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RESEARCH ARTICLE

The extent and impact of exotic vine invasions in fragmented mesic forests in Eastern Australia

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Abstract

Exotic vines threaten biodiversity causing damage to forest structure. We investigated the distribution of exotic vines across different patchily distributed plant communities. We surveyed patches of 12 threatened, mesic forest communities along the coastal plain in New South Wales, Australia to determine how exotic and native vine distribution and density were influenced by characteristics of forest patches and neighbouring land use. Vine density and stem widths were measured in quadrats in the edge and interior of patches. Canopy cover, number of dead trees, area to perimeter ratio and surrounding land use were recorded for each patch. Our results show that exotic vine assemblages were influenced by anthropogenic land use surrounding patches but not influenced by community type. Most exotic vine species were present across the whole region where surveys were undertaken. Exotic vines species were sometimes at high densities but had smaller stem widths than native species and there was no change in density from the edges into the interior. *Araujia sericifera* and *Ipomoea cairica* were the most prevalent exotic species and together with the fast edge growing *Anredera cordifolia* are of key concern. In contrast, native vine assemblages were species rich, with some individuals having large stem widths suggesting greater age and we found species composition varied with plant community type. Native vines showed continual recruitment and appeared more specialized to the attributes of each plant community. Surrounding anthropogenic land uses (residential, agricultural and industrial) were the most important factors predicting invasion of exotic vines and were more important than the length of edges. This suggests that the surrounding matrix characteristics were influencing degradation of the interior of these patches, rather than exotic vines invading along an invasion front from the edge. Exotic vines need to be controlled across the entirety of patches, rather than a focus on edge control practices.

KEYWORDS
forest edge, forest interior, invasive plants, land clearing, Liana, temperate forests

INTRODUCTION

Exotic vines pose a significant threat to biodiversity due to their fast growth allowing them to aggressively invade and degrade forests (Estrada-Villegas & Schnitzer, 2018; Letcher, 2014; Schnitzer, 2018). All vines, including exotic vines, can cause physical damage to host trees leading to changes in forest structure which can ultimately lead to canopy collapse (Estrada-Villegas &

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Schnitzer, 2018). Vine impact is related to density and biomass, as vines with higher biomass shade out more light (Llorens & Leishman, 2008), and invade more of the canopy of their host trees, leading to higher rates of branch breakage and mortality (Ingwell et al., 2010). Higher densities of vines also compete intensely for resources (Schnitzer & Carson, 2010), and can reduce overall forest biomass (Schnitzer et al., 2011). Exotic vine invasion can add to native vine impacts and lead to a large increase in damage causing degradation of the forests. While vines invade all forest types, they can be particularly damaging for closed and mesic forests where losses of canopy biomass significantly alters the structure and changes ground level climates (Paul & Yavitt, 2011; Schnitzer, 2018). In Australia, mesic forests include rainforests and eucalypt forests where the understorey is comprised of soft-leaved plants rather than sclerophyllous species.

Fragmentation of forests creates higher edge to interior ratios and vines, in general, are more abundant at the edge of forests (Campbell et al., 2018; Letcher, 2014), where high rates of disturbance create opportunities for establishment with small trees often acting as trellises (Putz, 1984; Schnitzer, 2018). Furthermore, fragmentation may have been reduced patch size increasing the edge to interior ratios. This edge effect is less pronounced as fragmentation increases and where patches have become highly degraded (Campbell et al., 2018) as, here, vines are able to take advantage of canopy openings from tree falls (Schnitzer & Carson, 2010) and can invade into the interior. Vines usually outcompete trees after disturbances as they can allocate more resources to energy capture and elongation than self-supporting plants (Mello et al., 2020). Extensive stem development can provide further opportunities for other vine individuals to establish, and can alter or stall forest succession (Paul & Yavitt, 2011). Therefore, communities that are more fragmented, that is, have higher edge to interior ratios, and are degraded as a result of other factors, should have a higher risk of impact and invasion by exotic vine species. However, if exotic vines are able to establish in the interior of a patch, their damage on host trees would cause disturbances and provide improved opportunities for vine invasion across the whole patch. Therefore, confirming whether exotic vine species invade from edges, or are found in the interior of a patch, is important in understanding their threat.

Increased isolation of forests is usually due to anthropogenic land use changing the landscape around a patch. This can provide a pathway for exotic vines to establish as an isolated forest surrounded by a residential or agricultural area has a higher chance of invasive weed propagules reaching the forest than if it was surrounded by intact vegetation (Vilà & Ibáñez, 2011). However, some exotic vine species may be able to invade into relatively undisturbed patches by having long-distance dispersal methods, such as wind-blown (Gassó et al., 2009) or vertebrate-dispersed seeds, and germination tolerance to low-light situations. Alternatively, seed may germinate on the edge and the vine may then degrade the forest through host plant damage providing opportunities for further germination further into the forest. Discerning how the surrounding landscape influences the assemblage of vine species is valuable in identifying the processes of invasion and key attributes which might influence exotic vine invasion.

Along the east coast of Australia, mesic and closed forests are often patchily distributed amongst more open eucalypt forests and woodlands, and are frequently disturbed, resulting in many communities being listed as threatened under the *Biodiversity Conservation Act 2016* (NSW Scientific Committee, 2006). These patches can be quite small in the natural landscape but there is no doubt that clearing has caused both a reduction in the size of remaining remnants and a change to surrounding vegetation. Knowledge of which exotic vine species are the main invaders for each

of these communities are required to prioritize management for particular species and mitigate the threat for individual communities but also for the region in general. We conducted surveys across 12 different closed and mesic forest plant community types which vary in canopy structure to determine which exotic vines were invaders of specific communities and which were more ubiquitous. Native vines are a natural element of all of these communities, but little is understood about their abundance or specificity for particular communities. Differences in the patterns of distribution of native and exotic vines may highlight important factors that influence exotic vine invasion. To this end, we investigated:

1. How native and exotic vine species differ in distribution and density in patches of closed forests,
2. How these plant communities differ in native and exotic vine assemblages and
3. How patch disturbance and surrounding land use influence the occurrence and distribution of exotic vines.

METHODS

Survey sites and design

Patches from 12 mesic and closed forest communities classified as threatened (as defined by the NSW *Biodiversity Conservation Act 2016*) were surveyed along the coastal region of New South Wales. They vary in canopy cover in terms of both the species forming the canopy (Table 1) and the degree of canopy closure (Figure 1). All occur naturally in small patches even in uncleared landscapes and are in stark contrast to the open woodlands that occur in surrounding drier areas. The vegetation communities that were surveyed ranged from subtropical rainforests to coastal floodplain forests and include taller moist open forests (Table 1).

Field surveys were conducted from June 2019 to March 2021. There were 129 patches of forest visited (Table 1). The number of patches surveyed for each threatened community was correlated with the available habitat in the landscape ($F_{1,10}=20.2$, $p<0.01$, $R^2=0.67$, Table 1). For example, Mount Gibraltar Forest only occurs on a small number of isolated pockets of a specific rock intrusion (microsyenite) in the Southern Highlands, and only two patches could be surveyed. In contrast, Swamp Oak Floodplain Forest is widespread along the NSW coast and 24 patches were surveyed.

Distribution of native and exotic vines in patches

Within a patch, interior and edge habitat were surveyed using up to ten 2 m $\times$ 50 m replicate quadrats, with the first quadrat set near the point of entry into the patch. Edge quadrats were within 0–10 m of the edge, while interior quadrats were at least 50 m from the edge. While there are a range of characteristics associated with edge effects up to 100 m (Campbell et al., 2018; Laurance et al., 2001), these distances were not sensible in the more disturbed and patchy landscapes in Eastern Australia where patch sizes were naturally much smaller. Like Mohandass et al. (2014), we chose edges and interior habitat at these distances as light levels were much greater across this distance and acute disturbances were more obvious up to 10 m from an edge. Furthermore, many patches were not large enough to sample over 100 m into the patch. Thus, our distances reflect a known change in light as well as allowing us to survey more fragments of each plant community to

TABLE 1 The plant communities surveyed in order of percentage cover visualized in Figure 1, their acronyms, dominant tree species and number of patches and quadrats surveyed.

Ecological community	Acronym	Dominant tree species	Remaining area (ha)[a]	No. patches surveyed	No. quadrats	No. native vine species	No. exotic vines species
Lowland Rainforest on Floodplain	LLRF	*Mallotus philippensis, Aphananthe philippensis, Argyodendron trifoliolatum*	<1000	11	76	46	11
Illawarra Subtropical Rainforest	ISRF	*Streblus brunionanus, Elaeodendron australe, Guioa semiglauca*	3400	11	47	22	12
Littoral Rainforest	LRF	*Acmena smithii, Cupaniopsis anacardiodes, Elaeodendron australe*	NA	18	116	38	14
Western Sydney Dry Rainforest	WSDRF	*Melaleuca stypheloides, Streblus brunionanus, Clerodendrum tomentosum*	338	9	26	20	10
Milton Ulladulla Subtropical Rainforest	MUSRF	*Streblus brunionanus, Elaeodendron australe, Alectryon tomentosum*	NA[b]	7	31	20	3
Pittwater Wagstaffe Spotted Gum Forest	PWSGF	*Corymbia maculata, Notelaea longifolia, Glochidion ferdinandi*	227	9	42	18	5
Swamp Sclerophyll Forest on Coastal Floodplains	SSF	*Eucalyptus robusta, Melaleuca quinquenervia, Glochidion ferdinandi*	11500	20	112	29	16
Subtropical Coastal Floodplain Forest	STCFF	*Lophostemon suaveolens, Corymbia intermedia, Melaleuca quinquenervia*	350	11	59	21	9
Swamp Oak Floodplain Forest	SOFF	*Casuarina glauca, Melaleuca quinquenervia*	10400	24	133	17	14
Robertson Basalt Tall Open Forest	RBTOF	*Eucalyptus fastigata, Acacia melanoxylon, Eucalyptus viminalis*	400	3	8	5	2
Moist Shale Woodland	MSW	*Eucalyptus tereticornis, Clerodendrum tomentosum, Breynia oblongifolia*	604	4	21	7	3
Mount Gibraltar Forest	MGF	*Eucalyptus fastigata, Eucalyptus viminalis, Melicytus dentata*	NA[b]	2	15	4	3
Total				129	686	74	27

Abbreviation: NA, not available.

[a]Data obtained from final determinations on NSW government website.

[b]Small patches all restricted to a single locality.

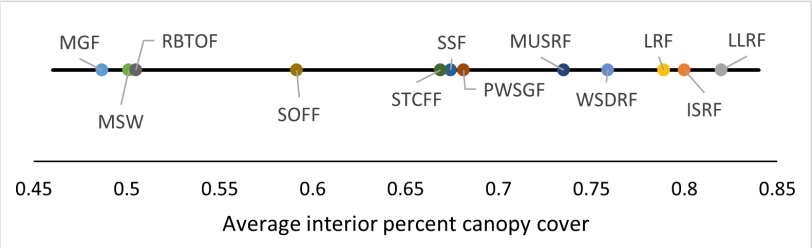


FIGURE 1 Average interior percent canopy cover of 12 plant communities surveyed along the NSW Coastal Plain. Abbreviations follow Table 1.

understand community changes in exotic vine abundance. Each quadrat was at least 50 m from the next. Despite our decisions on requiring 50 m distance for quadrats, some patches were still too small to enable interior habitat to be sampled and some were not big enough to complete the maximum number of quadrats in the edge or interior. However, overall the total number of quadrats surveyed for each community was closely correlated to the number of patches sampled ($F_{1,10} = 146.8$, $p < 0.01$, $R^2 = 0.93$) indicating a similar intensity of sampling.

Quadrats were rectangular to enable surveys to be undertaken in narrow patches and ran parallel to the nearest edge. Up to 10 quadrats in each habitat were surveyed in a patch. Within each quadrat we recorded the presence of exotic and native vine species, measured the number of vine stems above 2 m, identified vine stems to species, measured the diameter of stems at breast height (DBH, 1.3 m) of vine stems above 2 m, and the number of dead trees. DBH (stem width) was used as a proxy for vine biomass as an allometric relationship between dry biomass and DBH has been shown to occur in vines (French et al., 2017; Schnitzer et al., 2006); however, the accuracy of this relationship decreases significantly for large (greater than 140 mm DBH) stems (Schnitzer et al., 2006). Vines that were under 2 m tall were recorded for presence analyses, but not abundance nor stem width analyses.

Stem densities were calculated as stems per hectare. For each species, we calculated the density as the average number of stems per quadrat and then converted this to average stems per hectare.

We recorded canopy cover at six points within each quadrat, 0 m, 10 m, 20 m, 30 m, 40 m and 50 m along the long edge of the quadrat, using the HabitApp application (Scrufster, 2014) on a Samsung S8 smartphone. The phone was held at shoulder height with the camera facing the canopy, which takes a photo and HabitApp returns a percent cover estimate. These six values were averaged for each quadrat, and then used to see how exotic stem density differs amongst the surveyed communities due to their average canopy covers as a measure of invasion. However, as canopy covers include the foliage from exotic vines when they are present in the canopy, we only used canopy data from patches where less than six exotic vine stems were recorded when we categorized communities. This was averaged for each community (Figure 1).

Variation in vine assemblages amongst communities

We undertook 3-factor permutational multivariate analyses of variance (PERMANOVA) based on Bray Curtis similarity distances to determine if there were differences in composition of both native and exotic species, based on stem density, amongst plant communities and between interior and edge position (PRIMER-E V7). We excluded three communities

which had too few patches for analysis: Robertson Basalt Tall Open Forest (RBTOF), Moist Shale Woodland (MSW), Mt. Gibraltar Forest (MGF) (Table 1). Patch was nested within plant community and random. As there were patches with no exotic vines present, a dummy vine with a minimal value of one stem was added in every patch to allow for the inclusion of all patches in the analysis as described by Clarke et al. (2006). We permuted the residuals under a reduced model (999 permutations). We visualized differences amongst communities using a metric multidimensional plot of bootstrap averages for each patch. Similarly, PERMANOVA was also used to test changes in assemblages amongst communities and between edges and interiors, following transformation of the data to presence/absence data. Comparison of the results of these tests helped to identify if differences in assemblages were related to abundances of particular vine species or just the species present.

Finally, for the three widely distributed plant communities, swamp sclerophyll forest on coastal floodplains (SSF), swamp oak floodplain forest (SOFF) and littoral rainforest (LRF) (Table 1), we explored whether exotic vine assemblages differed between the northern subtropical patches and southern patches in temperate climates using PERMANOVA. The northern patches all occur within the NSW North Coast and South East Queensland bioregion while the southern patches are within the Sydney Basin and South East Corner bioregions. We were aware that some vine species had preferences for temperate or subtropical climates and wanted to investigate whether changes in exotic assemblages might vary broadly across the distribution of these widely distributed communities.

An analysis of variance (ANOVA) was used to test if there was a difference between stem densities between edges and interiors of patches for each species, with patch included as a block. Only species that were present in more than four sites were analysed. Bonferroni correction was also investigated to reduce Type 1 error rates. Mixed model ANOVAs were also undertaken comparing stem densities per ha in edges and interiors of sites for all exotic vines combined and all native vines combined.

The effect of patch disturbance and surrounding land use on vines

The percentage of anthropogenically modified areas (i.e. residential, industrial and agricultural area), native vegetation and water bodies in a 1 km area around each patch were calculated for the surrounding patch matrix. These percentages were determined using QGIS 3.16.3 (QGIS Development Team, 2017), by first creating 1 km buffers around each patch, then using shapefiles of native vegetation, land zoning and hydrology areas to find how much of the buffer is occupied by each landscape type. Patch size and the area to perimeter ratio of patches were calculated by drawing polygons over patches in QGIS. Edges were classified as breaks in vegetation within a patch, as well as changes in community. Therefore, roads and tracks traversing patches were included as an edge. We also calculated the area and area to perimeter ratio of all forest habitat including vegetation surrounding each site, so changes in community were not considered to be an edge for this metric. This was labelled area of vegetation, and area to perimeter ratio of vegetation while the size and ratio of the patch only were called area of site and area to perimeter ratio of patch. The density of dead trees in patches was included as a measure of patch disturbance, as dead trees allow for more light to penetrate the canopy providing opportunity for exotic vines to establish. In no cases did the dead trees appear to be

caused by vine invasion indicating that this was a characteristic that might influence invasion rather than be caused by invasion.

To see which patch characteristics most influenced exotic and native vine assemblages, a distance-based linear model (DISTLM) analysis was undertaken in PRIMER-E V7 (Anderson et al., 2008) using the density of stems per hectare for each species in each patch. DISTLM provides quantitative measures and tests of the variation explained by the predictor variables. To ensure limited multicollinearity in the models, we determined that the correlation coefficient between different environmental variables was lower than 0.7. We used Bray Curtis indices of similarity of stem density and selected the best model using adjusted R^2 values after 999 permutations. The best fitted model from all possible combinations for factors, was then placed into a distance-based redundancy analysis (dbRDA) and visualized in an ordination plot. For the environmental characteristics, we included the percentage of native vegetation in the surrounding matrix, percentage of anthropogenically modified land in the surrounding matrix categorized into agricultural, industrial and residential, percentage of water bodies in the surrounding matrix, the area to perimeter ratio of the patch, the density of dead trees and patch size. Again we excluded RBTOF, MSW and MGF as there were too few patches. These are the most open communities (Figure 1).

RESULTS

Distribution of native and exotic vines in patches

Across all communities, 101 vine species were recorded: 74 native vines and 27 exotic vines (Table 1). The most vine species in a habitat were recorded in lowland rainforest on floodplains (57 spp.; 46 native, 11 exotic spp.), while the most exotic species were recorded in SSF (16 spp.). Exotic vines were recorded in 66% of all patches and 34% of quadrats. The number of exotic species recorded for each community increased with the number of patches surveyed ($R^2 = 0.81$) reflecting a larger area of available habitat.

The average density of all vine stems across all patches was 1734 ± 76 (SE) stems/ha. In most communities, native stem density exceeded exotic stem density except for the three most open communities which had average canopy covers less than 60% (Figure 2). These communities were two open forests (RBTOF and MGF) and a moist shale woodland (MSW). Native and exotic stem densities appeared similar in SOFF (average canopy cover = 59%). Exotic vine density was generally very low compared to native vine density for all other communities, though the highest density (for both exotics and natives) was recorded for a subtropical rainforest (ISRF, average canopy cover = 80%). Across all communities, exotic vines accounted for 25% of the vine stems recorded.

Exotic vine stems per hectare and native vines stems per hectare did not differ between edge and interiors (exotic $F_{1,106} = 0.20$, $p = 0.66$; native $F_{1,96.1} = 1.18$, $p = 0.28$). When individual species were analysed separately, most species had no preference for edges (Table 2) and only one species (*Ipomoea cairica*) was more common when Bonferroni corrections were applied. Three other exotic vine species, and five natives had a tendency to have higher stem densities recorded on the edge than the interior (Table 2); exotic species were *Anredera cordifolia, Cardiospermum grandiflorum* and *Lonicera japonica*. Only one species, native *Marsdenia flavescens*, tended to have significantly higher stem density in the interior, although was also not significant when the Bonferroni correction was applied.

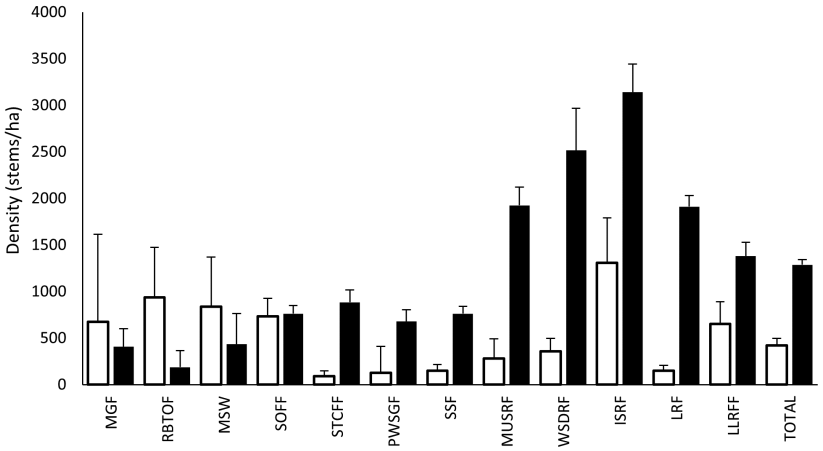


FIGURE 2 The average (±SE) density of exotic (open bars) and native (closed bars) vines recorded in plant communities. Average community canopy cover increases from left to right.

Similar patterns were seen with stem widths across communities with two of the most open communities being the only ones where average stem width was greater for exotics than natives (Figure 3a). Generally, the widest stems occurred in the rainforest communities (MUSRF, WSDRF, ISRF, LRF, LLRF), though SSF and SOFF also had wide native stems (Figure 3a). The average stem width for native and exotic vines across all patches was 13.2 mm (±0.16 SE) and 5.1 mm (±0.09 SE), respectively. Median widths for natives and exotics were 7.1 and 3.6 respectively. Also, 37% of native vine stems were greater than 10 mm, while only 10% of exotics were greater than 10 mm (Figure 3b).

Regardless of community, *Araujia sericifera* was the most widespread exotic vine, occurring in 24% of patches, followed by *Ipomoea cairica*, which occurred in 19% of patches; however, *I. cairica* was recorded in more plots than *A. sericifera,* 12% and 10% respectively. Some exotic vine species were not common (at <5 patches) but had high densities when they were present. For example, *Hedera helix* was only recorded in two patches (one each of MGF and RBTOF), though average stem density of those patches was 1093 (±585 SE) stems/ha. Two other species were also recorded at one patch each in LLRF; *Aristolochia littoralis* (1086 ± 496 stems/ha) and *Asparagus africanus* (600 ± 454 stems/ha).

Variation in vine assemblages amongst communities

For all communities, native and exotic vine assemblages did not differ between edge and interior regions (Table 3). Native vine assemblages showed clear differences amongst plant communities (Figure 4) which were maintained when presence/absence data were analysed. This indicates that differences in assemblages are largely associated with differences in the species present in plant communities, rather than being associated with changes in stem density. The greatest similarities in native assemblages occurred for the floodplain forests where *Parsonsia straminea* was particularly prevalent and dense. Bootstrapped means show separation amongst most communities, though substantial overlap occurred in the floodplain forests (SOFF, SSF and STCFF) (Figure 4a).

Similarly for exotic vine assemblages, there was a significant difference amongst communities; however, pairwise comparisons showed that many communities did not differ from each other (Table 3, Figure 4b).

TABLE 2 Average stems per hectare on the edges and interior, the percentage of patches and results from ANOVA testing for differences in stem density between edge and interior plots of each species with Bonferroni correction included. Asterisk denotes exotic species. Bold values denote significant differences at 5%. Underlined values are significant after Bonferroni correction is applied.

	EDGE	INTERIOR				
Species	**Stems/ha**	**Stems/ha**	**% patches**	**Error SD**	***F***	***p***
Species tending to be more common on edges						
*Anredera cordifolia**	442	168	16%	133	5.65	**0.032**
*Cardiospermum grandiflorum**	318	219	11%	76	8.1	**0.025**
*Ipomoea cairica**	864	307	19%	102	17.21	**<0.001**
*Lonicera japonica**	165	70	7%	28	9.6	**0.021**
Dioscorea transversa	67	20	5%	14	8.026	**0.037**
Cayratia clematidea	183	280	22%	66	5.126	**0.035**
Gynochthodes jasminoides	207	125	39%	39	5.228	**0.027**
Ripogonum album	370	258	16%	75	4.979	**0.039**
Smilax australis	482	280	40%	61	4.913	**0.032**
Stephania japonica	151	65	31%	38	4.391	**0.044**
Species tending to be more common in interior						
Marsdenia flavescens	95	58	6%	96	9.365	**0.028**
Species with no preferences for edges						
*Araujia sericifera**	549	312	24%	225	0.61	0.444
*Asparagus plumosus**	129	89	14%	60	0.26	0.626
*Delairea odorata**	638	355	16%	194	3.7	0.078
*Dolichandra unguis-cati**	152	669	4%	274	0.27	0.709
*Ipomoea indica**	187	243	9%	148	0.49	0.523
*Passiflora suberosa**	56	38	16%	25	4.1	0.07
*Passiflora subpeltata**	249	233	14%	137	2.1	0.18
*Solanum seaforthianum**	108	50	18%	76	0	0.986
Aphanopetalum resinosum	555	297	8%	149	2.126	0.179
Celastrus australis	439	518	22%	154	1.068	0.313
Cissus antarctica	188	193	33%	34	4.037	0.053
Cissus hypoglauca	252	319	22%	59	2.445	0.138
Cissus sterculiifolia	153	194	5%	38	0.383	0.563
Clematis aristata	165	80	9%	49	3.71	0.096
Cynanchum elegans	215	28	5%	115	0.141	0.723
Derris involuta	95	55	7%	32	0.326	0.589
Embelia australiana	112	197	4%	68	0.102	0.766
Eustrephus latifolius	165	208	29%	38	0.121	0.731
Geitonoplesium cymosum	125	142	43%	26	2.641	0.11
Hibbertia scandens	61	56	15%	30	0.03	0.865
Hoya australis	272	362	4%	86	7.103	0.056
Jasminum volubile	148	133	5%	172	2.186	0.213
Kennedia rubicunda	15	36	5%	17	0.072	0.8
Legnephora moorei	133	150	7%	74	0.68	0.437
Maclura cochinchinensis	76	51	33%	16	1.29	0.263
Marsdenia rostrata	225	664	29%	18	0.767	0.387
Pandorea jasminoides	47	5	4%	18	2.855	0.166
Pandorea pandorana	276	228	35%	56	0.279	0.601
Parsonsia straminea	359	319	68%	31	1.384	0.243
Parsonsia velutina	30	31	3%	28	0.003	0.961
Piper hederaceum	122	130	7%	44	0.881	0.376

(Continues)

TABLE 2 (Continued)

Species	EDGE Stems/ha	INTERIOR Stems/ha	% patches	Error SD	*F*	*p*
Sarcopetalum harveyanum	99	32	14%	22	0.621	0.444
Smilax glyciphylla	149	104	16%	45	1.908	0.189
Trophis scandens	233	297	29%	51	0.523	0.475

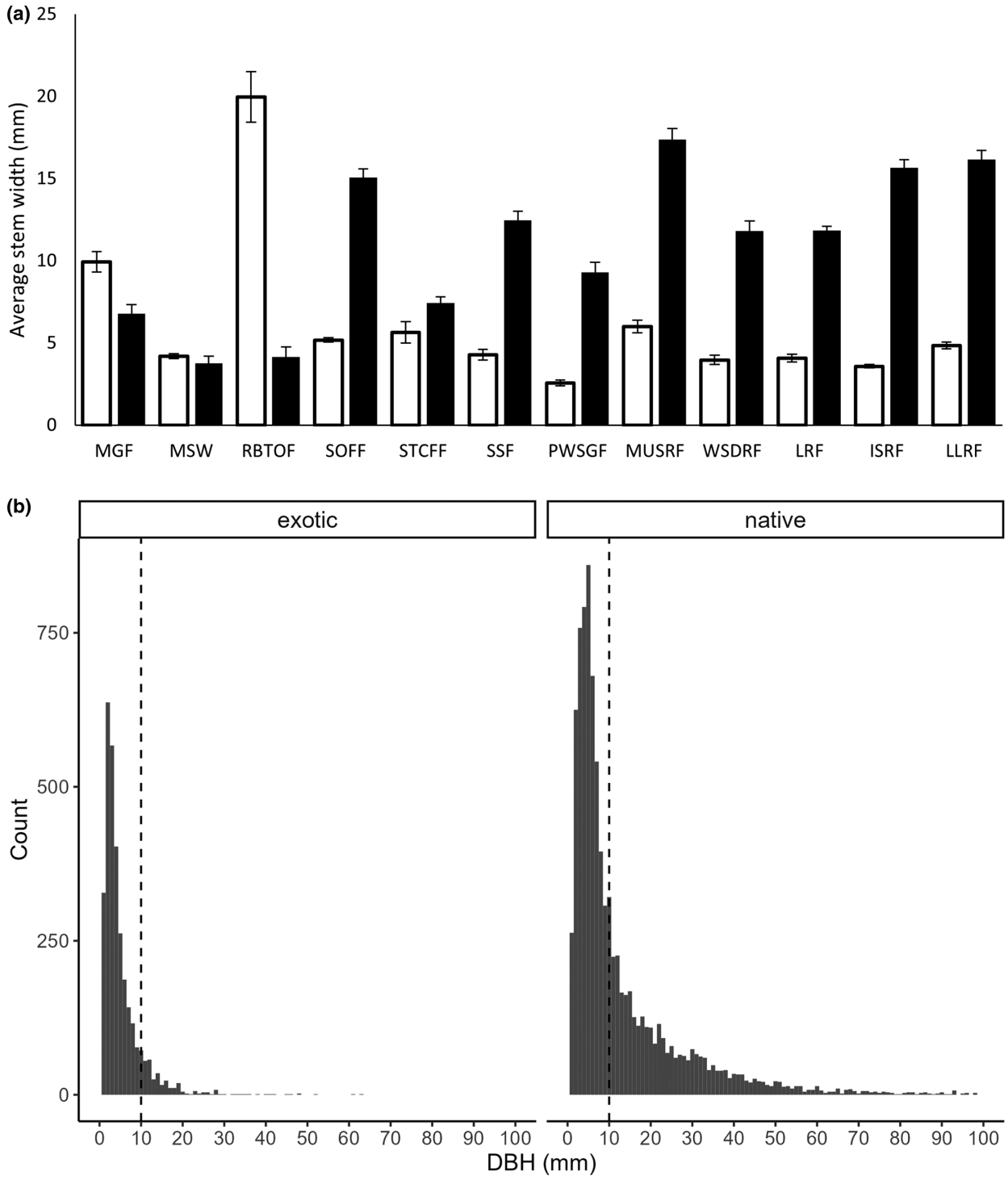


FIGURE 3 (a) The average stem width of exotic (open bars) and native (closed bars) vines in communities. Community canopy cover increases from left to right. (b) The distribution of stem widths recorded for exotic and native vine species. Vertical dashed line represents 10 mm, which is often used as a cut-off for vine inclusion.

TABLE 3 *F* tables from PERMANOVA analyses for comparisons of native and exotic vine assemblages amongst different plant communities (Community) and edge versus interior quadrats (EI). Patches were nested within community (Patch(Comm)). Bold values denote significant differences. P/A denotes analysis using presence/absence data where rare species become equivalent to common species. Res residuals.

		df	MS	Pseudo-*F*	*p* (perm)
NATIVE	**Community**	8	30570	**5.665**	**0.001**
Stems/ha	EI	1	3117.5	1.113	0.331
	Patch(Comm)	109	6780.9	**2.611**	**0.001**
	Comm × EI	8	3404.7	1.210	0.079
	Site(Comm) × EI	84	2860.9	**1.101**	**0.023**
	Res	374	2597.5		
	Community	8	23946	8.675	**0.001**
P/A	EI	1	1190.2	4.217	0.324
	Patch(Comm)	109	3662.2	**3.905**	**0.001**
	Comm × EI	8	1224.9	1.249	0.189
	Patch(Comm) × EI	84	989.8	1.055	0.267
	Res	374	937.9		
EXOTIC	**Community**	8	11779	**3.198**	**0.001**
Stems/ha	EI	1	2120.2	1.280	0.232
	Patch(Comm)	109	4627.4	**2.607**	**0.001**
	Comm × EI	8	1771.9	1.075	0.339
	Patch(Comm) × EI	84	1621.5	0.913	0.843
	Res	374	1775.1		
	Community	8	3865	**4.295**	**0.001**
P/A	EI	1	349.96	1.166	0.352
	Patch(Comm)	109	1176.1	**3.444**	**0.001**
	Comm × EI	8	326.92	1.099	0.339
	Patch(Comm) × EI	84	287.79	0.843	0.915
	Res	374	341.44		

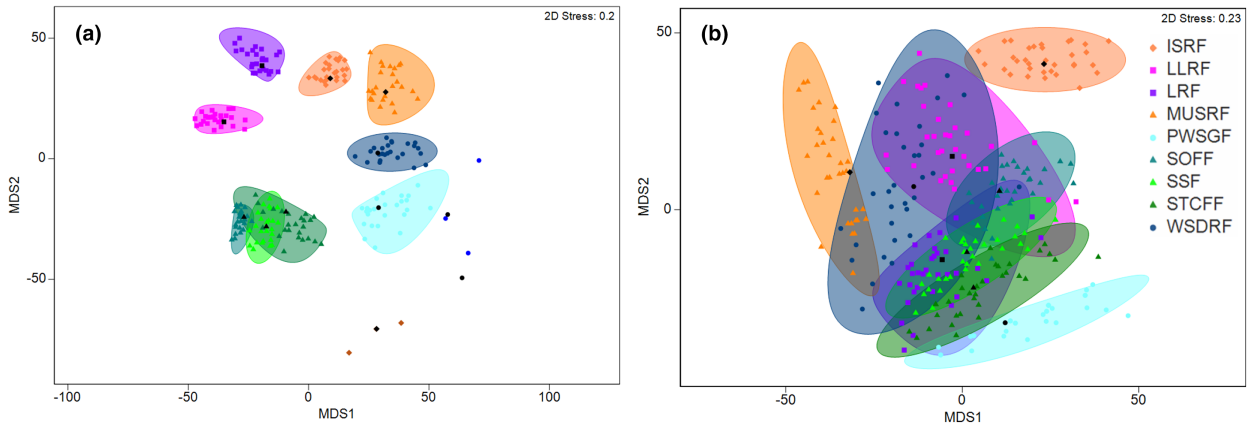


FIGURE 4 Two-dimensional scaling plots of bootstrapped averages of stem densities for (a) native and (b) exotic vine assemblages. Plots are based on permutational multivariate analysis of variance with 999 permutations. Colours represent the different plant communities following the defined abbreviations in Table 1.

Comparisons between exotic assemblages in the northern and southern patches of widespread plant communities identified only one difference. There was a difference in assemblages in SOFF (PERMANOVA: pseudo $F_{1,66} = 3.667$, $p = 0.013$), where *I. cairica* was prevalent and abundant in

the northern patches (occurring in 42% of patches with an average of 2320 (±1041 SE) stems/ha), while *A. sericifera* was abundant in southern patches (occurring in 29% of patches with an average of 1978.6 (±1473 SE) stems/ha). There was no difference in assemblages between northern and southern patches for SSF (pseudo $F_{1,65} = 1.275$, $p = 0.298$) or LRF (pseudo $F_{1,82} = 1.845$, $p = 0.978$).

The effect of patch disturbance and surrounding land use on vines

For native vine assemblages that had canopy covers over 60% (excluding the three communities with too few patches), the best distance-based linear model only explained 13% of the variation in the assemblages. Differences amongst assemblages were associated with changes in eight environmental variables included in the model but none were particularly important in explaining the differences (Table 4, dbRDA, Figure 5a). Only two environmental characteristics were not included in the best model: % average canopy, area of the patch. For exotic vine species the best model explained 11% of the total variation and included seven variables. The most influential factors were the nearness to water bodies, amount of vegetation, residential and industrial neighbouring land, reflected in the length of the vectors (Figure 5b).

DISCUSSION

Distribution of native and exotic vines in patches

We found differences in the distribution of exotic and native vines that closely reflected the age of establishment of individuals. The presence of native vines with wide stems suggest that plants had been established a

TABLE 4 Results from marginal tests of multivariate distance-based linear regression testing the effect of different environmental characteristics on changes in stem density of native and exotic vine assemblages. Only factors in the best model are presented. Bold text shows significant differences. Edge:int. is the edge to interior ratio of the vegetation.

Explanatory factor	Pseudo *F*	*p*	Proportion
Native assemblage			
Agriculture	**3.711**	**0.002**	**0.028**
Industrial	1.255	0.206	0.010
Residential	1.607	0.056	0.012
Vegetation	**2.748**	**0.002**	**0.021**
Water	**4.942**	**0.001**	**0.037**
Density of dead trees	**1.687**	**0.043**	**0.013**
Edge:int vegetation	**4.061**	**0.001**	**0.031**
Area of Vegetation	**2.435**	**0.001**	**0.019**
Exotic assemblage			
Agriculture	1.043	0.377	0.008
Industrial	**2.845**	**0.004**	**0.022**
Residential	**2.871**	**0.011**	**0.022**
Water	**2.675**	**0.009**	**0.021**
Average canopy	0.996	0.372	0.007
Edge:int vegetation	**3.130**	**0.005**	**0.024**
Area of Vegetation	**2.506**	**0.011**	**0.019**

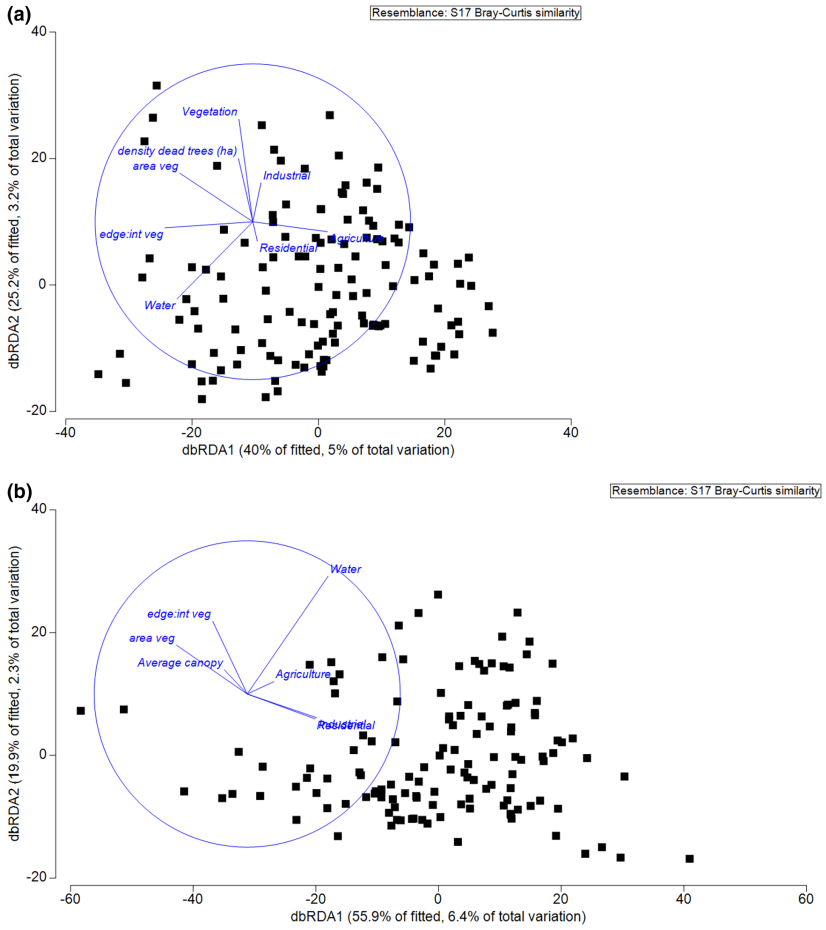


FIGURE 5 Distance based redundancy analysis of the best models identified from the distance-based linear modelling for (a) native and (b) exotic vine assemblages. Edge:int. veg = the edge to interior ratio of the vegetation, area veg = the area of the patch plus surrounding vegetation, average canopy = the average percent canopy cover, Water = % of area surrounding the patch that is water, Agriculture = % of the area surrounding the patch that is agricultural land use, Residential = % of the area surrounding the patch that is residential land use, Industrial = % of the area surrounding the patch that is industrial land use.

long time ago; however, there was still an abundance of individuals of native species with small stem widths, indicating continual recruitment within communities. Individuals of *Parsonsia straminea, Pandorea pandorana, Cissus antarctica* and *Trophis scandens* were often with large stems and likely to have been present for many years. Native vine assemblages did not differ between edges and interiors suggesting that edges do not have specific characteristics that might enhance establishment.

Exotic species had higher stem abundances but no very large individuals with large stem widths, reflecting more recent establishment and invasion. The vast majority of exotic stems were below 1 cm DBH, which would not have been included in some studies (e.g. Álvarez-Cansino et al., 2015; Campbell et al., 2018; Ingwell et al., 2010), but are now suggested to be included in standard protocols as diversity and abundance of vines increases when stems <1 cm are included (Gerwing et al., 2006). Vine stem width scales allometrically with dry biomass (French et al., 2017; Schnitzer et al., 2006, 2007), and the wider average stems of native vines suggest that native vines usually have higher biomass than exotic vines in communities. However, despite the low biomass, the high abundances of stems of some exotic vine species recorded conveys their ability to rapidly colonize

a patch. Exotic vines species with very high stem abundance are likely to increase their impact on the host community as foliage biomass increases with time. If left untreated these exotic vines will increase, degrade community structure and inhibit recruitment of native species (Ingwell et al., 2010; Paul & Yavitt, 2011). Gerwing and Farias (2000) calculated that a liana with a stem width of 2 cm has approximately the same leaf mass as a tree of 10 cm which has substantial impact on light availability for surrounding species (Gerwing & Farias, 2000). The species which recorded high stem densities, such as *Hedera helix, Ipomoea cairica, Anredera cordifolia*, *Araujia sericifera*, are likely to present the greatest threats to plant communities through canopy damage.

Both vine stem density and assemblages for both exotic and native vines were not different between interior and edge habitats. A similar pattern was found by Mohandass et al. (2014) and may be a result of the small distance between the edge and habitat classified as interior (>50 m) for both studies. The closed forests in our study are often very small patches and, in natural areas, are surrounded by drier habitats. In these situations, the small natural patch size may well have always been influenced by edges. In the present landscape, however, the edges often include land uses that have been modified by humans exposing these to a source of exotic species and stronger propagule pressure.

Interestingly, some species tended to have higher abundances along edges than in interiors, indicating a different response to edge effects for some species. In particular, widespread native (*Smilax australis* and *Gynochthodes jasminoides)* and exotic (*Ipomoea cairica*, *Anredera cordifolia*) species tended to have higher densities on the edge than interior, with edge densities being more than double for *I. cairica* and *A. cordifolia* than the interior. While these species established in the interior of the forests without high light (Bernich et al., 2023), they clearly showed a response to the increase in light. It is these species which may invade quickly as they are able to establish in both high- and low-light conditions which poses greater threats to forests near anthropogenically modified land. These species are likely to be highly dependent on anthropogenic movement of propagules in the modified surrounding landscape.

Variation in vine assemblages amongst plant communities

The richness of native vines in patches was higher than exotic vine richness, supporting the importance of vines in these forests. Native vine assemblages also differed strongly between all plant communities, except amongst the floodplain forests, suggesting that differences in distribution and biophysical properties in these communities were providing a filter for structuring native vine assemblages. Overall, 74 native species were recorded but some plant communities, particularly rain forests, had between 20 and 46 native vine species. Native vines form a characteristic and important part of rainforest communities (Marshall et al., 2020). Rainforest communities and floodplain communities also had a high average native stem width. Native biomass and damage resulting from native vines may well be greater in these communities as a natural part of the disturbance regime, although large vines can assist with canopy closure and recovery from small disturbances (Marshall et al., 2020). For fragmented forests that are highly degraded, control of native vines may need to be considered to avoid further structural damage.

There were fewer differences in the assemblages of exotic vines invading different plant communities despite a surprising diversity of exotic species (27

species). Exotic vines appear more generalized in their habitat requirements than native species, which is a trait used to infer invasiveness (Baker, 1974). Exotic vines may be able to invade different habitats due to being able to adapt to novel conditions quickly. For example, three exotic vine species that were commonly recorded in the surveys (*Anredera cordifolia*, *Araujia sericifera* and *Dolichandra unguis-cati*) were found to have higher phenotypic plasticity in leaf economy traits than three common and similar native vines (*Parsonsia straminea*, *Pandorea jasminoides* and *Hibbertia scandens*) which might help them to establish in a range of different environments (Osunkoya et al., 2014). Also, *Ipomoea cairica* has been shown to be tolerant of saline conditions in south China (Liu et al., 2016) and can have high rates of germination in warmer environments (Wang et al., 2011). Therefore, higher rates of phenotypic plasticity or adaptation might allow exotic vine species to establish in more habitats than natives, though further research is needed to confirm the link between phenotypic plasticity and invasiveness.

While we did find some differences in exotic vine assemblages, these changes were not large and suggest that prioritization of exotic vine management strategies can be consistent across the whole subtropical and temperate region surveyed. Specific management plans for each plant community can have the same key recommendations as the exotic vine community is largely the same. A couple of exceptions are noted. Firstly, very high invasions of *Hedera helix* were evident in cooler communities at higher altitudes reflecting the need for specific management of this species in this area. *Hedera helix* and *Delairea odorata* are able to withstand frosts and their native range is in temperate climates (Robison, 2006; Strelau et al., 2018). Secondly, while *Ipomoea cairica* was a particularly frequent invader in warmer areas, *Araujia sericifera* was more invasive in southern patches.

The effect of disturbance and surrounding land use on vine assemblages

Highly fragmented or disturbed patches usually have a higher abundance of vines (Campbell et al., 2018; Schnitzer, 2018), and our results suggest that the surrounding human activity had a significant influence on exotic vine invasion. Two results from this survey suggest that it is the landscape in which the fragment exists, rather than the edge which is facilitating invasion. Firstly, surrounding land use was a better predictor than the edge: interior ratio for stem density and there were few differences between the density of vines between edges and interiors. There is little evidence that many vine species largely spread into the forests from the edges. Instead both this survey and other experimental work (Bernich et al., 2023) identify that exotic vines are able to establish and grow in habitat away from the edges, and it is the increased propagule pressure associated with anthropogenic disturbances that is key to invasion (Vilà & Ibáñez, 2011). In a comparison of vine abundance between intact and fragmented forests, Campbell et al. (2018) found that vine abundance was higher in fragments and edge effects were less pronounced. Therefore, the highly fragmented nature of closed forests surrounded by increasing anthropogenic disturbance in this landscape will cause invasion in the whole fragment rather than invasion from the edge. This process does not seem to be related to increases in gaps in the forests as this characteristic did not influence exotic vine assemblages (i.e. dead trees per ha) in our study.

The species that is of particular concern in this respect is *Araujia sericifera,* a wind-dispersed species, where propagules can be transported into a greater range of landscapes without the assistance of humans (Gassó

et al., 2009) and where it is able to germinate across a range of temperatures (Vivian-Smith & Panetta, 2005) and establish in shaded environments (Bernich et al., 2023). As a result, this species is prevalent across the whole surveyed region in high densities and stem widths, in both the edge and interior of patches. There is the potential of widespread damage if management of this species is not prioritized.

Overall, the role of anthropogenic activities in exotic vine invasion is clear with disturbances impacting the whole fragment, increasing the invasion within the interior of fragments. Unlike native vine species, exotic vines were able to establish across many different habitats and pose a more generalized issue across the region. Our response to these patterns will need to include actions which reduce propagule pressure and management of invasions in the whole patch, not just the edges. High stem densities are likely to translate into much greater biomass and damage in the future and reducing stem densities will be important. Our work highlights some key species that pose current and future risks which should be prioritized.

AUTHOR CONTRIBUTIONS

Adam Bernich: Data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Kris French**: Conceptualisation, funding acquisition, methodology (equal), analysis, data curation (equal), writing, review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest by the authors.

DATA AVAILABILITY STATEMENT

Data will be provided in Dryad.

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