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ORIGINAL RESEARCH ARTICLE

Priority host plants for *Ceratitis capitata*, mediterranean fruit fly, based on the host reproduction number for surveillance, trade and eradication programs

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Abstract

Hosts of tephritids are known to vary in their capacity to support the life cycle from egg lay to adult. This capability is measured by the Host Reproduction Number (HRN) which the number of adults that emerge from one kg of fruit. Mediterranean fruit fly (Medfly) is one of the economically important fruit flies and is distributed worldwide. Many Medfly hosts are known but data to quantify their capacity to support the life cycle is scattered through many reports. Here, we reviewed published literature and found data on 146 potential hosts. We placed them in order of HRN and their Host Suitability Index. The HRN values ranged from bird plum (HRN = 1019) to three species of *Syzygium* which were non hosts (HRN = 0). The HRN order will help to inform and triage hosts for targeted surveillance and eradication programs and inform disinfestation activities associated with incursion response management, and for trade and risk mitigation.

Keywords Trade · Incursion · Exotic

Introduction

Trade and tourism are key to the economies of many countries. However, increasing international trade of fruit and vegetables, and increasing tourist travel has led to more frequent incursions of invasive plant pests (Robinson and McNeill 2022). Tephritid fruit flies are one of the most important invasive and destructive crop pests (Follett et al. 2021). Endemic tephritids cause direct losses, making fruit inedible and adversely impacting the ability to feed a growing world population (Bebber et al. 2014). Additionally, detections of exotic tephritid infestations (eggs, larvae, pupae) trigger regulatory responses to eradicate or contain the incursion (Hancock 2013). Importing countries impose stringent quarantine restrictions to prevent entry of potentially infested fruit or vegetables. Therefore, tephritids have the potential to damage national economies and disrupt both domestic and international trade in fresh fruit.

Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) is one of the world's most serious plant pests (Woods et al. 2005). It is a native of Africa but has spread to many parts of the world. In Australia, it is restricted to Western Australia (Woods et al. 2005; Dominiak and Mapson 2017) but the eastern Australian states are free from Medfly. Additionally, Medfly is not established in New Zealand (MacLellan et al. 2021). Many regions, including New Zealand and eastern Australia, are sensitive to potential incursions of Medfly.

The actual risk posed by Medfly is largely influenced by host species. Hosts can be infested with eggs, larvae or pupae but not all of these life stages become adult flies, even under ideal mass rearing conditions (Fanson et al. 2014). Different hosts are known to have varying capacity to support the tephritid life cycle from egg laying stage to emerged adults. This is measured by the number of adults that emerge from one kilogram of fruit (Cowley et al. 1992) and this metric was termed the Host Reproduction Number (HRN) (Dominiak 2022). The HRN can range from 0 to > 1000 (Dominiak 2022; Follett et al. 2021) placed these HRN into six major categories, based on the log of HRN and these categories were termed the Host Suitability Index (HSI). An additional category is non-host. In Australia, Hancock et al. (2000)

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listed 53 species as hosts of Medfly, however, there was no ranking based on the HRN to quantify host risk. Here we found data on 146 potential hosts of Medfly and placed these hosts in the order of reproductive capacity (HRN).

Materials and methods

We followed the methodology described by Dominiak (2022). In summary, Google Scholar was used as a search engine because it yields more results than other databases (Pozsgai et al. 2021). The main research term used was "Ceratitis capitata". Additional terms were added, such as "host" or "suitability" or "susceptibility" or "fruit" and similar terms in successive searches. We examined the results and we chose references if they provided useful data for HRN. Usually, useful references were contained in the first four pages of each search. The third search word was changed, based on the results in earlier searches.

To formulate the table containing hosts, HRN and HSI, we examined each reference for data of each host regarding the reproductive capacity to support adult fruit flies. Where possible, all fruit infestation results are standardized on an individual's HRN. Most data were based on field sampling. Unfortunately, not all papers reported the information required. Some papers reported infestations per fruit and provided insufficient information to calculate the adults/kg metric. Some papers reported infestation rates in graphs or figures and accurate interpretation was too difficult to obtain reasonable estimates. Other papers reported infestations of larvae or pupae per kg and this information is not reported here. Different papers report a range of HRN figures. In plant biosecurity, the worst-case scenario is always assumed to be the case. Therefore, we did not include any references that reported a HRN lower than the eventual highest HRN in Table 1. Within Table 1, the HRN is followed by the equivalent index (HSI) proposed by Follett et al. (2021).

We examined the published literature covering the HRN for Medfly and ranked host plants in descending order based on published HRN (Table 1). Additionally, we assigned each host into one of the potential six HSI categories: HRN = 0 is non host (NH); HRN = < 0.1 is very poor (VP); HRN = 0.1-1.0 is poor (P); HRN = 1.1–10.0 is moderately good (MG); HRN = 10.1–100 is good (G); and HRN = > 100 is very good (VG) (Follett et al. 2021). In our review, numbers of HRN > 20 were rounded out to the closest whole number. Numbers < 20 were converted to one decimal point. We chose the higher HRN where different numbers were reported for a particular host, reflecting the worst-case scenario for biosecurity regulation considerations. There is a broad range within G and VG and there was merit in subdividing these two categories into high and low (Follett pers. comm.), based around the midpoint of the category. Therefore, we added H or L to the G and VG hosts in Table 1.

Africa is the ancestral home of Medfly and data primarily came from Copeland et al. (2002). This was supplemented mainly by Grove et al. (2017; 2019). Liquido et al. (1990) was the primary source for Medfly hosts in Hawaii. Woods et al. (2005) was the source for Medfly hosts in Australia.

Results

We found HRN for 146 potential hosts of Medfly (Table 1). Of these, there were 40 host plants were in the "very good" category (seven hosts were categorised as "very good-high" (VG-H) (HRN > 500) and 33 hosts as "very good-low" (VG-L) (HRN between 100 and 500). We found 61 hosts as "good" (15 good-high (G-H) and 46 good-low (G-L)). Additionally, we found 34 hosts were "moderately good" host plants (MG), five as "poor" (P), zero host plants as Follett's "very poor" and six host plants were categorised as non-hosts (NH) based on the available data.

Discussion

Two previous reviews were regionally based and examined many tephritids in the Pacific (Follett et al. 2021) and Africa (Dominiak 2022). Our review appears to be the first to propose using HRN on a particular species (Medfly) with the potential to inform a range of management options. Tephritid movements occur through long distance jumps followed by local diffusion (Sadler et al. 2011; Florec et al. 2013) found that it was economically better to invest in better exclusion techniques than enhanced surveillance or enhanced eradication capacity. Hence, importers can use HRN to identify higher risk importations and prepare better risk mitigation strategies to minimise or eliminate incursions of Medfly. However, incursions may still occur. Therefore, surveillance programs could consider HRN to identify the more ideal hosts in which to hang traps. Additionally, exotic incursions are more likely to establish quickly in hosts with a high HRN such as papaya (*Carica papaya*) with a HRN = 650. These hosts should be targeted with control measures to optimise eradication success. Therefore, if VG and G feral host fruit were removed or treated, pest populations are likely to decline quickly and the emergency response will have a shorter duration, decreasing the cost of the eradication program (Hancock 2013).

This targeting of host fruit based on HRN is particularly important in countries such as New Zealand which has no tephritids (MacLellan et al. 2021). It may be less important where exotic incursions have to compete with established

Table 1 List of hosts of Mediterranean fruit fly showing Host Reproduction Number (HRN), Host Suitability Index (HSI) and the source paper

Host		Host Reproduction Number	Host Suitability Index	Source
Scientific name	Common name			
Berchemia discolour	Bird plum	1019	VG-H	Grove et al. (2017)
Carissa spinarum	Bush plum	884	VG-H	Grove et al. (2017)
Murraya paniculata	Mock orange	790	VG-H	Moquet et al. (2021)
Passiflora suberosa	Corky passion vine	747	VG-H	Moquet et al. (2021)
Solanum pseudocapsicum	Jerusalem cherry	664	VG-H	Liquido et al. (1990)
Carica papaya	Papaya	650	VG-H	Woods et al. (2005)
Terminalia catappa	Pacific almond	524	VG-H	Woods et al. (2005)
Malpighia glabra	Barbados cherry	434	VG-L	Woods et al. (2005)
Juglans regia	Walnut	367	VG-L	Liquido et al. (1990)
Solanum melongena	Eggplant	354	VG-L	Liquido et al. (1990)
Corallocarpus ellipticus	Gourd	348	VG-L	Copeland et al. (2002)
Prunus armeniaca	Apricot	341	VG-L	Liquido et al. (1990)
Chrysophyllum cainito	Star Apple	336	VG-L	Woods et al. (2005)
Solanum seaforthianum	Brazilian nightshade	333	VG-L	Copeland et al. (2002)
Annona muricata	Soursop	298	VG-L	Woods et al. (2005)
Ekebergia capensis	Cape ash	297	VG-L	Grove et al. (2017)
Carissa bispinosa	Karoo num-num	292	VG-L	Grove et al. (2017)
Terminalia petiolaris	Blackberry tree	276	VG-L	Woods et al. (2005)
Coffea racemosa	Rosemosa coffee	259	VG-L	Grove et al. (2017)
Solanum torvum	Turkey berry	250	VG-L	McQuate (2008)
Prunus serotine cf. capuli	Capuli cherry	237	VG-L	Copeland et al. (2002)
Garcina livingstonei	Imbe	235	VG-L	Grove et al. (2017)
Mangifera indica	Mango	228	VG-L	Woods et al. (2005)
Prunus persica	Peach	204	VG-L	Liquido et al. (1990)
Flueggea virosa	Goowal	188	VG-L	Copeland et al. (2002)
Fortunella japonica	Kumquat	178	VG-L	Liquido et al. (1990)
Coffea arabica	Coffee	176	VG-L	Liquido et al. (1990)
Mimusops zeyheri	Milk wood	171	VG-L	Grove et al. (2017)
Opilia amentacea	Opilia	170	VG-L	Copeland et al. (2002)
Psidium guajava	Guava	160	VG-L	Woods et al. (2005)
Thevetia peruviana	Yellow oleander	148	VG-L	Woods et al. (2005)
Carissa edulis	Bush plum	145	VG-L	Copeland et al. (2002)
Vepris simplicifolia	*	144	VG-L	Copeland et al. (2002)
Harpephyllum caffrum	Wild plum	141	VG-L	Grove et al. (2017)
Guettarda speciosa	Beach gardenia	134	VG-L	Copeland et al. (2002)
Elaeodendron sclucienfurthianum	*	132	VG-L	Copeland et al. (2002)
Acokanthera schimperi	Poison arrow tree	113	VG-L	Copeland et al. (2002)
Harrisonia abyssinia	*	122	VG-L	Copeland et al. (2002)
Juglans nigra	Black walnut	118	VG-L	Liquido et al. (1990)
Eugenia uniflora	Surinam cherry	111	VG-L	Grove et al. (2019)
Mimusops obtusofolia	Red milk wood	99	G-H	Copeland et al. (2002)
Azima tetracantha	Bee sting bush	97	G-H	Copeland et al. (2002)
Manilkara sansiharensis	*	97	G-H	Copeland et al. (2002)
Antidesma venisum	Tassle berry	96	G-H	Copeland et al. (2002)
Clausena anisate	Horsewood	94	G-H	Copeland et al. (2002)
Salacia elegans	*	88	G-H	Copeland et al. (2002)
Mimusops kummel	Red milk wood	87	G-H	Copeland et al. (2002)
Malus sylvestris	Apple	79	G-H	Liquido et al. (1990)
Miliusa braheri	*	71	G-H	Woods et al. (2005)
Prunus salicina x P. cerasifera	Methley plum	69	G-H	Liquido et al. (1990)
Pentarhopalopilia umbellulate	False cluster pear	67	G-H	Copeland et al. (2002)
Vepris nobilis	White ironwood	56	G-H	Copeland et al. (2002)
Coffea sp.	Coffee	53	G-H	Moquet et al. (2021)

Table 1 (continued)

Host		Host Reproduction Number	Host Suitability Index	Source
Scientific name	Common name			
Prunus domestica	Plum	51	G-H	Liquido et al. (1990)
Parinaric curatellifolia	*	50	G-H	Grove et al. (2017)
Bourreria petiolaris	*	42	G-L	Copeland et al. (2002)
Capparis sandwichiana	Puapilo	41	G-L	Liquido et al. (1990)
Polysphaeria parvifolia	*	40	G-L	Copeland et al. (2002)
Capsicum annuum	Bell pepper, capsicum	39	G-L	Liquido et al. (1990)
Manilkara sulcate	*	39	G-L	Copeland et al. (2002)
Gmelina arborea	Snapdragon tree	39	G-L	Woods et al. (2005)
Artabotrys monteiroae	Red hook-berry	34	G-L	Copeland et al. (2002)
Syzygium cordatum	Water berry	32	G-L	Grove et al. (2017)
Syzygium jambos	Jambos	27	G-L	Liquido et al. (1990)
Filicum decipiens	Treefern	27	G-L	Copeland et al. (2002)
Grewia trichocarpa	*	25	G-L	Copeland et al. (2002)
Lycopersicon lycopersicum	Common tomato	23	G-L	Liquido et al. (1990)
Pimento dioca	Allspice	22	G-L	Grove et al. (2019)
Manikara butugi	*	22	G-L	Copeland et al. (2002)
Psidium littorale	Strawberry guava	21	G-L	Liquido et al. (1990)
Euclea divinorum	Toothbrush bush	21	G-L	Copeland et al. (2002)
Eriobotrya japonica	Loquat	20	G-L	Liquido et al. (1990)
Wikstroemia phillyreifolia	Akia	19.8	G-L	Liquido et al. (1990)
Ficus carica	Common fig	18.6	G-L	Liquido et al. (1990)
Ludia mauritiana	*	18	G-L	Copeland et al. (2002)
Syzygium cumini	Java plum	17.9	G-L	Liquido et al. (1990)
Inga laurina	Inga	17.4	G-L	Moquet et al. (2021)
Diospyros kaki	Oriental persimmon	17.2	G-L	Liquido et al. (1990)
Drypetes gerrardii	Forest iron plum	17	G-L	Copeland et al. (2002)
Englerophytum magalismontanum	*	17	G-L	Grove et al. (2017)
Vepris trichocarpa	Furry fruited teclea	16.6	G-L	Copeland et al. (2002)
Capparis sepiaria	Wild caper bush	16	G-L	Copeland et al. (2002)
Capsicum frutescens	Chilli pepper	17.7	G-L	Moquet et al. (2021)
Strychnos henningsii	Red bitter berry	15.4	G-L	Copeland et al. (2002)
Sideroxylon inerme	White milkweed	14.1	G-L	Copeland et al. (2002)
Mimusops elengi	Spanish cherry	13.9	G-L	Moquet et al. (2021)
Momordica charantia	Bitter melon	13.8	G-L	Liquido et al. (1990)
Scaevola plumieri	Gullfeed	13.7	G-L	Copeland et al. (2002)
Malpighia punicifolia	Acerola	13.1	G-L	Liquido et al. (1990)
Olea woodiana	Forest olive	13	G-L	Copeland et al. (2002)
Drypetes natalensis	Natal iron plum	13	G-L	Copeland et al. (2002)
Dovyalis caffra	Kei-apple	12	G-L	Grove et al. (2017)
Flacourtia indica	Batoko plum	12	G-L	Copeland et al. (2002)
Cascabela thevetia	Yellow oleander	11.9	G-L	Moquet et al. (2021)
Rubus lucidus	Blackberry	11.9	G-L	Liquido et al. (1990)
Santalum sp.	Sandalwood	11.1	G-L	Liquido et al. (1990)
Cordia sebestena	Scarlet cordia	11	G-L	Woods et al. (2005)
Physalis peruviana	Poha	11	G-L	Liquido et al. (1990)
Pithecellobium dulce	Madras thorn	10.9	G-L	Moquet et al. (2021)
Scaevola sericera	Beach naupaka	10.5	G-L	Copeland et al. (2002)
Pouteria viridis	Green sapote	10.2	G-L	Liquido et al. (1990)
Flagellaria guineensis	Bababia	9.6	MG	Copeland et al. (2002)
Ximenia caffra	Sour plum	9.4	MG	Copeland et al. (2002)
Annona cherimola	Cherimoya	8.9	MG	Liquido et al. (1990)
Eugenia uniflora	Surinam cherry	8.1	MG	Liquido et al. (1990)
Cyphomandra betacea	Tree tomato	8.1	MG	Liquido et al. (1990)

Table 1 (continued)

Host		Host Reproduction Number	Host Suitability Index	Source
Scientific name	Common name			
Solanum muricatum	Pepino	8.0	MG	Liquido et al. (1990)
Monodora grandidieri	*	7.7	MG	Copeland et al. (2002)
Mimusops bagshawei	*	7.7	MG	Copeland et al. (2002)
Coccinia microphylla	Red gourd	7.7	MG	Copeland et al. (2002)
Lamprothamnus zanguebaricus	*	6.9	MG	Copeland et al. (2002)
Prunus africana	African cherry	6.5	MG	Copeland et al. (2002)
Euphoria longan	Longan	6.3	MG	Liquido et al. (1990)
Acokanthera oppositifolia	Bushman's poison	5.5	MG	Copeland et al. (2002)
Casimiroa edulis	Sapote	5.4	MG	Liquido et al. (1990)
Spondias cytherea	Wi apple	5.3	MG	Liquido et al. (1990)
Citrus x tangelo	Tangelo	4.4	MG	Liquido et al. (1990)
Clausena lansium	Wampi	4.2	MG	Liquido et al. (1990)
Psidium cattleianum	Strawberry guava	4.1	MG	Grove et al. (2019)
Citrus maxima	Pummelo	4.1	MG	Liquido et al. (1990)
Citrus x paradisi	Grapefruit	3.9	MG	Liquido et al. (1990)
Citrus reticulata	Tangerine orange	3.7	MG	Liquido et al. (1990)
Persea americana	Avocado	3.2	MG	Liquido et al. (1990)
Phyllanthus acidus	Otaheite gooseberry	2.9	MG	Liquido et al. (1990)
Annona reticulata	Custard apple	2.6	MG	Liquido et al. (1990)
Blighia sapida	Akee	2.2	MG	Liquido et al. (1990)
Citrus sinensis	Orange (Navel and Valencia)	2.2	MG	Liquido et al. (1990)
Parinaric macrophylla	Nonda	2	MG	Woods et al. (2005)
Passiflora ligularis	Sweet granadilla	1.8	MG	Liquido et al. (1990)
Calophyllum inophyllum	Kamani	1.8	MG	Liquido et al. (1990)
Opuntia ficus-indica	Cactus	1.8	MG	Liquido et al. (1990)
Musa x paradisiaca	Banana	1.4	MG	Liquido et al. (1990)
Syzygium malaccense	Mountain apple	1.4	MG	Liquido et al. (1990)
Oxyantlus zanguebaricus	*	1.2	MG	Copeland et al. (2002)
Pyrus communis	Pear	1.1	MG	Liquido et al. (1990)
Artocarpus altilis	Breadfruit	0.9	P	Liquido et al. (1990)
Citrus limon	lemon	0.8	P	Liquido et al. (1990)
Averrhoa carambola	Star fruit	0.7	P	Moquet et al. (2021)
Citrus aurantiifolia	Lime	0.6	P	Liquido et al. (1990)
Citrus australasica	Finger lime	0.2	P	Follett et al. (2022)
Acca sellowiana	Feijoa	0	NH	Grove et al. (2019)
Plinia caujifora	Jaboyicaba	0	NH	Grove et al. (2019)
Psidium friedrichsthalianum	Costa Rican guava	0	NH	Grove et al. (2019)
Syzygium guineense	Water berry	0	NH	Grove et al. (2019)
Syzygium paniculatum	Magenta cherry	0	NH	Grove et al. (2019)
Syzygium samarangense	Java plum	0	NH	Grove et al. (2019)

* = no common name

tephritids with higher HRNs in those same hosts (Copeland et al. 2006; Dominiak and Mapson 2017).

We found 40 VG hosts capable of supporting > 100 adults per kg of fruit. Within this group, papaya, Pacific almond, mango, coffee and guava were major hosts. Good hosts was the largest category (41.7%) with 61 hosts. Surveillance and incursion managers should be aware of these species to optimise surveillance or eradication activities. Additionally, the use of HRN to inform and triage surveillance targets should consider factors such as typical size (kg) of fruit. Also, it is unclear whether the HRN translates to the attractiveness of the fruit and preferential selection by Medfly.

The seven hosts with the highest HRN (HRN = VG-H) would be preferred hosts for surveillance including bird plum, bush plum, mock orange, corky passion vine, Jerusalem cherry and Pacific almond (Table 1). However, any host with a HRN > 100 would be ideal hosts for surveillance (40 hosts). In any incursion, these hosts should be fruit stripped to prevent any further rapid Medfly population development. For domestic and international trade, the HRN could be used to vary disinfestation protocols, particularly in a Systems Approach (Dominiak 2019). For instance, should limes (HRN = 0.6) be required to undergo the same treatment as papaya (HRN = 650) where the risk is about 1000 times greater. Additionally, the temperature mediated disinfestation period might be shortened for low HRN commodities to achieve the same biosecurity outcome (e.g. - a given probit level in a Systems Approach). Shorter treatment times would result in a lower carbon footprint of commodities and minimise the impact on global climate change.

In Australia, Hancock et al. (2000) listed 53 potential hosts of Medfly, but there was virtually no ranking of HRN. Based on our review (see Table 1 for details), ten of these hosts were VG hosts, seven were G hosts, 12 were MG hosts and one was a NH. Many authors report hosts of Medfly but not all record the HRN metric: many authors report adults per fruit with no reference to weight of individual fruit. The HRN metric needs to be included in future reports if trade, surveillance and eradication programs are to be optimised. Additionally, knowledge of high HRN hosts would inform eradication managers to rapidly reduce endemic Medfly populations.

It is important to reflect that this host list is not exhaustive. There are many hosts of Medfly referenced in literature that have not been included in this review due to unavailability of data to quantify reproductive capacity. Also, it is important to acknowledge that even though the data suggests that some are potential NH hosts, these hosts need to be considered carefully. For example, feijoa is commonly considered a Medfly host (Argov and Gazit 2008) but we could not find HRN data for feijoa in Africa. Therefore, NH should not be ruled out as a host based on the presented data alone. It is known that factors such as climate, altitude, competition with other fruit fly species and time of year of sampling can influence number of flies found and may account for some NH results.

Here, we have reported the worst-case HRN however these number may not apply to all circumstances. Medfly are found in abundance at lowland and high elevation sites (> 2,100 m ASL) however Medfly were seldom found in lowland areas after the introduction of *Bactrocera dorsalis* (Hendel) (Copeland et al. 2002). Medfly has a high tolerance of dry conditions compared to *B. dorsalis* (Hassani et al. 2016) and is capable of withstanding low temperatures (Badii et al. 2015). Therefore, the HRN may be lower than our reported figures based on the local environment, particularly at the margins of its range. Conversely, the HRN may be higher in ideal environmental situations. We encourage all fruit fly researchers to report, where possible, the HRN for all tephritids so that management and trade can be optimised. For example, commercial consignments of papaya, egg plant, apricot, mango and peach needs to be treated before export because of their high HRN. Conversely, based on our findings, low HRN commodities such as feijoa, finger lime, star fruit, pear and banana may require minimum disinfestation before export. Alternatively, these commodities would be suitable for a *Systems Approach* to production and not require any disinfestation due to their low HRN (Dominiak 2019).

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Declarations

Conflict of interest The authors declared that there are no conflicts of interest.

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