural and semi-natural systems which has the potential of delivering ecosystem service spillover (Schindler & Hilborn, 2015; Schindler *et al.*, 2015). Though models like FunBumble might become more robust through sophisticated model building and improved parameter estimates in future for the dominant and intermediate species, but not for the potential dominant (*B. distinguendus*) or potential intermediate (*B. sylvarum* & *B. distinguendus*) species that has become rare in the last 50 years, essentially because the extinction events are non-random at low evenness levels which characterises contemporary community composition when compared to historic high evenness levels (Wilsey & Polley, 2004). The inappropriate application of portfolio theory for "optimised management" is being criticised in financial systems. Because, very little empirical data is being used for training the model, that is best fit only in hindsight (data-fitting), rather than forecasting or prediction (Gigerenzer, 2016). And such criticisms are applicable to ecological systems too, since both are uncertainty prone as against the usual assumptions of risk. Since last 100 years, understanding about the distinction between the risk and uncertainty has been increasingly debated and recognized in economic systems, which applies very much to the management decisions of the ecological systems too (Knight, 1921; O'Donnell, 2017). The normative unsuitability of portfolio models as prediction tools for the pollinator community's ecosystem service delivery enhancement in natural and semi-natural systems, invites the exploration of alternate normatively best performing management tools than the optimised management option provided by the portfolio

theory. Such, alternate best performing decision-making tool has been already identified empirically, also competitively tested against mean-variance portfolio model in the financial management discipline and the tool is said to be a heuristic called 1/N or equal weights heuristic, which employs a precautionary approach to achieve temporal stability in portfolio returns (DeMiguel *et al.*, 2009).

Before opting such normative tools, there is a need to understand what caused the wedge in gaining understanding about the species abundance distribution and human decision-making in ecological sciences. For example, what made Doak *et al.*, (1998) in their seminal theoretical paper on portfolio effect to use equal abundance for all portfolio components? While Schindler *et al.*, (2015) rightly rejected it saying this is not feasible in natural systems (See. Supplement box of Schindler *et al.*, (2015)), and rightly interpreted the above seminal paper's use of equal abundances as being heuristic, but regrettably their complete rejection of this as mere heuristic had led to failure in exploring possible cognitive explanations hidden behind such adaptive heuristic. The adaptive nature of this heuristic could be descriptively explained by bounded rationality paradigm of cognitive sciences (Simon, 1979; 1990) using the framework of ecological rationality (Gigerenzer *et al.*, 2011), which is not dealt in this report, since it's beyond the scope of this study's objective.

Perfect evenness is not possible in both natural and semi-natural biological and financial systems, since it's strictly between the log-normalish and log-seriesish distribution, which are not determined or manipulable by the decision of an individual's investment action. The potential reason for past unrealistically high evenness in both in-situ and simulation experiments is due to the human cognition's intrinsic aspiration of demonstrating importance of diversity's ability in provisioning potential overyielding and stabilising performance in functions of productivity. Therefore, maximal evenness in those experiments confounded the human cognitive belief (human belief/value of equal importance ascribed to diverse functional traits in a given species pool) with the realistic count-based species abundance distributions of portfolio components. This confounding between the abstract cognitive decision's abundance structure & absolute abundance distribution structure of portfolio components needs to be explicitly discussed to progress towards robust decision making under scenarios of global change, which had been regrettably missed in all critical analysis (Schindler & Hilborn, 2015; Schindler *et al.*, 2015) about limitations of portfolio theory and limitations of maximal evenness approach that begun in seminal paper of Doak *et al.*, (1998).

Therefore, by placing equal importance on all species based on belief of equal importance or equal value for all species irrespective of its direct or indirect ecosystem service benefits, decision-maker decides to protect all species, that includes the protection of vulnerable and sensitive rare species as prime objective of conservation. The bias of conserving primarily the rare species, could contribute to the potential restoration of bumble bee community structure & stability of ecosystem service delivery through indirect "unintended mechanisms". Though the ecosystem service delivery is an insufficient argument for conservation as suggested by Kleijn *et al.*, (2016), pro-sociality kind of con-

servation or precautionary approach potentially serve ecosystem services through unintended mechanisms by dampening the selective and non-selective stressors (Aburto-Oropeza *et al.*, 2008). This method of protection of all species is characteristically called as protected area or reserved habitat, which are well established as precautionary approach or precautionary principle.

As of now the belief dimension of portfolio investments had not been discussed independently from financial/capital resource dimension of distributable investments. Though, interestingly the seminal paper on portfolio concept by Nobel laureate Harry Markowitz, (1952) does start with two stage classification of decision-making process in any portfolio investment, the first stage received least attention when compared to second stage. The first stage is classified as "the observations and experience ending with belief" (Frahm, 2015), and this first stage belief acts as the decision-making precursor for second stage portfolio selection, which begins the selection of best performing portfolio and its investment structure. Further on, the seminal paper departs to discuss in-depth about this second stage decision-making process of portfolio selection, whereas the first stage belief dimension of decision-making remained unexplored. So, based on the ecological rationality (*Sensu:* Gigerenzer, 2016) of the system for which portfolio decisions are made, the first stage decision making either results into the second stage action of portfolio selection (as in the case of distributable investment of financial resources) or remains in the first stage itself translating into non-distributable investment, depending on the ecological rationality of respective systems (When abundance structure is non-distributable and when species abundance distribution is between log-normalish and log-seriesish distribution). For example, in biological systems (Natural, Semi-natural and Managed production systems) the decision making precursor either ends as first stage belief itself causing protection (reserves or protected area) as the investment action (in natural and semi-natural systems) which goes blind about the portfolio component's abundance distribution and engages only in investment activities that are reducing selective and non-selective stressors, or progresses into the second stage portfolio selection through manipulation of the frequency distribution of species abundances, as in the farm management actions of the manipulable production systems.

Thus, under the dimension of belief-based investments, the 1/N heuristic gets initiated into a novel non-distributable investment form called "Equal-Belief" heuristic, which needs further investigations for its significance in support of precautionary principle across diverse complex adaptive socio-ecological systems.

4.3 Implications for Conservation & Crop Production Systems

4.3.1 For Crop production systems

In the systems of agricultural intensification, active management measures that promote the nest sites, floral resources for the wild bumble bee pollinator community of diverse functional traits needs to be managed based on the insights from ecological investigations, using evidence-based knowledge

about the species-specific habitat and resource requirements of each well studied dominant, co-dominant and intermediate bumble bee species.

4.3.2 For conservation: ecosystem service spillover/subsidy systems

Conservation-ecosystem service subsidy systems could be considered analogous to conservation biological control programmes, these systems employ 1/N heuristic as the prime tool of wild bumble bee pollinator community management in semi-natural grassland reserves or semi-natural woodlands or natural forests. These systems target the conservation of all demographic identities dominant, intermediate and rare, through allocating equal value of importance beyond the target ecosystem service delivery-based conservation management optimisation. Such 1/N heuristic application made in the appropriate landscape, ecological and environmental contexts could strive to eliminate both selective & non-selective stressors, would not only restore the potential dominant and intermediate species, additionally increases the turnover of species abundance in production systems through subsidy or spillover of wild bumble bee community into production ecosystem's thereby relatively improved evenness levels causing ecosystem service stability improvement as an unintended benefit out of employing a heuristic decision of 1/N equal-belief heuristic in coupled natural & semi-natural agro-ecosystems.

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5. Conclusion

The increasing interest on ecological integrity is encouraging investigations about multiple dimensions of biodiversity. This simulation modelling investigation of varying evenness levels effect on biodiversity, productivity and stability has contributed understanding about the impact of bumble bee community composition shifts. The primary conclusion of this study is that, realistic evenness & realistic community structure dimension of ecological integrity, has positive relationship with biodiversity, productivity and stability. At high evenness (HE, for example 1940's) scenarios, the negative selection effect caused selection of unproductive species enables positive contribution of LT co-dominants, thereby causing low magnitude increases in productivity, high magnitude increases in stability and increased species co-existence resulting in overyielding of red clover seeds. Especially in the presence of HE both portfolio effect and species asynchrony increases with large magnitude, therefore that results in large magnitude stability of red clover seed yield. Very, importantly the increase in number of co-dominant identity as evenness level increases, does contribute to the resultant increase in the productivity. The negative selection effect coupled with positive contribution of co-dominance identities in the realistic high evenness *B. terrestris* dominance identity scenarios are a biodiversity enhancing and buffering species co-existence mechanism in red clover production system, which could function efficiently provided selection pressures as well as non-selective pressures or stressors on community composition reduces in the regional, local and landscape scale ecosystems and environments. Important conservation implications of the results from experimental scenarios is implementing floral resource & nesting site facilitation for long tongue intermediate species in crop production systems.

Especially, realistic evenness level, realistic community structure investigation context of this study facilitates, investigation of limitations of portfolio concept application in the biodiversity conservation management. Bounded rationality paradigm of decision-making proposes the satisficing dimension and rejects the potential optimising management decisions of bumble bee community composition and suggests the application of novel normative and adaptive tool namely 1/N heuristic based equal-belief or equal-value heuristic for rare and endangered biodiversity conservation. In summary, this study calls for protection of natural and semi-natural habitats to reap potential benefits from unintended mechanisms of equal-belief heuristic, by reduction in magnitude of both selective and non-selective stressors at the target bumble bee habitats.

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A.Appendix

FunBumBle Script

```
setwd("C:/Users/Vivek/Documents/EvNnS/CSV files/Evenness csv")

rd40<-read.csv(file = "rd40.csv", header=TRUE) ### Original 1940's Data

###1940's Scenario with evenness levels and Pollinator Identity

rd40HEter<-read.csv(file = "rd40HEter.csv", header=TRUE)
rd40HEpas<-read.csv(file = "rd40HEpas.csv", header=TRUE)
rd40HEdis<-read.csv(file = "rd40HEdis.csv", header=TRUE)
rd40HEhor<-read.csv(file = "rd40HEhor.csv", header=TRUE)
rd40MEter<-read.csv(file = "rd40MEter.csv", header=TRUE)
rd40MEpas<-read.csv(file = "rd40MEpas.csv", header=TRUE)
rd40MEdis<-read.csv(file = "rd40MEdis.csv", header=TRUE)
rd40MEhor<-read.csv(file = "rd40MEhor.csv", header=TRUE)
rd40LEter<-read.csv(file = "rd40LEter.csv", header=TRUE)
rd40LEpas<-read.csv(file = "rd40LEpas.csv", header=TRUE)
rd40LEdis<-read.csv(file = "rd40LEdis.csv", header=TRUE)
rd40LEhor<-read.csv(file = "rd40LEhor.csv", header=TRUE)

rd60<-read.csv(file = "rd60.csv", header=TRUE) ### Original 1960's Data

###1960's Scenario with evenness levels and Pollinator Identity

rd60HEter<-read.csv(file = "rd60HEter.csv", header=TRUE)
rd60HEpas<-read.csv(file = "rd60HEpas.csv", header=TRUE)
rd60HElap<-read.csv(file = "rd60HElap.csv", header=TRUE)
rd60HEhor<-read.csv(file = "rd60HEhor.csv", header=TRUE)
rd60MEter<-read.csv(file = "rd60MEter.csv", header=TRUE)
rd60MEpas<-read.csv(file = "rd60MEpas.csv", header=TRUE)
rd60MElap<-read.csv(file = "rd60MElap.csv", header=TRUE)
rd60MEhor<-read.csv(file = "rd60MEhor.csv", header=TRUE)
rd60LEter<-read.csv(file = "rd60LEter.csv", header=TRUE)
rd60LEpas<-read.csv(file = "rd60LEpas.csv", header=TRUE)
rd60LElap<-read.csv(file = "rd60LElap.csv", header=TRUE)
rd60LEhor<-read.csv(file = "rd60LEhor.csv", header=TRUE)

rd2010<-read.csv(file = "rd2010.csv", header=TRUE) ### Original 2010's Data

###2010's Scenario with evenness levels and Pollinator Identity

rd2010HEter<-read.csv(file = "rd2010HEter.csv", header=TRUE)
rd2010HElap<-read.csv(file = "rd2010HElap.csv", header=TRUE)
rd2010MEter<-read.csv(file = "rd2010MEter.csv", header=TRUE)
rd2010MElap<-read.csv(file = "rd2010MElap.csv", header=TRUE)
rd2010LEter<-read.csv(file = "rd2010LEter.csv", header=TRUE)
rd2010LElap<-read.csv(file = "rd2010LElap.csv", header=TRUE)

setwd("C:/Users//Documents/EvNnS")

####funbumble is the function to replicate the simulation experiment with
different input data sets.

funbumble <- function(data){
  out <- matrix(ncol = nrow(data), nrow = 100)
  efficiency <- data[,4]
  floret <- 250
  Totalvisits <- 236540 ##visit/flower head/100m2/year
```

```r
  mean_visits <- Totalvisits * (data[,"prop_abundance"]/100)
  #sum(mean_visits) look that this should be near the total value.
  visits <- mean_visits
  for (t in 1:100) {
    #created a random "year" quantile, where 0.25 is a bad year (in the 25%
quantile) and 0.75 is a good one.
    year_se <- rnorm(1,0.50, 0.10) #

    for (s in 1:nrow(data)){
      #calculate species visits based on this year probability using qnorm
      #I adjust the new mean so it is non linearly related to the old one,
but only slightly affected by it
      new_mean <- mean_visits[s] + (sqrt(abs(visits[s]-mean_vis-
its[s]))*sign(visits[s]-mean_visits[s]))
      #I use jitter to add some noise around the quartile and the new mean
here
      visits[s] <- qnorm(jitter(year_se, 10), mean = new_mean, sd =
data[s,"se_visits"])}
    seeds <- visits*(floret*efficiency)
    seed_yield_kg <- seeds/550000 ### According to Mcgregor. S. E., 1976 book
(Insect Pollination in crops) 1 kg of redclover seeds contains approximately
5,50,000 seeds
    out[t,] <- seed_yield_kg
  }
  scatter.smooth(rowSums(out),xlab="Year",ylab="Seed yield in kg/100m2")
  #return(View(out))
  out}


#######cv function
cv <- function(x) {
    ( 100*sd(x)/mean(x) )
}


######Function for Funbumble output

fbbleoutput<- function(data){
  data_Yield<- funbumble(data)
  x <- rowSums(data_Yield)
  answer <- data.frame(mean(data_Yield),cv(data_Yield))
  #(mean(data_Yield)) is quite stable now! ### mean redclover seeds in kg/100
m2 field & cv(data_Yield))
  names(answer)[[1]]<-"mean yield"
  names(answer)[[2]]<-"cv yield"
  return (answer)
}


##### Executing the function "fbbleoutput" for multiple dataset...

U <-list(rd40HEter,rd40HEpas,rd40HEdis,rd40HEhor,rd40ME-
ter,rd40MEpas,rd40MEdis,rd40MEhor,rd40LEter,rd40LEpas,rd40LEdis,rd40LE-
hor,rd60HEter,rd60HElap,rd60HEpas,rd60HEhor,rd60ME-
ter,rd60MElap,rd60MEpas,rd60MEhor,rd60LEter,rd60LElap,rd60LEpas,rd60LE-
hor,rd2010HEter,rd2010HElap,rd2010MEter,rd2010MElap,rd2010LEter,rd2010LElap)

fbumble_U<-sapply(U,fbbleoutput)
```

Sample Scenarios

Meta-Scenarios & Evenness Levels for FunBumble Modelling

Table: A-3: Scenario design sample

1940 HE *B. distinguendus*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	6	4		0.53
3	sy.St.B.lap.I	7.22	2.2		0.5
4	sy.Lt.B.pas.D	10	2.6		0.48
5	sy.Lt.B.dis.D	20	1.7		0.44
6	sy.Lt.B.hor.D	10	2.6		0.49
7	sy.Lt.B.sub.I	9.6	5.7		0.41
8	sy.Lt.B.syl.I	9	4		0.46
9	sy.St.B.hyp.R	7.5	2.6		0.52
10	sy.St.B.pra.R	7.5	4		0.54
11	sy.SLt.B.spp.R	8	2.6		0.48
12	sy.St.robbing.D	5.18	4		0.1

1940 HE *B. terrestris*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	12	4		0.53
3	sy.St.B.lap.I	7.22	2.2		0.5
4	sy.Lt.B.pas.D	10	2.6		0.48
5	sy.Lt.B.dis.D	10	1.7		0.44
6	sy.Lt.B.hor.D	10	2.6		0.49
7	sy.Lt.B.sub.I	9.6	5.7		0.41
8	sy.Lt.B.syl.I	9	4		0.46
9	sy.St.B.hyp.R	7.5	2.6		0.52
10	sy.St.B.pra.R	7.5	4		0.54
11	sy.SLt.B.spp.R	8	2.6		0.48
12	sy.St.robbing.D	9.18	4		0.1

1940 ME *B. distinguendus*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	5.70	4		0.53
3	sy.St.B.lap.I	5.59	2.2		0.5
4	sy.Lt.B.pas.D	10.00	2.6		0.48
5	sy.Lt.B.dis.D	48.00	1.7		0.44
6	sy.Lt.B.hor.D	11.50	2.6		0.49
7	sy.Lt.B.sub.I	3.00	5.7		0.41
8	sy.Lt.B.syl.I	4.00	4		0.46
9	sy.St.B.hyp.R	2.50	2.6		0.52
10	sy.St.B.pra.R	2.00	4		0.54
11	sy.SLt.B.spp.R	3.00	2.6		0.48
12	sy.St.robbing.D	4.71	4		0.1

1940 ME *B. terrestris*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	28.80	4		0.53
3	sy.St.B.lap.I	5.59	2.2		0.5
4	sy.Lt.B.pas.D	9.50	2.6		0.48
5	sy.Lt.B.dis.D	10.00	1.7		0.44
6	sy.Lt.B.hor.D	11.50	2.6		0.49
7	sy.Lt.B.sub.I	3.00	5.7		0.41
8	sy.Lt.B.syl.I	4.00	4		0.46
9	sy.St.B.hyp.R	2.50	2.6		0.52
10	sy.St.B.pra.R	2.00	4		0.54
11	sy.SLt.B.spp.R	3.00	2.6		0.48
12	sy.St.robbing.D	20.11	4		0.1

1940 LE *B. distinguendus*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	3.00	4		0.53
3	sy.St.B.lap.I	2.58	2.2		0.5
4	sy.Lt.B.pas.D	4.50	2.6		0.48
5	sy.Lt.B.dis.D	75.00	1.7		0.44
6	sy.Lt.B.hor.D	6.50	2.6		0.49
7	sy.Lt.B.sub.I	2.00	5.7		0.41
8	sy.Lt.B.syl.I	2.20	4		0.46
9	sy.St.B.hyp.R	0.80	2.6		0.52
10	sy.St.B.pra.R	0.35	4		0.54
11	sy.SLt.B.spp.R	0.65	2.6		0.48
12	sy.St.robbing.D	2.42	4		0.1

1940 LE *B. terrestris*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	45.00	4		0.53
3	sy.St.B.lap.I	2.58	2.2		0.5
4	sy.Lt.B.pas.D	5.00	2.6		0.48
5	sy.Lt.B.dis.D	4.50	1.7		0.44
6	sy.Lt.B.hor.D	6.50	2.6		0.49
7	sy.Lt.B.sub.I	2.00	5.7		0.41
8	sy.Lt.B.syl.I	2.20	4		0.46
9	sy.St.B.hyp.R	0.80	2.6		0.52
10	sy.St.B.pra.R	0.35	4		0.54
11	sy.SLt.B.spp.R	0.65	2.6		0.48
12	sy.St.robbing.D	30.42	4		0.1

1940 HE *B.hortorum*

	A	B	C		D
1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	6.00		4	0.53
3	sy.St.B.lap.I	7.22		2.2	0.5
4	sy.Lt.B.pas.D	10.00		2.6	0.48
5	sy.Lt.B.dis.D	10.00		1.7	0.44
6	sy.Lt.B.hor.D	20.00		2.6	0.49
7	sy.Lt.B.sub.I	9.60		5.7	0.41
8	sy.Lt.B.syl.I	9.00		4	0.46
9	sy.St.B.hyp.R	7.50		2.6	0.52
10	sy.St.B.pra.R	7.50		4	0.54
11	sy.SLt.B.spp.R	8.00		2.6	0.48
12	sy.St.robbing.D		5.18	4	0.1

1940 ME *B. hortorum*

	A	B	C		D
1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	5.70	4		0.53
3	sy.St.B.lap.I	5.59	2.2		0.5
4	sy.Lt.B.pas.D	10.00	2.6		0.48
5	sy.Lt.B.dis.D	11.50	1.7		0.44
6	sy.Lt.B.hor.D	48.00	2.6		0.49
7	sy.Lt.B.sub.I	3.00	5.7		0.41
8	sy.Lt.B.syl.I	4.00	4		0.46
9	sy.St.B.hyp.R	2.50	2.6		0.52
10	sy.St.B.pra.R	2.00	4		0.54
11	sy.SLt.B.spp.R	3.00	2.6		0.48
12	sy.St.robbing.D	4.71	4		0.1

1940 LE *B. hortorum*

1	species	prop_abundance	se_visits		mean_eff
2	sy.St.B.ter.D	3.00	4		0.53
3	sy.St.B.lap.I	2.58	2.2		0.5
4	sy.Lt.B.pas.D	4.50	2.6		0.48
5	sy.Lt.B.dis.D	6.50	1.7		0.44
6	sy.Lt.B.hor.D	75.00	2.6		0.49
7	sy.Lt.B.sub.I	2.00	5.7		0.41
8	sy.Lt.B.syl.I	2.20	4		0.46
9	sy.St.B.hyp.R	0.80	2.6		0.52
10	sy.St.B.pra.R	0.35	4		0.54
11	sy.SLt.B.spp.R	0.65	2.6		0.48
12	sy.St.robbing.D	2.42	4		0.1

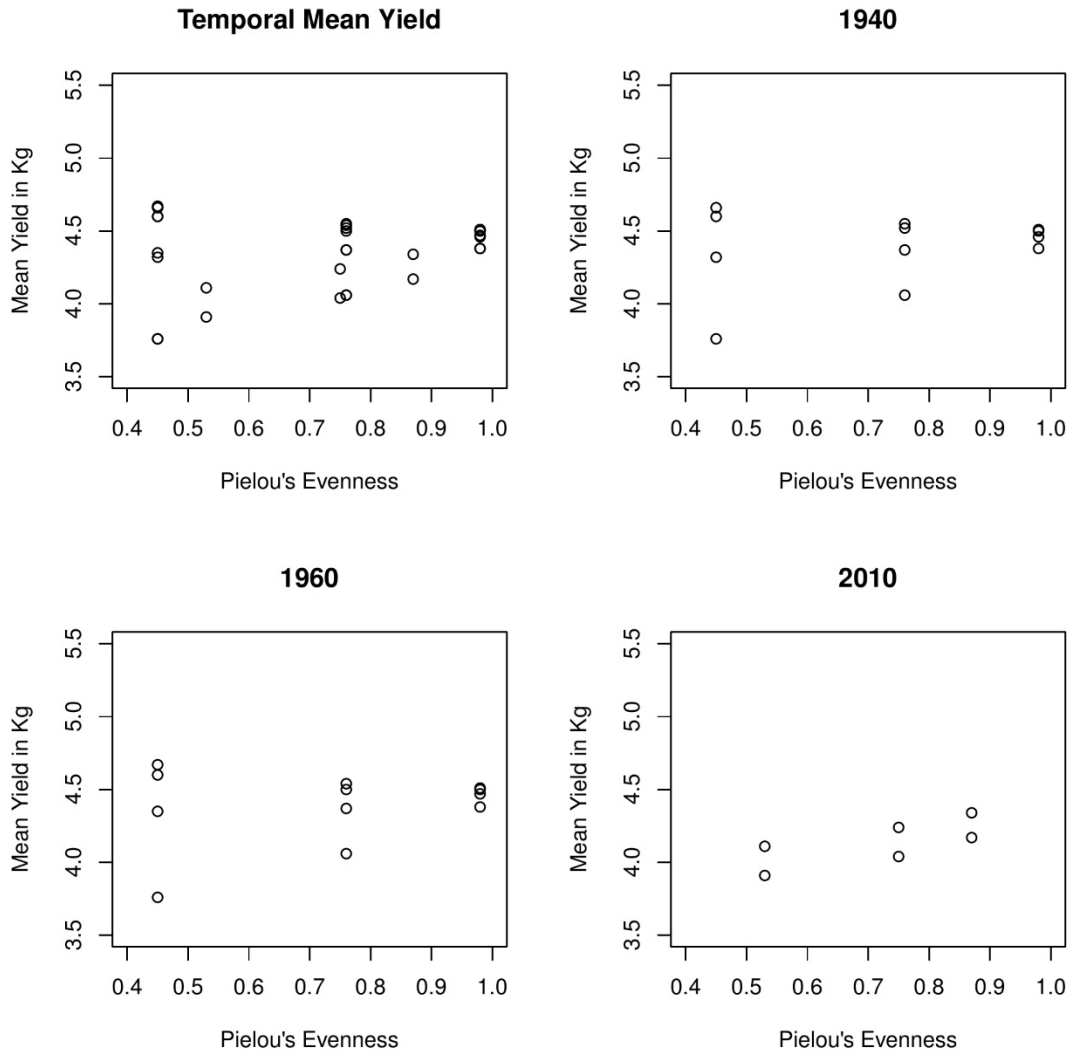# Meta-Scenarios Plots of Community Structure

Evenness Level Meta-Scenarios Plots

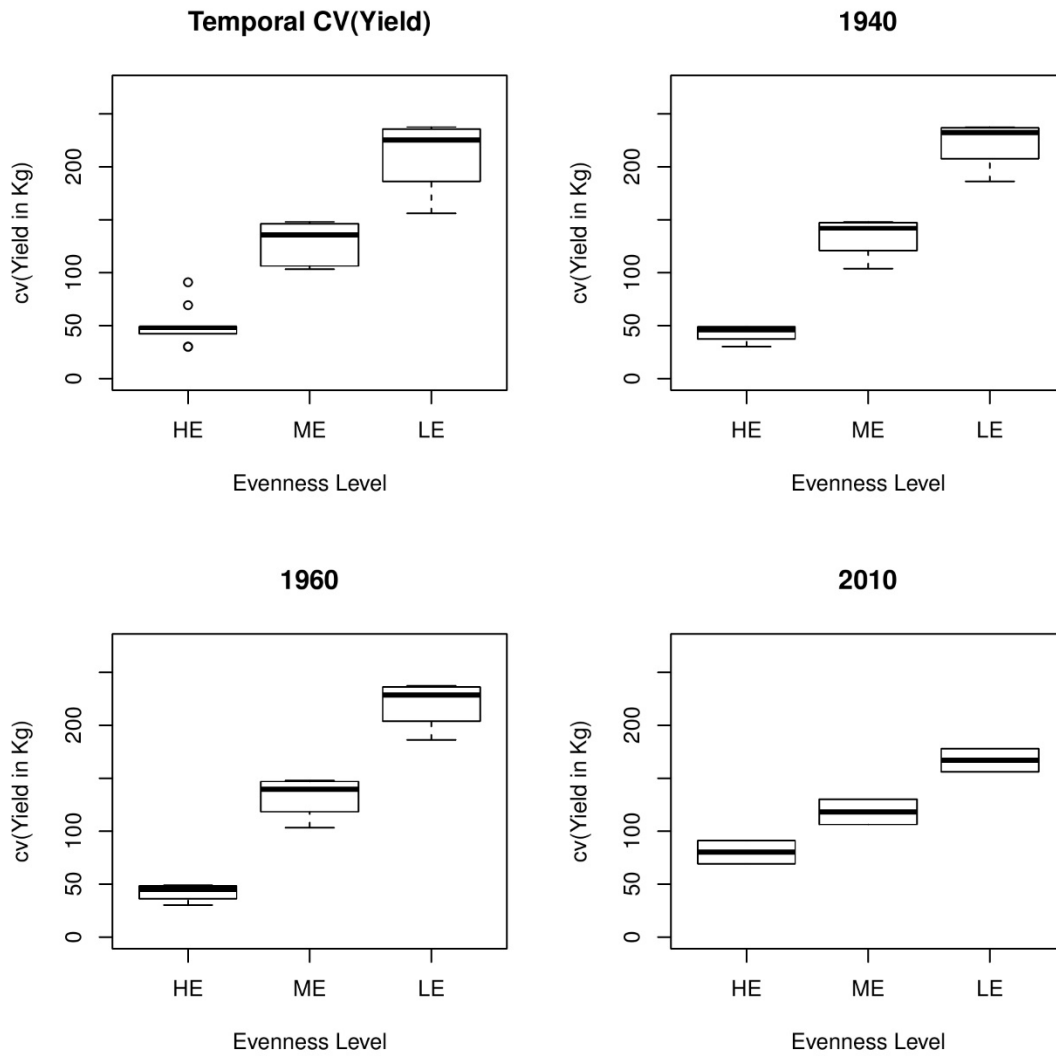CV(yield) in kg Vs Pielou's Evenness Index
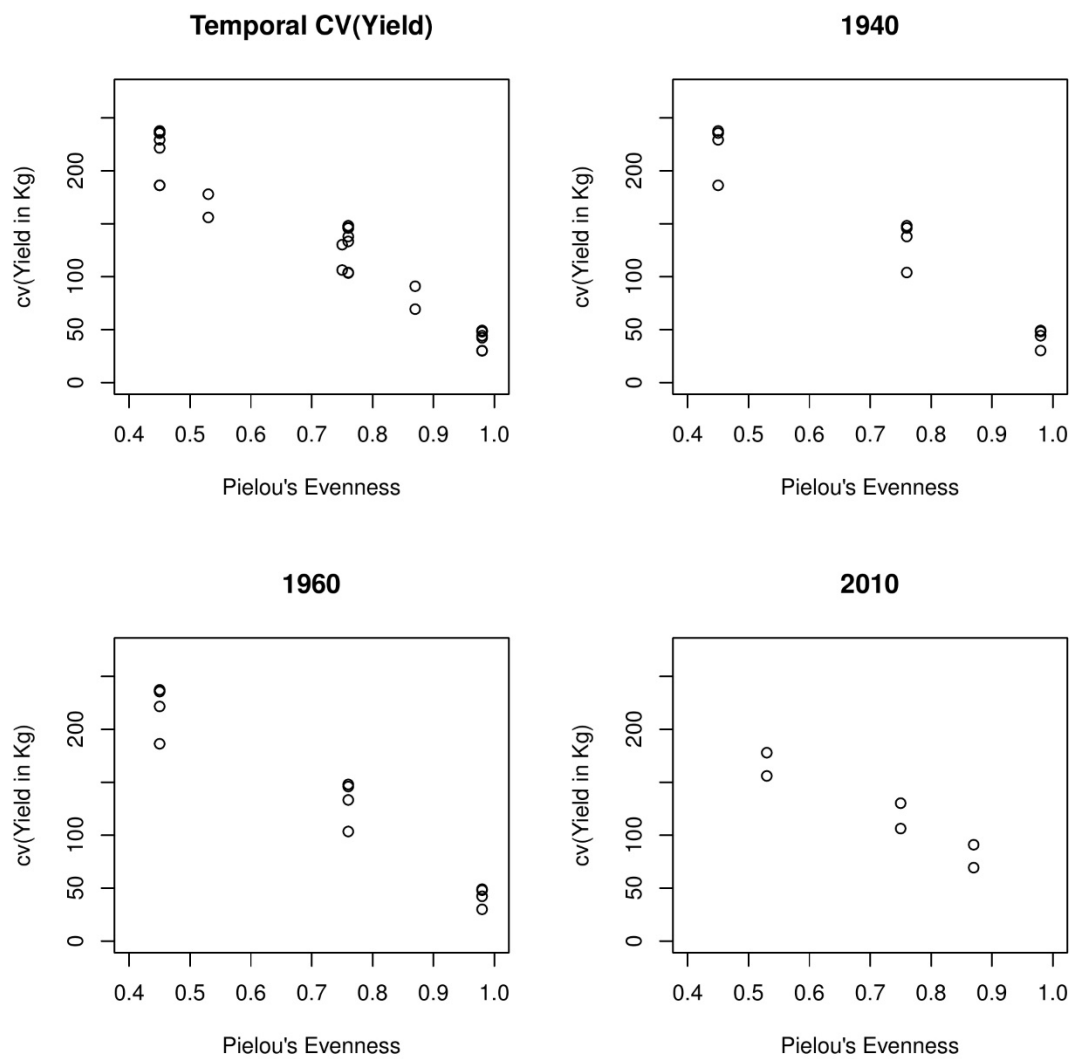
FigA1. 8: *Aggregated meta-scenario & meta-scenarios scatterplot comparison of 100 years temporal CV(Yield) in kg aggregated across dominance level and dominant species identity scenarios plotted against pielou's evenness index.*

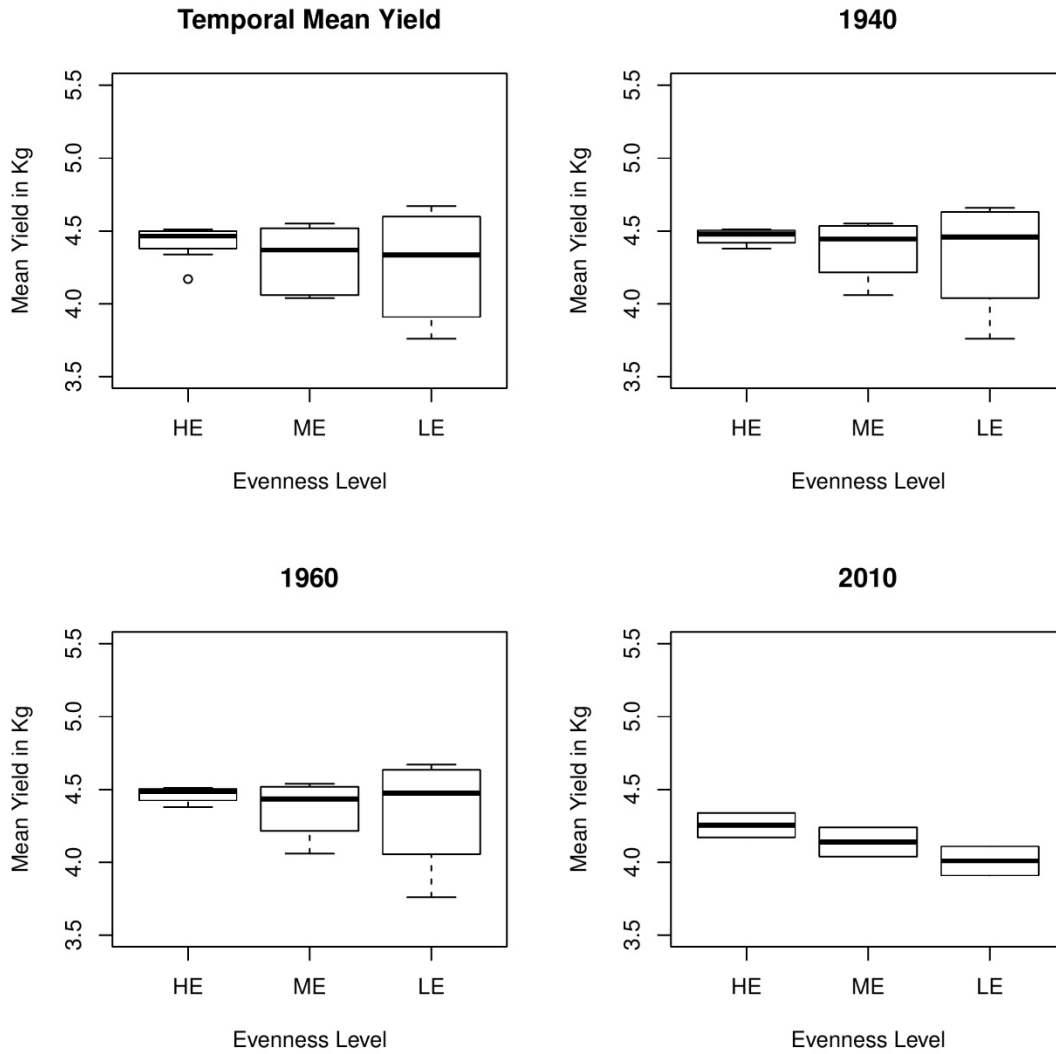Mean Yield in kg Vs Pielou's Evenness Index

FigA1. 9: Aggregated meta-scenario & meta-scenarios scatterplot comparison of 100 years temporal mean(Yield) in kg aggregated across dominance level and dominant species identity scenarios plotted against pielou's evenness index.

CV(yield) in kg Vs Evenness Level

FigA1. 10: Aggregated meta-scenario & meta-scenarios comparison of 100 years temporal CV(Yield) in kg aggregated across dominance level and dominant species identity scenarios plotted against evenness levels. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.
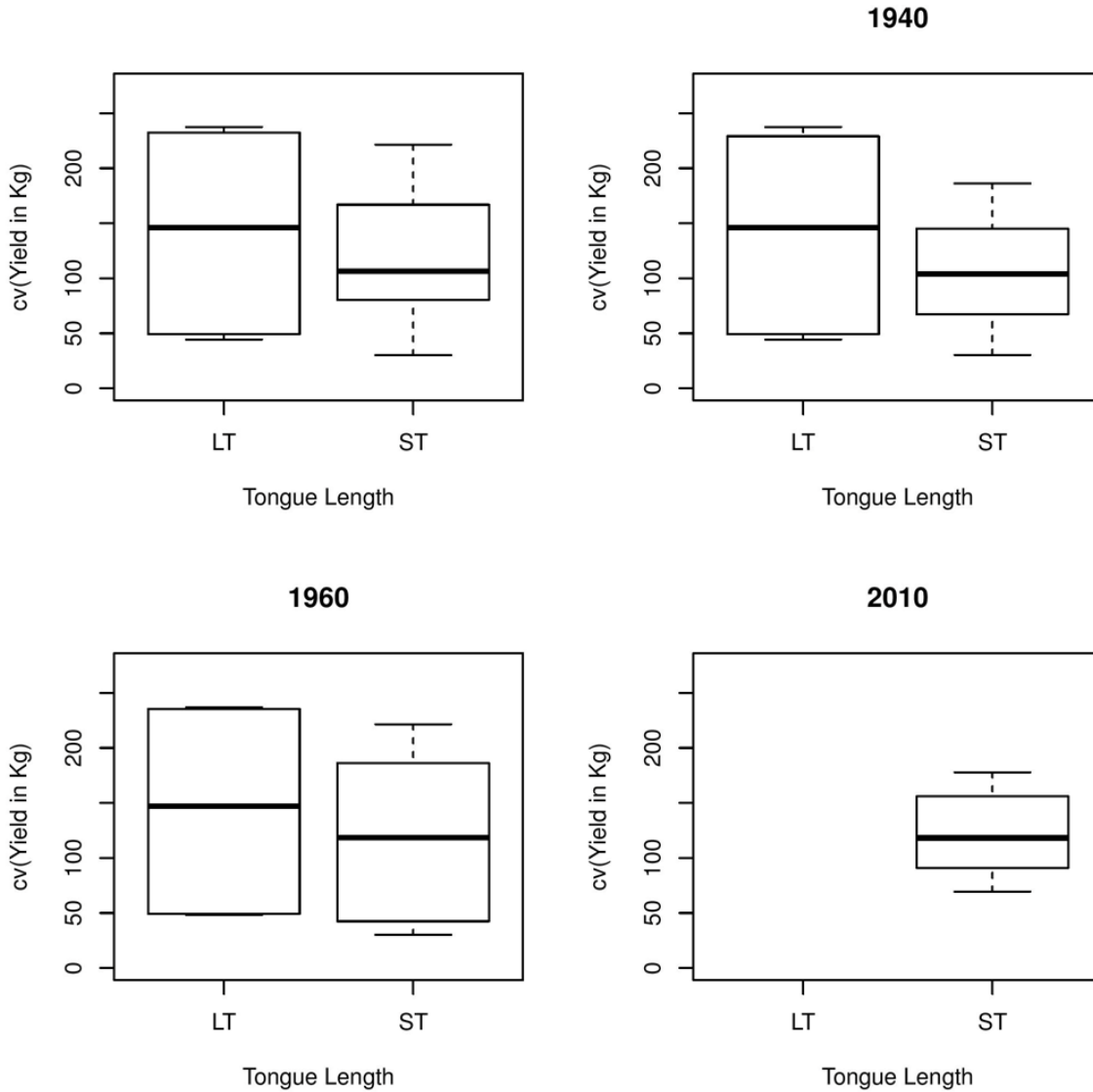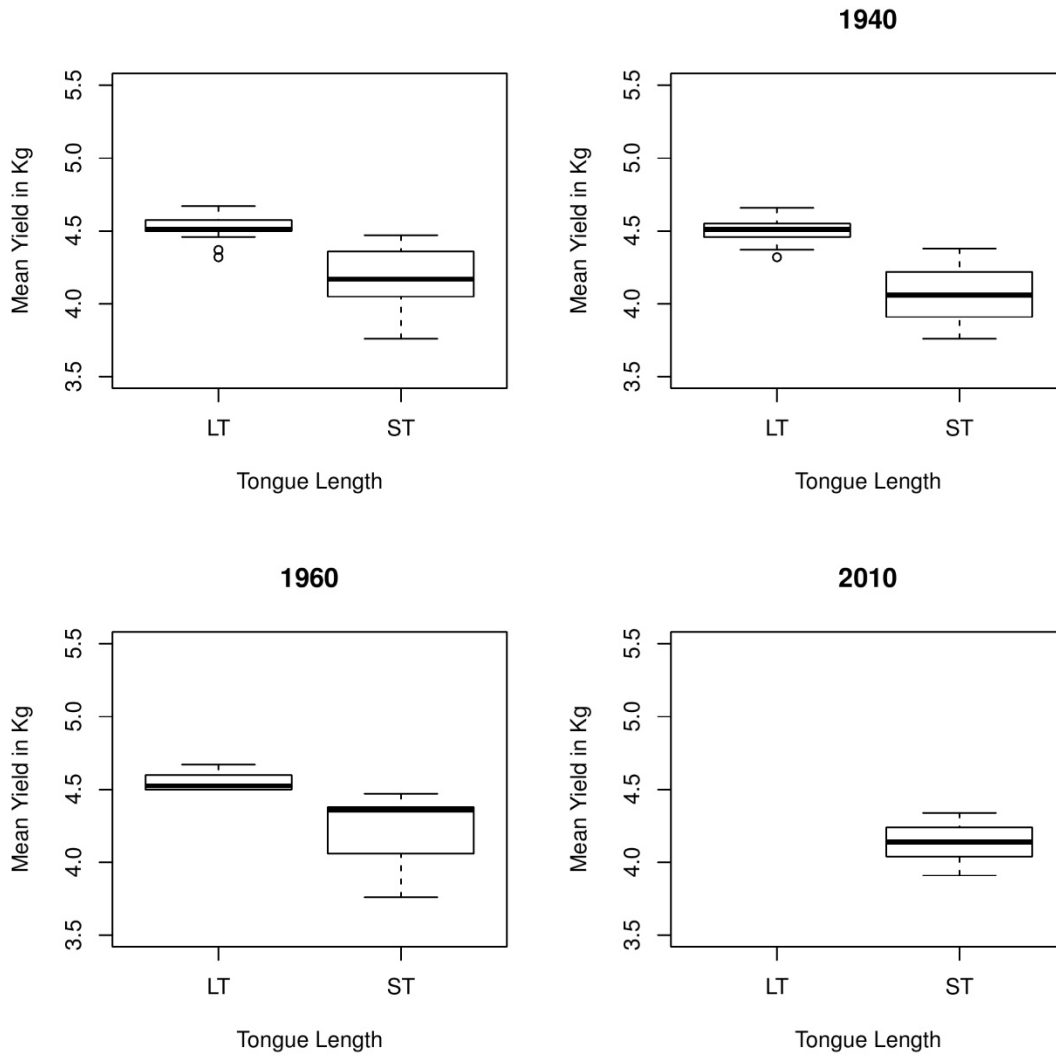
Mean Yield in kg Vs Evenness Level

FigA1. 11: Aggregated meta-scenario & meta-scenarios comparison of 100 years temporal mean(Yield) in kg aggregated across dominance level and dominant species identity scenarios plotted against evenness levels. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.

Tongue Length Identity Meta-Scenarios Plots

CV(yield) in kg Vs Tongue Length

FigA1. 12: Aggregated meta-scenario & meta-scenarios comparison of 100 years temporal CV(Yield) in kg aggregated across evenness levels, dominance levels and dominant species identity scenarios, plotted against tongue length trait. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.
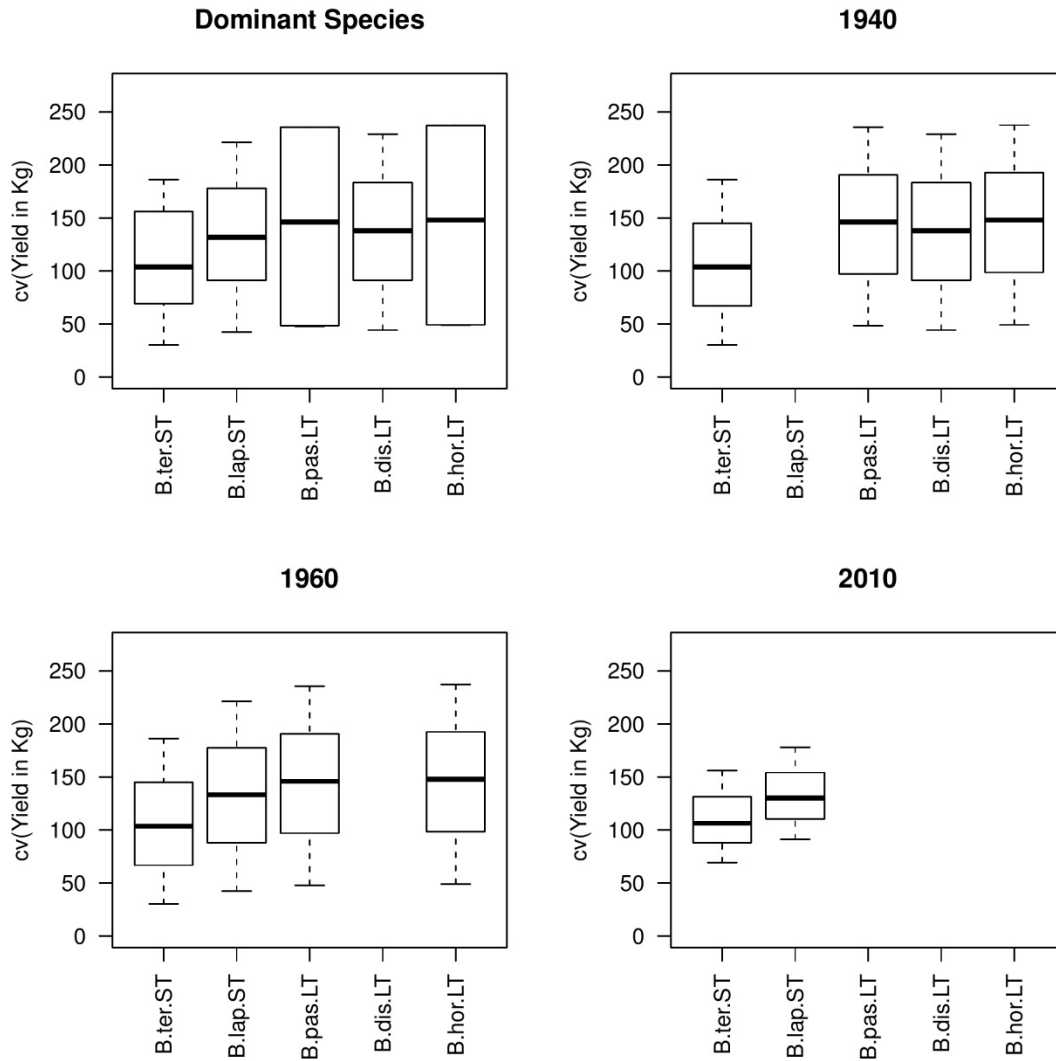
Mean Yield in kg Vs Tongue Length

FigA1. 13: Aggregated meta-scenario & meta-scenarios comparison of 100 years temporal mean(Yield) in kg aggregated across evenness levels, dominance levels and dominant species identity scenarios, plotted against tongue length trait. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.
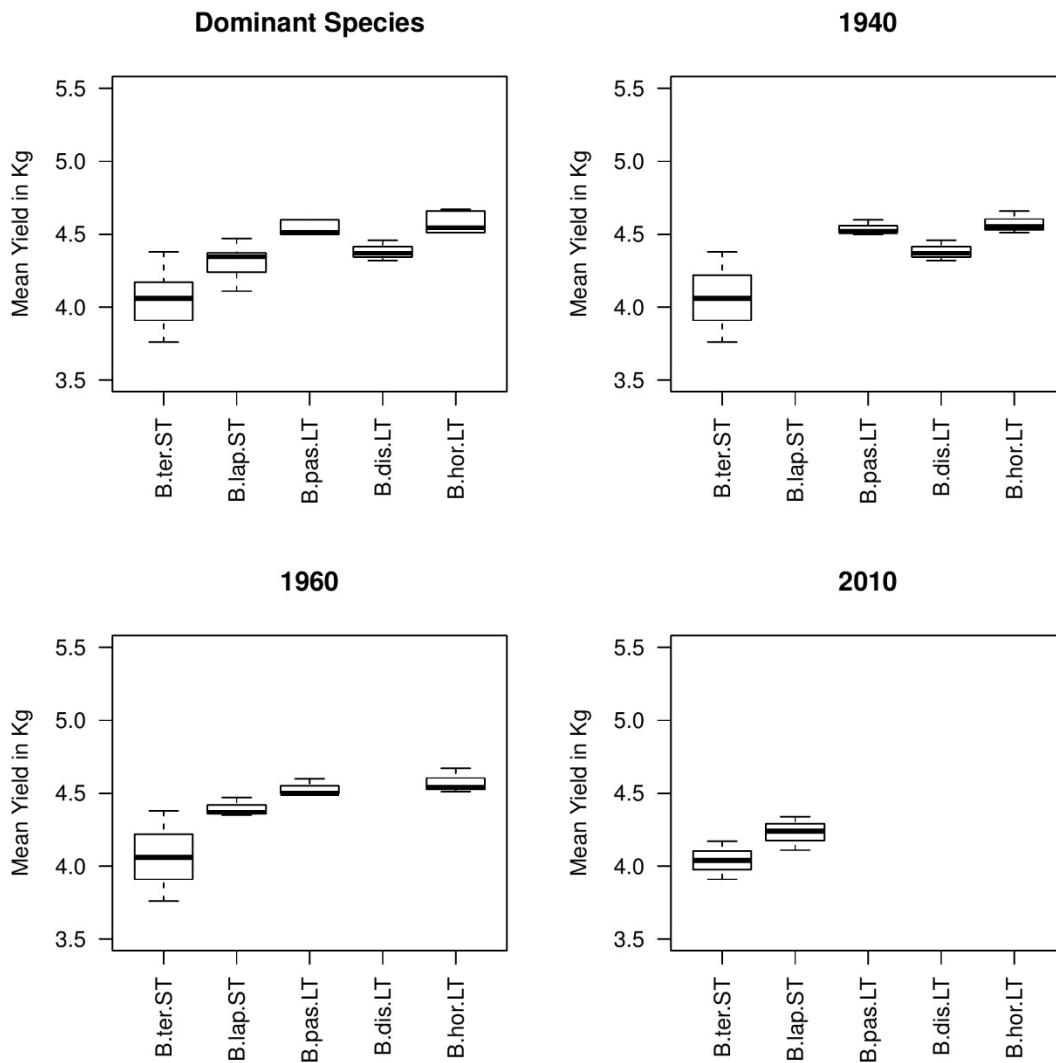
Dominance identity Meta-Scenarios Plots

CV(yield) in kg Vs Dominance Identity

FigA1. 14: Aggregated meta-scenario & meta-scenarios comparison of 100 years temporal CV(Yield) in kg aggregated across dominant species identity scenarios, across evenness and dominance levels plotted against dominant species identity. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.

Mean Yield in kg Vs Dominance Identity

FigA1. 15: Aggregated meta-scenario & meta-scenarios comparison of 100 years temporal mean(Yield) in kg aggregated across dominant species identity scenarios, across evenness and dominance levels plotted against dominant species identity. The box-plots show the median (horizontal line in the box) value. The bottom and top of the box are the first and third quartiles. The whiskers show either maximum or minimum values. Observations outside the range of the whiskers are plotted individually.