

Research Article

Spatial Stratification of Internally and Externally Non-Pollinating Fig Wasps and Their Effects on Pollinator and Seed Abundance in *Ficus burkei*

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Fig trees (*Ficus* spp.) are pollinated by tiny wasps that enter their enclosed inflorescences (syconia). The wasp larvae also consume some fig ovules, which negatively affects seed production. Within syconia, pollinator larvae mature mostly in the inner ovules whereas seeds develop mostly in outer ovules—a stratification pattern that enables mutualism persistence. Pollinators may prefer inner ovules because they provide enemy-free space from externally ovipositing parasitic wasps. In some Australasian *Ficus*, this results in spatial segregation of pollinator and parasite offspring within syconia, with parasites occurring in shorter ovules than pollinators. Australian figs lack non-pollinating fig wasps (NPFW) that enter syconia to oviposit, but these occur in Africa and Asia, and may affect mutualist reproduction via parasitism or seed predation. We studied the African fig, *F. burkei*, and found a similar general spatial pattern of pollinators and NPFWs within syconia as in Australasian figs. However, larvae of the NPFW *Philocaenus barbarus*, which enters syconia, occurred in inner ovules. *Philocaenus barbarus* reduced pollinator abundance but not seed production, because its larvae replaced pollinators in their favoured inner ovules. Our data support a widespread role for NPFWs in contributing to factors preventing host overexploitation in fig-pollinator mutualisms.

1. Introduction

Mutualisms are reciprocally beneficial interspecific interactions [1, 2], and a well-known system is that between fig trees (*Ficus* spp.) and their agaonid wasp pollinators [3–6]. In return for pollination, the wasps gall some fig ovules, which are then eaten by the larvae. About half (300+) of *Ficus* species are monoecious, where both male flowers and ovules are present in the same syconium (enclosed inflorescence or “fig”). Within monoecious syconia, ovules are highly variable in length [7–10]. Long (inner) ovules have short styles and mature near the centre of the syconium, whereas short (outer), long-styled ovules mature nearer the outer wall (see Figure 1). Female pollinating wasps (foundresses) lay their eggs by inserting their ovipositors down the flower styles. At maturation, wasp galls are clustered at the syconium’s centre [4, 6, 9–13] with seeds at the outer wall. This spatial stratification of pollinating wasps and seeds enables mutualism stability, although the mechanisms preventing the wasps from galling all ovules are unclear.

Mechanisms proposed to explain spatial partitioning of pollinator galls and seeds are based on biased oviposition (e.g. [12]) or biased offspring survival (e.g. [13–15]). Ovipositing foundress wasps may favour inner ovules because of shorter handling times offered by the short styles [10, 12]. Interference competition between foundresses, which further slows oviposition [16], and limited longevity [13, 16] means that wasps die before all ovules are galled. Like most mutualisms [17, 18], the fig-pollinator system is exploited by third parties, which mainly consist of non-pollinating fig wasps (NPFWs) that attack with their long ovipositors from outside of the syconium and, depending on the species, exert costs onto either mutualist by parasitism or seed predation. Pollinator offspring in outer ovules are more prone to parasitism by NPFWs than those in inner ovules. In three morphologically and phylogenetically distinct Australasian *Ficus*, this results in additional spatial stratification of pollinator and parasitic NPFW galls, showing that inner ovules provide pollinator offspring with “enemy-free space” [13]. Additionally, female pollinators in outer ovules are

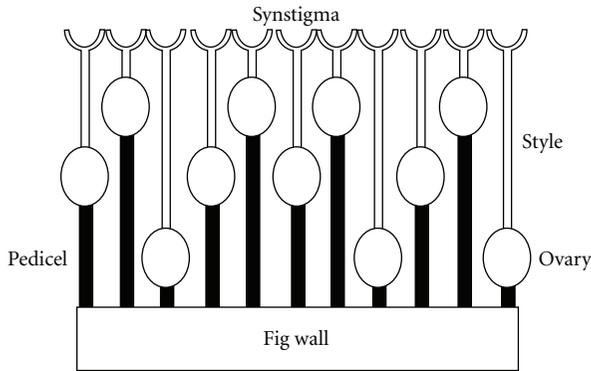


FIGURE 1: Variation in style and pedicel length in female flowers of monoecious *Ficus* (adapted from Dunn et al. [13]).

unlikely to be released from their galls by males [15]. Clearly, biased oviposition and biased survival are not mutually independent mechanisms, because biased survival is likely to contribute to selection for biased oviposition [13].

In addition to externally ovipositing NPFWs, some *Ficus* support non-pollinating wasps that oviposit similarly to the pollinators [5]. Some of these internally ovipositing non-pollinating fig wasps (henceforth “INPFWs”) gall ovules and have herbivorous larvae [19], whereas others rely on the presence of pollinating wasps to develop [20, 21]. Joussetin et al. [22] found that some INPFWs are passive pollinators of the trees so they can have positive or negative effects on both mutualists [21, 23–25]. However, the ovule layers INPFWs favour for oviposition, if any, are unknown. Because they oviposit at the same time as pollinators, and from inside the receptive syconium, INPFWs may use the same flowers as pollinators and thereby compete with or kill them.

This study was designed to answer three questions regarding the African endemic fig species *F. burkei*, its pollinating wasp *Elisabethiella stuckenbergi*, its externally ovipositing parasitic NPFWs, and the INPFW, *Philocaenus barbarus*. (1) Within syconia, are INPFW galls clustered in the same inner ovules favoured by the pollinators? (2) Is there spatial stratification of pollinating and parasitic NPFWs within the syconia of *F. burkei*—a fig species from a clade absent from Australasia? (3) Are INPFWs costly to the mutualists?

2. Materials and Methods

2.1. Study Species. *Ficus burkei* is an evergreen or semi-deciduous tree, which grows up to eight metres high. It is found in savannah woodland, wet or dry forests and as a planted shade tree in suburbia, and has a natural range that extends from South Africa to Ethiopia and Senegal [26]. *Ficus burkei* is actively pollinated by *Elisabethiella stuckenbergi* (Grandi) although *Alfonsiella brongersmai* (Wiebes) and *A. longiscapa* (Joseph) have also been recorded as pollinators. Another 25 (non-pollinating) wasp species are associated with *F. burkei* [27]. Two of these, *Crossogaster odorans* (Wiebes) and *Philocaenus barbarus* (Grandi), are INPFWs. In the syconia collected for this study, *E. stuckenbergi* was the only pollinator and *P. barbarus* the only INPFW present.

2.2. Collection of Syconia and Data Recording. During January and February 2007, we collected 28 early male flower phase *F. burkei* syconia (just prior to female wasp emergence [28]) from four trees at two different sites in South Africa. Immediately after removal from the tree, all syconia from that tree were placed into a plastic container filled with 80% ethanol.

On return to the laboratory, each syconium was carefully divided into eighths using a razor blade and fine forceps. For 18 syconia, each ovule was carefully removed with fine forceps. All ovules for a particular segment were placed into a watch glass containing 100% ethanol for categorisation and measurement. For the remaining 10 syconia, we again sliced each syconium into eighths and then subsampled ovules for further analysis by systematically removing every fourth ovule, starting from one end of a syconium segment and then working towards the opposite end (see [13] for details). Actual and estimated total numbers of seeds and wasps using this method are unlikely to differ significantly [29].

The length of each selected ovule was measured to the nearest 0.01 mm using an eyepiece graticule mounted on a binocular microscope. Ovule length was determined as pedicel length plus the length of the seed or wasp gall, excluding what remained of the style. Pedicel length was not used for two reasons: (1) some outer ovules have no pedicels, which would result in many zeros in the dataset, (2) there is often no distinct landmark where the pedicel joins the seed or gall, making accurate, repeatable measurements difficult [13, 15]. The numbers of female pollinators (foundresses) and INPFWs that had been present in each syconium when it had been receptive could not be accurately counted. This was because their heads and bodies had disintegrated, probably due to the characteristic tight packing of the developing seeds and wasp galls during the interfloral stage in *F. burkei* (D. W. Dunn and J. M. Cook, personal observations).

After measurement, each ovule was assigned to one of four categories: (1) *seed*: pollinated ovules that had developed into seeds, (2) *pollinator*: ovules with galls containing pollinator wasps (*E. stuckenbergi*), (3) *NPFW*: ovules with galls containing externally ovipositing NPFW species of similar size to pollinators that are parasitoids or inquillines (*Philotrypesis parca* and *Sycoryctes/Sycoscapter* spp.), and (4) *INPFW*: ovules with galls containing *P. barbarus*. Not all syconia contained wasps from all categories (Table 1). Because one of our aims was to identify any spatial stratification of seeds, pollinators, externally ovipositing NPFWs, and INPFWs, we did not include syconia that contained large galling wasps or their parasites (Otiteselline, Epichrysomalline, or Eurytomidae) (see also [13]). These rare species of large wasps effectively form a separate, independent component of the fig wasp community (e.g. [30]).

To test if the ovules used by *E. stuckenbergi* or *P. barbarus* were constrained by the lengths of their ovipositors, we measured the total body and ovipositor lengths of individuals of both species from the collected syconia, to the nearest 0.01 mm. Total body length was measured as the distance from the front of the head to where the ovipositor joins the abdomen. The length of each ovipositor was measured after its removal from the ovipositor sheath [11]. To take

TABLE 1: Summary of the wasps found in the 28 *Ficus burkei* syconia dissected for the study. Each row represents the possible combinations of pollinating wasps, externally ovipositing parasitic NPFWs (*Philotrypesis/Sycoscapter/Sycoryctes*), and *P. barbarus* in a syconium (i.e. row one represents syconia that only contained *E. stuckenbergi*). All 28 syconia produced seeds. The mean numbers (\pm S.E.) of wasps when present, and seeds, are given in the five columns to the right, along with ANOVA test results. * $P < 0.05$; ** $P < 0.001$. Tests presented as significant remain so after sequential Bonferroni correction for multiple, non-independent tests. Different letters indicate a significant difference between groups (Fisher’s LSD post hoc tests).

	All wasps	<i>P. barbarus</i>	Pollinators	NPFWs	Seeds
<i>E. stuckenbergi</i> (ES)	103.75 \pm 17.86 ^a	—	103.75 \pm 17.86 ^a	—	40.00 \pm 12.67
<i>P. barbarus</i> (PB)	0	0	—	—	0
NPFWs	0	—	—	0	0
ES + PB	0	0	0	—	0
ES + NPFWs	100.59 \pm 5.57 ^a	—	92.41 \pm 9.69 ^a	8.18 \pm 3.63	61.29 \pm 6.15
PB + NPFWs	0	0	—	0	0
ES + PB + NPFWs	72.00 \pm 8.68 ^b	33.86 \pm 5.60	32.43 \pm 4.38 ^b	5.71 \pm 2.41	46.71 \pm 12.68
ANOVA: <i>F</i>	4.28*	—	25.11**	2.81	1.59

these measurements, we used the same eyepiece graticule and microscope (at 20x magnification) used for the ovule measurements. Syconium length and width were measured to the nearest 0.05 mm using Vernier calipers, to enable syconium volume to be estimated. Any loose wasps in the lumen (mainly male *E. stuckenbergi*) were counted.

2.3. *Statistical Analyses.* We analysed our data with R statistical software [31]. For tests involving counts, data from those syconia from which a quarter of the ovules were sampled were quadrupled [29]. We confirmed the accuracy of this method by creating two models prior to our final analyses; one used only counts from 18 whole syconia and the other used counts from all 28 syconia. In each case, the same general trends were apparent, so we present results from the larger dataset.

We explored the effects of gall occupants on ovule length within syconia using general linear models, where ovule length was the dependent variable and gall occupant, site, and fig volume were the independent variables.

We also explored the effect of *P. barbarus* on wasp and seed production, by constructing five generalised linear models with Poisson (count data) or binomial (proportional data) error structures. The dependent (response) variables used were (1) the total number of wasps other than *P. barbarus*, (2) the number of pollinator wasps, (3) the proportion of pollinator wasps out of all wasps, (4) the total number of NPFWs, and (5) the number of seeds, per syconium. When models exhibited overdispersion, quasi-Poisson error structures were used [32].

For all models, we initially included the independent (explanatory) variables “site” and “tree” as factors to account for unmeasured variance between localities and trees [13–15, 33], and fig volume as a covariate. The inclusion of fig volume in this manner removed the need to use “fig” as an additional nested factor within “tree.” Where appropriate, models were simplified by backwards elimination by the removal of non-significant terms followed by a χ^2 test (where data were not overdispersed), or by an *F*-test (where overdispersion was present). This was to ensure that such removals did not significantly increase the residual error of

the model [32]. Variables that remained in the final models have been highlighted in the results.

3. Results

3.1. *Spatial Stratification of Wasps and the Ovules Used by P. barbarus.* Across our complete data set, INPFWs (*P. barbarus*), pollinators (*E. stuckenbergi*), externally ovipositing non-pollinating wasps (NPFWs), and seeds were significantly spatially stratified within syconia ($F_{3,2717} = 53.97$, $P < 0.001$; site: $F_{1,2717} = 100.32$, $P < 0.001$; fig volume: $F_{1,2717} = 23.23$, $P < 0.001$). On average, ovules containing *P. barbarus* galls were longer than those containing pollinators, which in turn were longer than those that had become seeds or contained the galls of NPFWs. The galls of NPFWs were those nearest to the outer wall of the syconium (Figure 2(a)). However, in syconia in which *P. barbarus* was absent, pollinators galled longer ovules than when *P. barbarus* was present ($F_{1,1337} = 91.18$, $P < 0.001$; site: $F_{1,1337} = 46.99$, $P < 0.001$; fig volume: $F_{1,1337} = 14.12$, $P < 0.001$, Figure 2(b)). The effects of different occupants on ovule length were independent of any effects of differences between the two sites and fig volume because each of these predictors remained in our final models.

3.2. *Does P. Barbarus Influence Pollinator and Seed Production?* Within the 28 syconia dissected, *P. barbarus* was not present unless *E. stuckenbergi* and parasitic NPFWs were also present (Table 1). Four syconia (14.29%) contained only *E. stuckenbergi*, 17 (60.71%) contained NPFWs and *E. stuckenbergi*, and seven (25%) contained NPFWs, *P. barbarus* and *E. stuckenbergi*. These frequencies of occurrence (including the additional four possible wasp combinations) differed significantly from an even distribution, showing that all wasps were unlikely to occur independently of each other ($\chi^2 = 56.50$, $P < 0.001$). Seed production was not significantly correlated with *P. barbarus* ($r_s = -0.196$, $P = 0.32$), NPFW ($r_s = 0.143$, $P = 0.47$), or pollinator abundances ($r_s = 0.048$, $P = 0.84$). This was reflected by no difference in seed numbers in syconia in which *P. barbarus* was present or absent (Proportion Deviance Explained, PDE = 0.25,

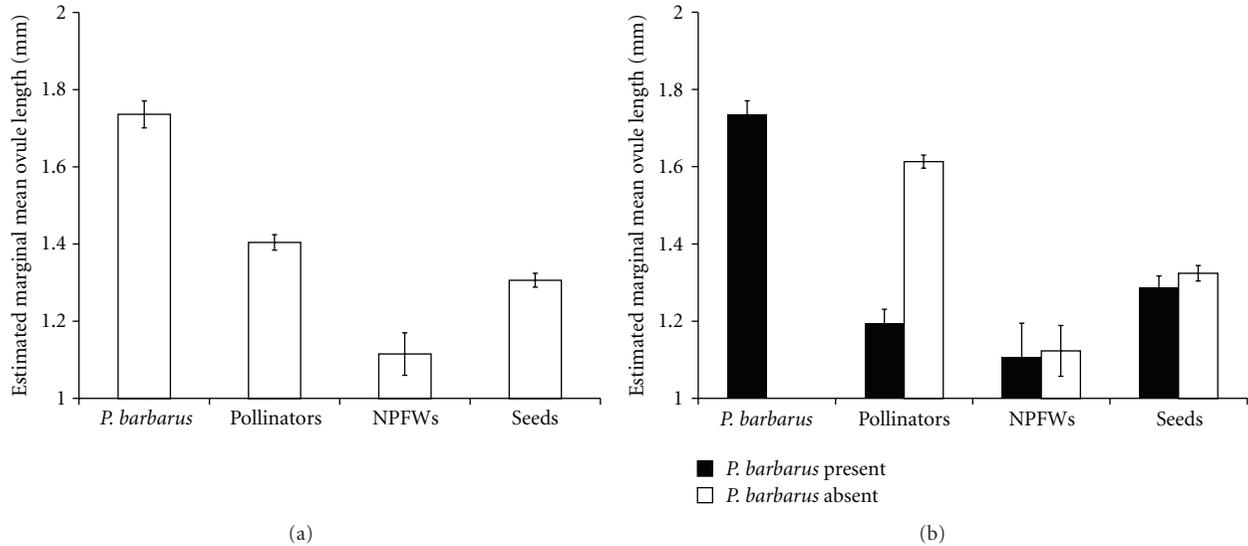


FIGURE 2: Mean (\pm S.E.) lengths of flowers with galls containing INPFWs (*P. barbarus*), pollinators (*E. stuckenbergi*), the externally ovipositing parasitic wasps *Philotrypesis parca* or *Sycoryctes/Sycoscapter* spp. (NPFWs) or seeds. (a) all data; (b) data split by the presence (black bars) or absence (white bars) of *P. barbarus*. Estimated marginal means are presented and are thus independent of the effects of “site” and “syconium volume” (Dunn et al. [15]).

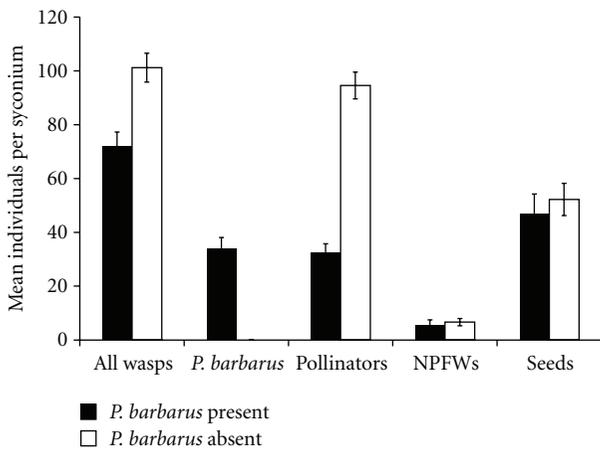


FIGURE 3: Mean abundance (\pm S.E.) per syconium of all wasps, the INPFW (*P. barbarus*), pollinating wasps (*E. stuckenbergi*), the externally ovipositing parasitic wasps (*Philotrypesis parca* or *Sycoryctes/Sycoscapter* spp.) (NPFWs), and seeds. Black bars represent syconia in which *P. barbarus* was present; white bars represent syconia in which *P. barbarus* was absent.

$t_{26} = -0.79$, $P = 0.44$; Figure 3), or between syconia containing different combinations of wasps (Table 1). *Philo-caenus barbarus* abundance was negatively correlated with pollinator abundance ($r_s = -0.741$, $P < 0.001$), and the total abundance of all wasps ($r_s = -0.496$, $P < 0.01$) per syconium, whereas pollinator abundance was positively correlated with the total abundance of all wasps ($r_s = 0.910$, $P < 0.001$).

Syconia containing *P. barbarus* thus had significantly fewer pollinators (PDE = 0.71, $t_{26} = -7.04$, $P < 0.001$; Figure 3), reduced proportions of pollinators (mean \pm S.E. = 0.22 ± 0.02 (present); 0.50 ± 0.03 (absent); PDE =

0.58, $t_{26} = -5.68$, $P < 0.001$), and significantly fewer wasps overall (P.D.E. = 0.32, $t_{26} = -3.01$, $P < 0.01$; Figure 3), than syconia in which *P. barbarus* was absent.

Patterns of pollinator and *P. barbarus* occurrence and abundance appeared to be independent of external parasitic NPFW abundance, which did not differ between syconia containing *P. barbarus* or not (PDE = 0.42, $t_{23} = 0.20$, $P = 0.84$; Table 1). In syconia containing only pollinators and NPFWs, total wasp abundance did not differ significantly to those in which only pollinators were present (Table 1). However, when *P. barbarus* was present, the total number of all wasps was lower than expected if *P. barbarus* offspring simply replaced pollinator offspring on a one for one basis (Figure 2; Table 1).

3.3. Body Size and Ovipositor Length of Pollinators and INPFWs. *Elisabethiella stuckenbergi* females were significantly smaller (mean body length \pm S.E. = 1.30 ± 0.004 mm) and had significantly longer ovipositors (mean ovipositor length \pm S.E. = 1.18 ± 0.003 mm) than female *P. barbarus* (mean body length \pm S.E. = 1.41 ± 0.007 mm; $t_{174.41} = -10.62$, $P < 0.0001$; mean ovipositor length \pm S.E. = 0.58 ± 0.007 mm; $t_{313.37} = 76.81$, $P < 0.0001$).

4. Discussion

Our study has three main findings. (1) As predicted, *P. barbarus* galls are clustered in long, inner ovules. Moreover, galled ovules containing *P. barbarus* are significantly longer than those containing pollinators. (2) There is spatial stratification of pollinators, parasitic externally ovipositing NPFWs, and seeds in the mature syconia of *F. burkei*. (3) *Philo-caenus barbarus* did not affect seed production but did reduce pollinator abundance.

Our data suggest that *P. barbarus* replaces pollinators in inner ovules and exerts a cost onto *F. burkei* by reducing the abundance of its pollen vectors. In the passively pollinated *Ficus curtipes*, *F. paracamptophylla*, and *F. consociata*, INPFWs pollinate as well as [20], or possibly better than [9] the associated agaonid. However, this is unlikely to be the case in actively pollinated fig species such as *F. burkei*. We show that the inner ovules of *F. burkei* are favoured by pollinator and *P. barbarus* foundresses. *Philocaenus barbarus* must compete with pollinators for these innermost ovules, due partly to constraints imposed by its short ovipositor. *Philocaenus barbarus* probably also has to rely on pollinators to facilitate entry to figs due to its large size [21]. This is suggested by the fact that *P. barbarus* only occurred in syconia that also contained *E. stuckenbergi*. Alternatively, entry after the “legitimate” agaonid pollinator may ensure a degree of pollination and reduce the risk of syconium abortion ([34, 35] but see [24, 30]), and/or increase the likelihood that all *P. barbarus* offspring develop fully [36, 37]. Finally, we cannot rule out that *P. barbarus* may be a parasite that usurps the galls of pollinators rather than inducing its own.

The stratification of parasitic NPFWs and pollinating wasps in *F. burkei* syconia is similar to that in three species of Australasian *Ficus* two from the *Malvanthera* section of the *Urostigma* and one from the taxonomically distinct *Sycomorus* subgenus [13]. Within *Ficus*, *F. burkei* resides in the *Galoglychia* section of the *Urostigma*, which is endemic to Africa [38] and diverged from the *Malvanthera* approximately 45 million years ago [39]. Our finding in *F. burkei* thus widens the potential that externally ovipositing parasitic NPFWs have in biasing pollinator mortality in outer ovules, which will add to the factors that result in pollinator gall and seed stratification and ultimately mutualism stability across different *Ficus* lineages [12, 13, 15]. Moreover, our stratification data do not support the hypothesis of West and Herre [14], who suggested that outer, long-styled ovules are intrinsically “unbeatable” and immune to wasp development. In our samples, wasp galls clearly occur across the full range of ovule lengths (Figure 2), as has been shown in some other *Ficus* species [13].

Interference competition by conspecifics during oviposition is predicted to slow pollinator oviposition, and hence help prevent ovule overexploitation [12, 16]. If *P. barbarus* is an herbivorous galler, it might thus have the potential to act as a “proxy foundress.” Additionally, *P. barbarus* may be able to physically dominate *E. stuckenbergi* due to its larger size [40, 41]. Pollinator numbers in syconia with *P. barbarus* are reduced more than would be expected if *E. stuckenbergi* offspring are simply being replaced with *P. barbarus* (Figure 3). This result is consistent with *P. barbarus* indirectly reducing the oviposition rates of the pollinators. However, we found no difference in seed production between *P. barbarus* infested and non-infested syconia—a result similar to that found for another INPFW species [21]. Moreover, *P. barbarus* does not seem to use ovules that would otherwise become seeds. The direct reduction in the total number of pollinators produced when *P. barbarus* is present in a syconium translates to a reduction in *Ficus* male function, and thus a cost to the plant.

Investigations into the precise trophic levels of INPFWs such as *P. barbarus*, and any effects they may have on pollinator oviposition behaviour, are likely to be of value to future studies examining the effects of non-pollinating wasps on fig-pollinator mutualists.

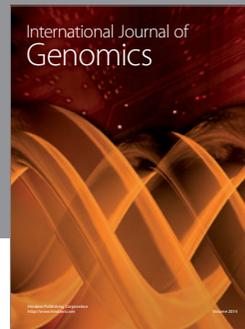
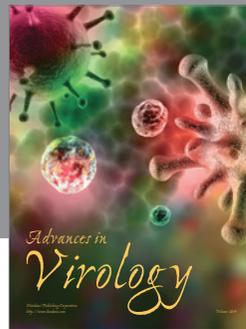
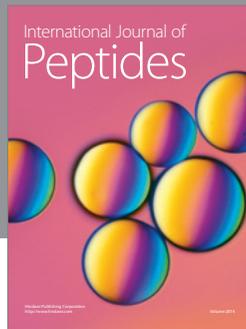
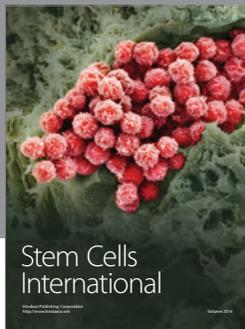
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